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# Untangling the complexities of larval Antarctic krill overwintering success under climate change

**Zephyr T. Sylvester [1,2,*], Devi Veytia [3,4,5], Alexis A. Bahl [6,7], Dominik Bahlburg [8,9], Deborah Benkort [10], Sophie Bestley [3,4], Bulut Cagdas [11], Alison C. Cleary [12,13], Andrew Constable [12,14,15], Stuart Corney [3,4], Bettina A. Fach [11], Nicole Hellessey [3,16], Simeon L. Hill [13], Nadine M. Johnston [13], Sara Labrousse [17], Benjamin Merkel [18], Eugene J. Murphy [13], Roshni C. Subramaniam [14,19,15], Sally Thorpe [13], Ben Raymond [4,12]**

[1]Environmental Studies Department, University of Colorado Boulder, Boulder, CO 80305, United States of America
[2]Institute of Arctic and Alpine Research, Boulder, CO 80305, United States of America
[3]Institute for Marine and Antarctic Studies, Hobart, Tasmania 7000, Australia
[4]Australian Antarctic Program Partnership, Hobart, Tasmania 7001, Australia
[5]FRB-CESAB, Fondation pour la Recherche sur la Biodiversité, 34000 Montpellier, France
[6]Department of Earth, Ocean and Atmospheric Sciences, The University of British Columbia, Vancouver V6T 1Z4 , Canada
[7]Institute for the Oceans and Fisheries, University of British Columbia, Vancouver V6T 1Z4 , Canada
[8]Technische Universität Dresden, 01062 Dresden, Germany
[9]Helmholtz Centre for Environmental Research, 04318 Leipzig, Germany
[10]Institut des sciences de la mer de Rimouski (ISMER)- Université du Québec à Rimouski, Rimouski, Quebec G5L 2Z9, Canada
[11]Institute of Marine Sciences, Middle East Technical University, Erdemli-Mersin 33731, Turkey
[12]Australian Antarctic Division, Department of Climate Change, Energy, the Environment and Water, Kingston, Tasmania 7050, Australia
[13]British Antarctic Survey, Cambridge CB3 0ET, United Kingdom
[14]Centre for Marine Sociology, University of Tasmania, Hobart, Tasmania 7001, Australia
[15]Sydney Institute of Marine Science, Sydney, New South Wales 2088, Australia
[16]Bigelow Laboratory for Ocean Sciences, East Boothbay, Maine 04544, United States
[17]Laboratoire d'Océanographie et du Climat, Paris 75005, France
[18]Akvaplan-niva, Fram Centre, Langnes, 9296 Tromsø, Norway
[19]CSIRO Environment, Hobart, Tasmania 7004, Australia

*Corresponding author. Environmental Studies Department, University of Colorado Boulder, Boulder, CO 80305, USA. E-mail: zephyr.sylvester@colorado.edu

## Abstract

Antarctic krill (*Euphausia superba*) are integral to Southern Ocean pelagic ecosystems. Winters with extensive sea ice have been linked to high post-larval krill recruitment the following spring, suggesting that sea ice plays a critical role in larval overwinter survival. As the ocean warms and sea ice declines under climate change, understanding the mechanisms linking sea ice and krill recruitment is increasingly urgent. To address this, we developed a qualitative network model (QNM) that integrates evidence-based and hypothesized interactions to explore larval overwinter survival and growth under future climate scenarios in the southwest Atlantic sector. Our model highlights habitat-specific impacts, with substantial declines predicted for the North Antarctic Peninsula continental shelf due to reduced autumn primary productivity and warming. In contrast, survival may improve in open-ocean habitats under cooler scenarios that enhance sea-ice-associated processes, such as food availability and refuge. The inclusion of hypothesized mechanisms, such as sea-ice terraces providing refuge from predation, strengthened these conclusions and highlighted critical uncertainties, including the influence of glacial melt on food web dynamics. These findings demonstrate the value of QNMs in complementing quantitative approaches, offering a framework for identifying critical mechanisms, addressing knowledge gaps, and guiding future field and laboratory studies to improve predictions of krill responses to climate change.

*Keywords:* Antarctic Peninsula; *Euphausia superba*; qualitative network model; recruitment; Southern Ocean

## Introduction

Antarctic krill (*Euphausia superba*, hereafter 'krill') is a key species in Southern Ocean pelagic ecosystems (Murphy et al. 2016). Krill support higher predators of high conservation importance, such as seals, penguins, and whales (Nicol and Foster 2016, Trathan and Hill 2016, Johnston et al. 2022, Hill et al. 2024, Kawaguchi et al. 2024), and play a role in ocean biogeochemistry, contributing to nutrient cycling that sustains primary production, as well as the global carbon cycle (Khatiwala et al. 2009, Cavan et al. 2019). Furthermore, krill are commercially valuable, supporting the Southern Ocean's largest and currently expanding fishery, which is mainly concentrated in the population center of krill: the southwest Atlantic sector (Nicol and Foster 2016, Meyer et al. 2020). Given the global significance of krill, maintaining their population levels and their ecological relationships with dependent and related species are guiding principles for the sustainable management of the krill fishery and the conservation of Southern Ocean ecosystems as mandated by the Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR) (CCAMLR 1980).

The current and anticipated impacts of climate change are placing new demands on krill management and conservation planning (Meyer et al. 2020, Yang et al. 2022). Krill are highly adapted to the seasonal sea-ice cycles that characterize the Southern Ocean's climate (Nicol et al. 2006). In recent years, circumpolar winter sea ice has shown pronounced changes, with low sea-ice extent anomalies since 2016 (Ludescher et al. 2019, Purich and Doddridge 2023), and regional hotspots of sea-ice loss (Fetterer et al. 2017, Ludescher et al. 2019, Maksym 2019). Larval krill may be particularly vulnerable to these changes, as the episodic occurrence of optimal sea-ice conditions has been linked to strong recruitment events the following spring (Siegel and Loeb 1995, Quetin and Ross 2003). Recent trends characterized by an increasingly positive Southern Annular Mode and decreasing sea-ice extent preceding low krill recruitment years could indicate that winter climate is becoming less favourable for larval survival (Saba et al. 2014, Atkinson et al. 2019). If past correlations are extrapolated into the future using climate model projections, recruitment failures are expected to continue (Gillett and Fyfe 2013, Roach et al. 2020, Ichii et al. 2023) in response to increased ocean warming near the Antarctic coast (Bracegirdle et al. 2020). Improving model relationships between environmental drivers and sensitive aspects of krill population dynamics, such as overwinter survival and growth of larvae, is essential for advancing scientific understanding and guiding research to support management under changing environmental pressures, as CCAMLR has yet to address climate change in its fisheries policies.

Quantitative modelling frameworks are an approach to advance biophysical modelling by capturing increased complexity in the life history of krill and exploring biophysical mechanisms influencing their spatiotemporal population dynamics (e.g. Murphy et al. 2012, 2016, Green et al. 2023). Biophysical models of larval krill overwinter survival covering a broad spectrum of spatiotemporal scales have provided different but complementary insights (Green et al. 2021, Veytia et al. 2021). Green et al. (2021) focused on biophysical relationships quantified at a regional scale to predict areas of high-quality spawning habitats. However, to provide inferences at regional and seasonal scales, quantitative models must simplify underlying finer-scale mechanisms, often using statistical relationships parameterized by data with patchy spatio-temporal coverage and relatively coarse spatial resolution (Perry et al. 2019).

These simplified finer-scale mechanisms likely play an important role in how larvae are impacted by changing sea-ice ecosystems, with supporting evidence often coming from short-term observational studies (Supplementary Table 1). However, data from these studies are often incompatible with parameterizing quantitative models, which require relationships quantifying how these mechanisms interact and integrate over a full winter season to influence growth and survival outcomes. This remains a critical knowledge gap and challenge for building mechanistic realism into quantitative models. For example, observations of larval krill feeding on sea ice algae support the hypothesis that ice algae are an overwinter food source (Hamner et al. 1989, Bernard et al. 2019). Yet, the relative importance of ice algal availability in comparison to correlated environmental factors, such as predator refuge availability, is uncertain. These mechanisms could become decoupled in the future due to shifts in sea ice dynamics, where changes in sea ice formation or melt patterns might reduce the overlap between sea ice algae availability and predator refuges, potentially altering the habitat's capacity to simultaneously provide food and protection for larval krill (Melbourne-Thomas et al. 2016). These uncertainties lead to diverging modelling scenarios, with differing implications for how krill larval survival and recruitment respond to climate change and raise questions about the potential roles of ecological feedback cycles (Ward 2020, Veytia et al. 2021, Hill et al. 2024).

In modelling contexts where a high level of mechanistic complexity is desired but quantitative knowledge is imprecise, qualitative network models (QNMs) are a useful tool. QNMs represent mechanistic interactions as either positive or negative, rather than quantitatively (e.g. through linear effects or nonlinear functions), and thus can achieve a degree of complexity that is often limited in quantitative models. QNMs can be used to explicitly address research questions examining the impact of 'hypothesized mechanisms', i.e. knowledge gaps or competing hypotheses, on predicted outcomes. By developing models with alternate configurations, the predicted outcomes can be compared across models to determine sensitivity to hypothesized mechanisms and/or evaluated against known outcomes to determine the most plausible conceptual model (Dambacher et al. 1999). In this paper, we use a QNM approach to explore drivers of larval krill overwinter growth and survival across a range of future climate scenarios in the southwest Atlantic sector of the Southern Ocean—a key area for krill biomass and the international krill fishery and of relevance to CCAMLR. As the relative importance of different environmental drivers can vary across oceanographic habitats (Reiss et al. 2017, Walsh et al. 2020, Johnston et al. 2022, Hill et al. 2024), we examine these processes across three different habitat zones occupied by krill in this sector ('high latitude shelf', 'low latitude shelf', and 'open ocean'). We accommodate our imprecise, conceptual understanding of hypothesized mechanisms for the relationship between sea ice and krill overwinter growth and survival by parameterizing them as qualitative interactions (Raymond et al. 2011, Melbourne-Thomas et al. 2012). We use our QNMs to explore the following key questions:

1. What mechanisms could contribute to regionally variable environmental drivers influencing the overwinter growth and survival of larval krill in different habitats?
2. How does the inclusion of hypothesized mechanisms impact results under a range of climate change scenarios?
3. Which of these hypothesized mechanisms shows the largest influence on overwinter growth and survival of larval krill?

## Materials and methods

### Qualitative network modelling approach

QNMs provide simplified representations of ecosystems, like in the Southern Ocean, built upon an interaction matrix of differential equations (Dambacher et al. 2002, Melbourne-Thomas et al. 2012, Puccia and Levins 1985). QNMs rely on a qualitative understanding of how variables in a system interact, indicated by whether interactions are positive (+), negative (−), or neutral (0, i.e. no interaction), providing conceptual linkages between key ecosystem variables (Levins 1974, 1998, Montaño-Moctezuma et al. 2007, Hosack et al. 2008, Raymond et al. 2011, Melbourne-Thomas et al. 2012). The methodology can therefore facilitate the modelling of complex communities when the information about the precise effect size of interactions is limited (Levins 1966, Dambacher et al. 2002). QNMs can be represented visually using signed digraphs of the interaction matrix, composed of a network of community members and processes ('nodes'), connected via mechanisms represented by signed interactions ('edges') indicating whether a positive (→) or negative (•) effect is exerted from one node onto another. The interaction matrix can be used to infer the qualitative response of each node (increase, decrease, or no change) to a sustained ('press') perturbation applied to one or more nodes. These responses incorporate both direct and indirect (i.e. a node acting upon another via one or more intermediate nodes) effects and can be calculated by matrix inversion (e.g. Bender et al. 1984) or simulation-based methods (Raymond et al. 2011, Melbourne-Thomas et al. 2012).

The simulation-based approach applied in this study began with model validation that tests the QNM for mathematical stability and ecological validity, supported by direct evidence. This was done by assigning randomized weights to all edges with qualitative values, thus perturbing the system from equilibrium, and sampling the output. The sampling was evaluated for mathematical stability based on eigenvalues and ecological validity based on established research. Once the model was determined as valid, sampling was repeated until a prespecified number of samples had been generated. These samples were then aggregated to provide a plausible representation of the system as a baseline. Having established the baseline, a specific set of perturbations were applied to the model, and the resulting response of the system could be quantified. The approach of using multiple simulations to conduct press perturbation experiments enables uncertainty about linkages to be captured within a single model while allowing incorporation of prior knowledge to inform model selection (as detailed in Dambacher et al. 2003, Raymond et al. 2011, Melbourne-Thomas et al. 2012). Additional characterization was added to the model by creating various configurations, such as indicating the certainty of the linkage between nodes. Using this framework, a sustained change (press perturbation) can be applied to a node or combination of nodes, and the qualitative responses (positive, negative, no change) of all nodes are simulated.

## Qualitative network modelling development

We identified 24 nodes to include in the network model, representing community members (e.g. 'Sea ice algae', 'Small copepods') and ecosystem processes or properties (e.g. 'Sea ice convergence', 'Ice thickness'). These nodes were connected by 77 edges, representing the positive or negative interactions between them (Supplementary Table 1). There were 71 evidenced interactions and 6 hypothesized interactions that influence the overwinter larval growth and survival (LGS) of krill based on existing literature (Fig. 1). Larval growth and larval survival are the two response nodes at the core of the QNM reflecting our core objective of understanding the factors influencing the overwintering processes. The remaining nodes in the model were categorized into functional groups. Habitat nodes, such as depth of sea bed, glacial melt, and latitude, were perturbed to simulate different habitat scenarios (see 'Simulating habitat variability'). Climate driver nodes—including factors such as autumn primary production, temperature, wind stress, and various sea ice-related processes—were perturbed to simulate the effects of climate change (see 'Simulating climate change scenarios'). Biological nodes encompassed the various organisms and biogenic compounds, including dimethyl sulphide (DMS), pelagic algae, and small copepods, which interacted within the ecosystem. Biogeochemical and ecological process nodes, like mixed layer depth (MLD), nutrients, and marine snow, represented key processes that drove ecosystem dynamics. Finally, interaction nodes, such as predation risk and competition, were included to capture the pressures influencing krill survival. To ensure clarity and consistency throughout the analysis, a comprehensive glossary of terms was provided to define each node in detail (see 'Glossary of Terms'). The interactions between nodes (edges) were assigned a qualitative direction (1 = positive, −1 = negative, 0 = no linkage) to translate the model into a qualitatively specified community matrix based on the signs of the edges. In addition to the direction of the edges, additional classifications were assigned to each edge to capture scientific certainty regarding the nature of the relationship between nodes as either evidenced or hypothesized. Rationale for each edge is detailed in Supplementary Table 1, and the classification of interactions is described in the later section: 'Simulating Mechanistic Uncertainty'. Using the simulation-based approach (see Supplementary Material: 'community matrix process'), a stable baseline representation of the important processes governing LGS in Southern Ocean ecosystems without any specific influences from habitat types, climate change, or mechanistic uncertainty was produced from the QNM.

## Press perturbations: simulating responses to habitat and climate change scenarios

Following the model validation process, the QNM was perturbed to simulate the impact of habitat variability and different climate scenarios on the responses of LGS. Once perturbed, the change from the baseline in the system because of environmental variability from both habitat nodes and climatological nodes could be quantified.

### Simulating habitat variability

We bounded the scope of our QNM within the Southwest Atlantic sector of the Southern Ocean due to the significant nature of the Antarctic Peninsula (AP) region across ecological, scientific, and commercial contexts. The AP is an ecologically significant region (Trathan and Hill 2016, Perry et al. 2019) where fishing efforts and other commercial activities, such as tourism, are heavily concentrated (Nicol et al. 2012, Nicol and Foster 2016). Notably, the northern tip of the AP is considered a vital krill population center (Atkinson et al. 2017, Perry et al. 2019), with the highest concentration of observational data on krill, making inferences about this area particularly robust (Henley et al. 2019). To capture the region's variability, we perturbed the QNM to simulate conditions to define three different habitat types within the AP sector: the northern AP represented as 'low latitude shelf', the southern AP represented as 'high latitude shelf', and the adjacent habitat off the shelf represented as 'open ocean'. In this context, the term 'perturbation' refers to the directional change applied

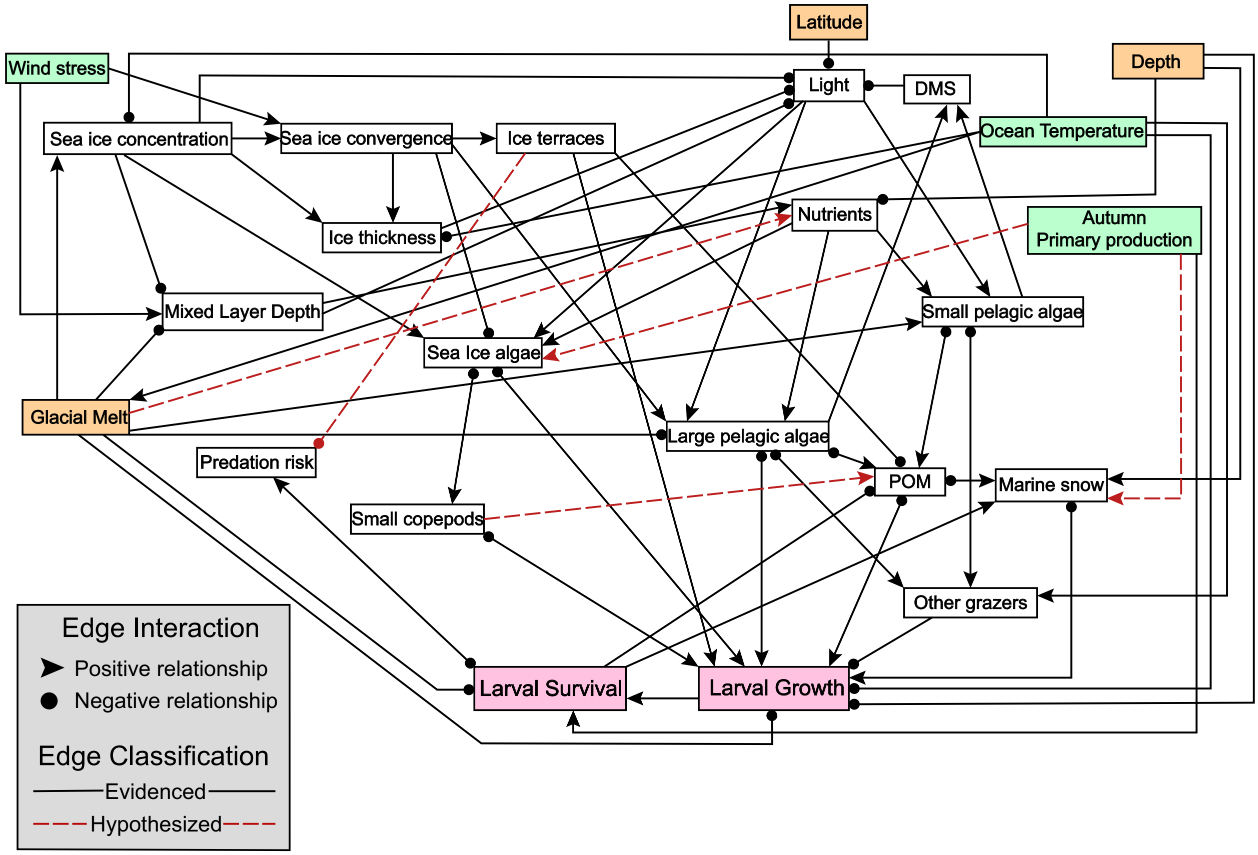


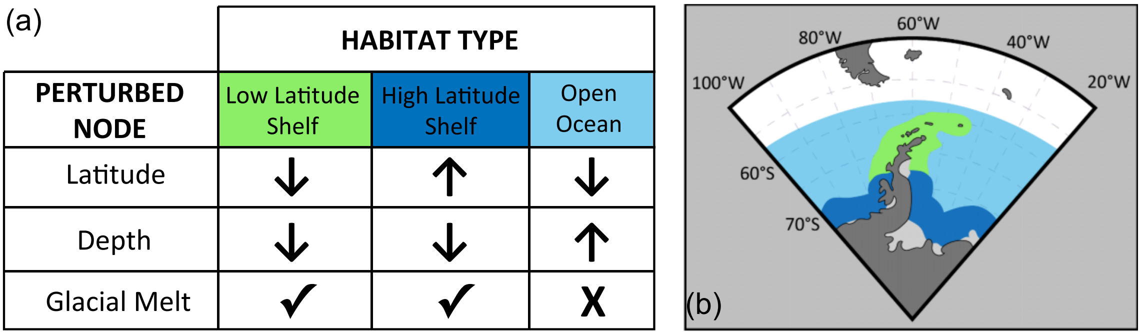
**Figure 1.** Visual representation of the QMN for overwinter LGS as a signed digraph with nodes represented in boxes and edges represented by signed lines. The response nodes, Antarctic krill LGS, are indicated in pink. Nodes simulated by changes (press perturbations) to create specific habitat zones are indicated in orange, while green nodes are simulated by press perturbations to create climate change scenarios. The direction(s) of an interaction are indicated by the symbol at the end of an edge. Interactions with a symbol at each end indicate that the interaction goes in both directions. The line type (full or dashed) indicates the classification of the edge as either evidenced or hypothesized. Nodes are described in the glossary; edges are described in more detail in Supplementary Table 1.

to model nodes (e.g. shallower depths or higher latitudes) to simulate baseline environmental variability. Importantly, these changes are not inherently positive or negative but serve to explore their influence on system responses in combination with other factors. The model building process identified latitude and (ocean) depth as the two primary large-scale drivers of environmental variability in the southwest Atlantic sector, which varied by the three habitat types. For example, latitude and depth both drive habitat variability in the marine environment: over winter, higher latitudes experience fewer hours of daylight (negative perturbation), shallower depths have greater nutrient availability (negative perturbation) due to increased vertical mixing and represent high latitude shelf areas, which suggest increased benthic habitat accessibility. When perturbed together, these drivers delineate a unique representation of habitat of the high latitude shelf habitat zone, due to the geography of the coastline of the AP that juts northward into a lower latitude than other shelf habitats around the Antarctic continent (Fig. 2). Additionally, melt from continental glaciers was included as a secondary habitat driver, as it is only present in the model when the depth was shallow (i.e. the high- and low-latitude continental shelf habitats).

## Simulating climate change scenarios

Directional perturbations (increase, decrease or no change) were applied to model nodes identified as 'climate drivers'—temperature, primary productivity (PP), wind strength, and sea ice—to construct five plausible future climate change scenarios (Table 1). Rather than serving as detailed forecasts, these scenarios function as simplified yet scientifically grounded representations of potential future states in the Southwest Atlantic sector. Model projections [e.g. from the Coupled Model Intercomparison Project (CMIP) Phases 5 and 6] and observational records consistently indicate that Southern Ocean temperatures will continue to increase as climate change intensifies (Morley et al. 2020). While the long-term trend leans towards warming, short-term or regional cooling anomalies have been observed historically and may recur in the future, justifying scenarios that include both increased and decreased temperature conditions. Similarly, annual PP is projected to increase with future warming and changes in light and nutrient regimes (Leung et al. 2015, 20; Laufkötter et al. 2015, Boyd 2019). There is less certainty, however, regarding trends in autumnal primary production (PP) where complex processes, such as phenological shifts in iron availability and grazing pressure, introduce uncertainties in how autumnal PP will respond in the future. To reflect these unknowns, scenarios include both increases and decreases in autumnal PP as simplified representations of plausible future states.

Winds represent a more constrained aspect of the scenarios. Projections generally point to strengthening westerly winds under future climate change, driven by poleward shifts in



(a)

| PERTURBED NODE | HABITAT TYPE<br>Low Latitude Shelf | <br>High Latitude Shelf | <br>Open Ocean |
|---|---|---|---|
| Latitude | ↓ | ↑ | ↓ |
| Depth | ↓ | ↓ | ↑ |
| Glacial Melt | ✓ | ✓ | X |

**Figure 2.** 'Antarctic krill habitat zones' within the southwest Atlantic sector of the Southern Ocean used within the modelling simulation. Panel A depicts how habitat zones were defined within the simulation: habitat zones (columns) are simulated by applying combinations of press perturbations (either increase ↑ or decrease ↓) to nodes characterizing habitat (rows; see orange boxes in Fig. 1). The presence or absence (as indicated by an 'x' or a '✓') of glacial melt is simulated by removing the glacial melt node from the model structure; no press perturbation is applied directly. Panel B gives a physical representation of where the habitat zones are simulated by the qualitative press perturbations. The open ocean habitat zone is indicated in light blue, while the high latitude shelf habitat zone is indicated by dark blue shading, and the low latitude shelf habitat zone is highlighted in green and is representative of the north AP.

**Table 1.** The climate change scenarios simulated in this study by applying combinations of press perturbations (either sustained increase ↑ or decrease ↓) to climate driver nodes.

| Climate change scenario | | | Perturbed model node | | | |
|---|---|---|---|---|---|---|
| ID | Short name | Description | Water temp. | Wind | Autumn PP | Sea ice |
| A | Temp+ & PP+ | Warmer, increased PP | ↑ | ↑ | ↑ | ✓ |
| B | Temp+ & PP− | Warmer, decreased PP | ↑ | ↑ | ↓ | ✓ |
| B.2 | No sea ice & Temp+ & PP− | Scenario B with total sea ice retreat | ↑ | ↑ | ↓ | X |
| C | Temp− & PP+ | Cooler, increased PP | ↓ | ↑ | ↑ | ✓ |
| D | Temp− & PP− | Cooler, decreased PP | ↓ | ↑ | ↓ | ✓ |

No press perturbation was applied to sea ice directly; therefore the 'x' and '✓' indicate whether the node is absent or present in the model structure. Note: when sea ice is absent ('x'), then associated sea ice nodes and edges (including sea-ice concentration, convergence, terraces, thickness and sea ice algae) are also absent.

atmospheric circulation (Bracegirdle et al. 2020, Morley et al. 2020). While it is possible for wind strength to remain unchanged or weaken in specific regions or time periods, these outcomes are far less common in the literature. As a result, the scenarios in this study only included increased wind strength to reflect the most widely supported and consistent prediction. For sea ice, the consensus points to an overall decline, yet recent variability—record highs followed by record lows and unprecedented wintertime minima—demonstrates that future conditions could be highly dynamic (Stammerjohn et al. 2012, Hobbs et al. 2016, Parkinson 2019, Purich and Doddridge 2023, Hobbs et al. 2024). Scenarios B and B.2 therefore incorporate both the presence and absence of sea ice to represent the possible outcomes resulting from these opposing changes in sea-ice.

By selecting perturbations that reflect the most widely supported trends—warming temperatures, generally increasing PP, and strengthening winds—while also incorporating plausible deviations (cooling temperatures, reduced PP) and the dynamic variability of sea ice conditions, the resulting scenarios capture a range of scientifically grounded future states. The inclusion of both the presence and absence of sea ice reflects its uncertain trajectory and recent extremes, while the focus on increased wind strength aligns with the strongest projections in the literature. Together, these scenarios serve as qualitative 'bookends' that enable an exploration of how key climate drivers might influence krill overwinter survival under varying plausible conditions in the Southwest Atlantic sector.

To simulate the system under climate change, the three main climate drivers of ocean temperature, wind stress, and autumn PP were identified. The model responds to climate-driven perturbations as follows (see Supplementary Table 1 for additional details): Increasing temperature (↑Temp) negatively impacts thermodynamically driven sea ice formation and has a positive impact on glacial melt, large pelagic algae, and other grazers, as well as directly negatively influencing larval krill growth via increased metabolism. Increasing wind stress (↑Wind) increases sea ice convergence (and indirectly sea ice thickness and terracing) and deepens the MLD. Increasing autumn PP (↑PP) directly and positively impacts larval krill survival (and potentially sea ice algae and marine snow). Due to the temporal limitations of the model, the variable autumn PP was used to explore changes in climate drivers that could have a meaningful impact on wintertime responses. In this scenario, autumn PP is considered a proxy for the primary production that becomes embedded in sea ice during its formation (sea ice algae), increasing scavenging availability. Implemented within the model, this theory couples sea ice algae concentrations with autumn PP rather than winter PP.

When the QNM was pressed to represent potential climate change scenarios for each habitat zone, the resulting changes were quantified by comparing the observed responses to the baseline results for the respective habitat zone. The metric used for quantification of change from one model state to the other is presented as relative change in net response, where

(1) net response = % of simulations predicting an increase − % of simulations predicting a decrease;
(2) relative change in net response = Net response$_{\text{future}}$ − Net response$_{\text{past}}$.

A negative relative change in net response therefore indicates that the variable responds more negatively under the specific climate change scenario than compared to the respective baseline perturbation (and vice versa for positive relative change). Additionally, since the net responses for the baseline habitat zone perturbations ranged from 0 to 100, relative change can therefore range from −200% to +200%. This means that a −200% relative change would indicate that the baseline simulations returned all positive responses, and the climate change scenario perturbation responses were all negative, and a +200% relative change would indicate the opposite.

### Simulating mechanistic uncertainty

Lastly, to understand the effects of uncertainty within the model, each model edge was classified as either 'evidenced' (i.e. the sign of the interaction was supported by direct evidence) or 'hypothesized' (i.e. in the absence of direct evidence, the sign was deduced following the rationale given in Supplementary Table 1). These classifications were based on the IPCC Guidance for the Fifth Assessment Report on Consistent Treatment of Uncertainties (Mastrandrea et. al 2011). 'Evidenced' interactions are those with evidence and support (measured, observed), such as the fact that krill larvae have been observed feeding on ice algae, and ice algae have been found in their stomachs. 'Hypothesized' interactions are inferred but not directly observed or measured. For example, it is thought that sea ice cavities have an energetic benefit for larval krill by providing refuge from currents. The impacts of uncertainty on model predictions can be explored by alternatively omitting and including hypothesized edges. This process produces a range of predictions of krill overwintering survival and growth explicitly accounting for mechanistic uncertainty. Conceptually, this is the comparison with a hypothetical 'known' system as opposed to a representation of the complete system 'as understood'. Thus, it provides a firm basis for assessing the consequences of uncertain interactions like habitat differences and different climate change scenarios.

By applying this method to the combinations of press perturbations described in Table 1 and Fig. 2, the following scenarios were simulated: (1) A historical baseline, where differences in LGS were simulated across the three habitat zones (without any perturbation to the climate drivers); (2) Climate change scenarios, where the three habitat zones were crossed with the five climate change scenarios. To explore the effects of adding hypothesized mechanisms on the simulation results, all the scenarios were simulated twice, first including only evidenced edges and second including both evidenced and hypothesized edges.

Two sensitivity analyses explored the relative influence of our analytical choices on LGS. The first looked at the effects of individual habitat zones and climate drivers. Since multiple nodes are perturbed simultaneously to produce the different habitat zones and climate scenarios, we simulated the press perturbations to individual driver nodes in isolation to identify if a particular node was driving an observed response. The second analysed the effects of individual hypothesized edges. Since all hypothesized edges were added simultaneously to the model structure in the second simulation run, we complemented this analysis by adding hypothesized edges one at a time to examine their incremental effect. To acknowledge that the effect of an edge will likely vary depending on the structure of the model at the time it is added, we permuted the edge-adding sequence (across all possible permutations for 6 edges = 720 permutations), and at each step, the resulting change in growth and survival was recorded. This analysis was performed for each habitat zone and possible climate change scenarios.

## Results

### Habitat variability: baseline for comparisons

Baseline results showed that conditions for larval krill growth and survival (LGS) were most favourable in the low-latitude shelf habitat, where shallow depths provide greater nutrient availability and habitat accessibility. In contrast, conditions were least favourable in the open ocean, characterized by deeper depths and the absence of nutrient inputs from glacial melt. In the baseline habitat configurations, growth provides the sole connection between habitat nodes and survival. As such, the simulated changes in LGS were the same, and the results are reported as a single response of LGS. The low-latitude shelf exhibited the highest habitat suitability for larval krill, as reflected by the +70% net response in LGS, while the open ocean habitat exhibited the least suitability (−29% net response), likely due to its deeper depths and lack of glacial melt-derived nutrient inputs (Fig. 3). The high-latitude shelf habitat demonstrated intermediate suitability (+30% net response), driven by a balance between limited daylight hours, glacial melt contributions, and nutrient accessibility from shallower depths.

The sensitivity analysis determined that the individual habitat drivers of latitude and depth impacted LGS similarly (Supplementary Fig. 1). In isolation, when either driver was negatively perturbed, LGS responded positively. The interactions between these two drivers logically followed this relationship. Moderate impacts on LGS resulted when one factor was positive while the other was negative. The largest number of positive outcomes for growth and survival occurred when both drivers were positive.

### Climate change scenarios

Climate change scenarios revealed habitat-specific responses in LGS, with the most pronounced negative impacts occurring in the low-latitude shelf habitat under all scenarios. Across all habitat zones, larval survival was most sensitive to decreases in autumn primary production. Changes in temperature and wind stress produced more complex, opposing effects across habitats, with negative impacts across LGS with every change in the low latitude shelf habitat. Unlike the baseline conditions, climate change scenarios introduced direct relationships between environmental drivers (e.g. temperature, PP) and both response variables, leading to divergent responses between growth and survival.

The diverging results were most prevalent in the open ocean habitat, where baseline results showed a net −29% response in LGS (Fig. 3), but when climate change scenarios were

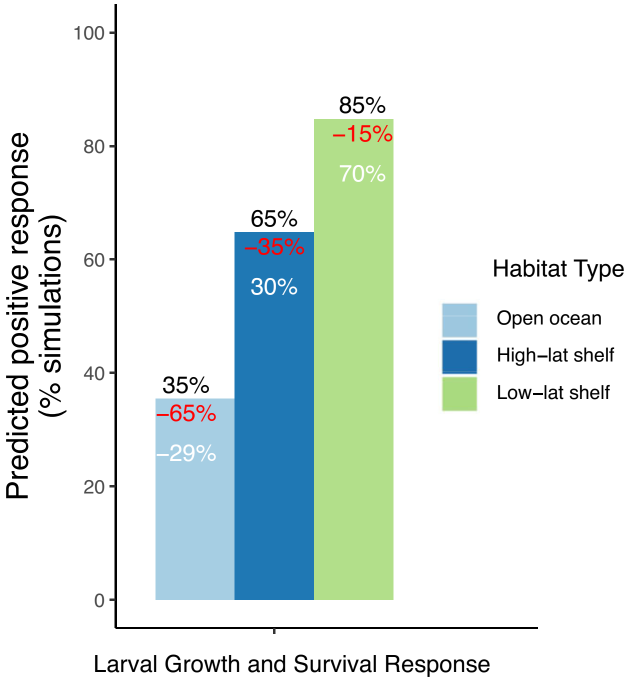


**Figure 3.** Habitat variability in larval Antarctic krill growth and survival. The height of the bars represents the percentage of simulations (*n* = 5000) predicting positive growth and survival in response to press perturbations simulating habitat variability (see Table 1). Text annotations within each bar represent the % of simulations predicting a positive response (black), negative response (red), and the net response (positive–negative, white).

applied, larval growth responses exhibited less relative change compared to larval survival. Open ocean habitat survival responses varied with survival responses increasing 51% under scenario A, not changing under scenario B, or decreasing 48% under scenario B.2 (Fig. 4). Within the open ocean habitat, the positive survival responses in scenarios A and C appear to be driven by the direct link between autumn PP and survival, while growth remained least impacted, likely due to the direct relationship between temperature and growth (Fig. 1). Further investigation showed that positive relative change in the growth response co-occurred with positive relative change in the nutrient response variable and negative relative change in the sea-ice concentration response variable (Supplementary Fig. 2). This result highlights the importance of direct versus indirect interactions in the model. Larval growth, directly influenced by temperature, exhibits less relative change because indirect benefits from increased nutrients and reduced sea ice cannot fully compensate for the stronger negative metabolic impacts of suboptimal temperature conditions. In contrast, larval survival benefits directly from increases in primary production, leading to more pronounced responses under scenarios where PP improves.

The responses of LGS to the climate change scenarios in the shelf habitats (low and high latitude) were primarily negative, indicating reductions in habitat suitability for LGS. In the high latitude habitat, LGS was reduced the most under scenarios A as well as B but showed little change under scenarios C and D (relative change <30%, Fig. 4). In particular, habitat suitability for larval survival declined by nearly 80% under scenario B. These results highlight how temperature-driven changes in glacial melt directly reduce larval survival and reduce overall habitat suitability for LGS.

In the low latitude habitat, the net responses in LGS experienced large decreases (>−70%) in relative change from baseline responses under all possible scenarios (scenarios A, B, and B.2), indicating a substantial decline in habitat suitability for larval overwintering. The largest decreases in larval growth were observed under scenarios A (net decrease of 82%) and B.2 (net decrease of 90%). These results suggest that warming temperatures and reduced primary production, both of which characterize these scenarios, create conditions that are less favourable for larval growth. The largest decrease in net response overall was for survival (decrease of 142%), indicating that while the baseline simulations returned mostly positive responses, the climate change scenario perturbation responses were mostly negative. These findings underscore how the low-latitude shelf habitat, which initially provides the most favourable baseline conditions due to nutrient availability and accessibility, becomes more unsuitable under climate change scenarios.

Analysis of individual climate drivers revealed distinct habitat-specific responses in the model, highlighting the specific influences of autumn PP, ocean temperature, and wind stress on LGS (Fig. 5). Increases in autumn PP drove increases in larval survival relative to their baseline levels, especially within the open ocean and high latitude shelf habitats, while decreases resulted in less suitable conditions for survival declines across all habitat zones. The relative change in net larval growth from perturbing autumn PP was less pronounced in comparison to the survival response. These results are most likely due to the direct relationship between survival and autumn PP, which provides key energy stores for surviving (rather than growing) overwinter.

The high- and low-latitude shelf habitats displayed similar responses, with declines in LGS when temperature or wind stress were increased. The reduction in habitat suitability for larval survival was more pronounced under warming temperatures that exacerbated the negative impacts of glacial melt on survival. Conversely, in the open ocean habitat, growth and survival responses showed a 35% increase when temperature was increased, or wind stress was decreased. This suggests that moderate warming may improve metabolic rates, while reduced wind stress stabilizes the water column and nutrient retention, creating more favourable conditions for LGS in the open ocean habitat. The opposing habitat variation in relative change responses in the open ocean habitat is due to the complexity within the model and the specific response variables that experienced higher amounts of relative change (Supplementary Fig. 4). For example, when the open ocean habitat was perturbed with increased wind stress, the relative change in the response variables for sea ice terraces, sea ice convergence, sea ice thickness, and MLD were all positive, while the light response variable experienced negative relative change. With reduced wind stress, the opposite occurred, but there was little to no relative change in the light response (Supplementary Fig. 4).

## Effects of mechanistic uncertainty

Including hypothesized mechanisms in the model resulted in minimal changes to most habitat and climate change scenarios, with the largest differences observed in the open ocean habitat and under specific climate scenarios. These results highlight the importance of certain hypothesized relationships, such as the role of glacial melt in nutrient availability and the refugia effect of ice terraces, in shaping larval

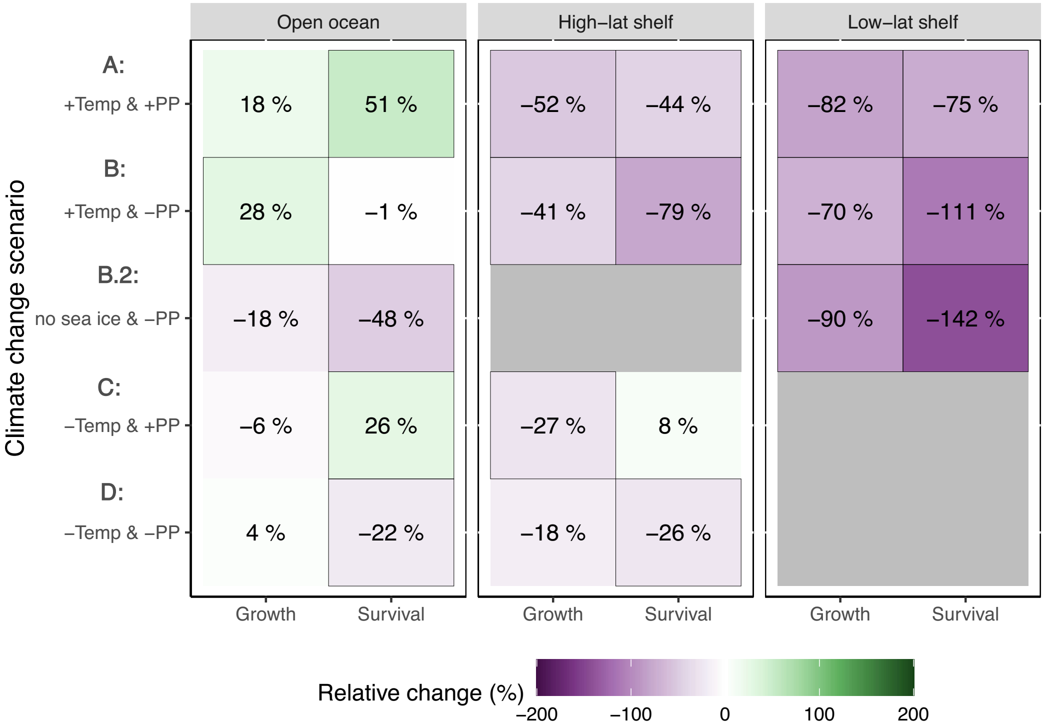


**Figure 4.** Impacts of climate scenarios on LGS for each habitat type. The shaded cells display the net response (% positive–% negative simulations) relative to baseline (Fig. 3) of krill growth and survival. Boxes are outlined if the change is over 15%. These responses were predicted using the model configuration that only included evidenced mechanisms for five climate change scenarios and three habitat zones. Grey cells were not simulated. The climate scenarios A–D refer to the press perturbations detailed in Table 1.

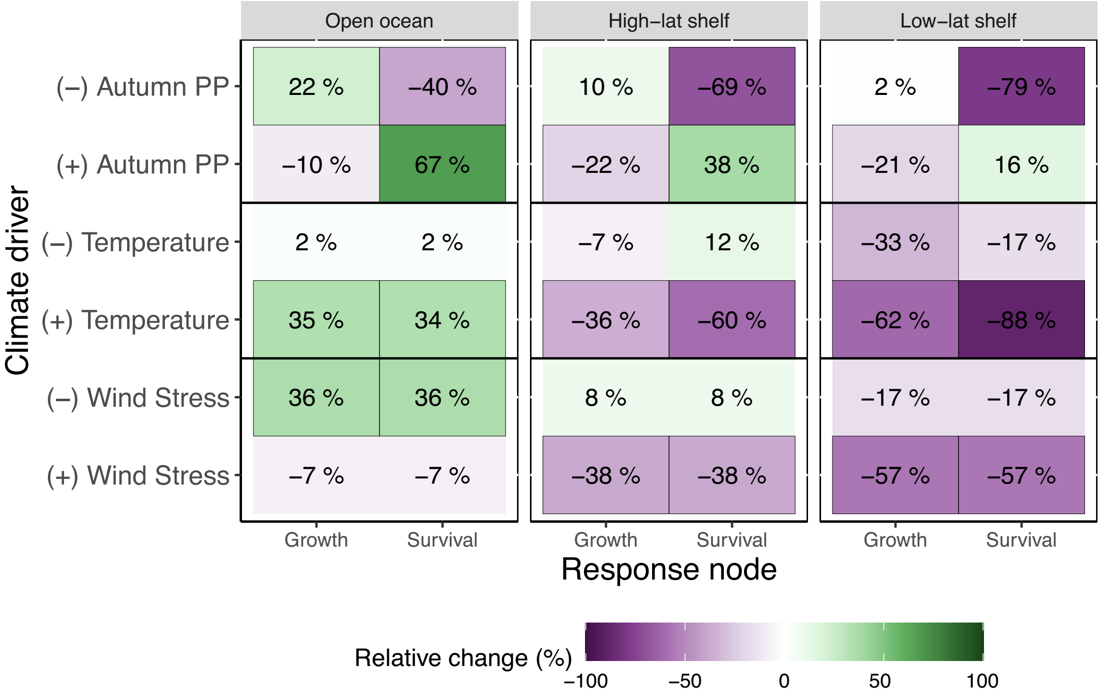
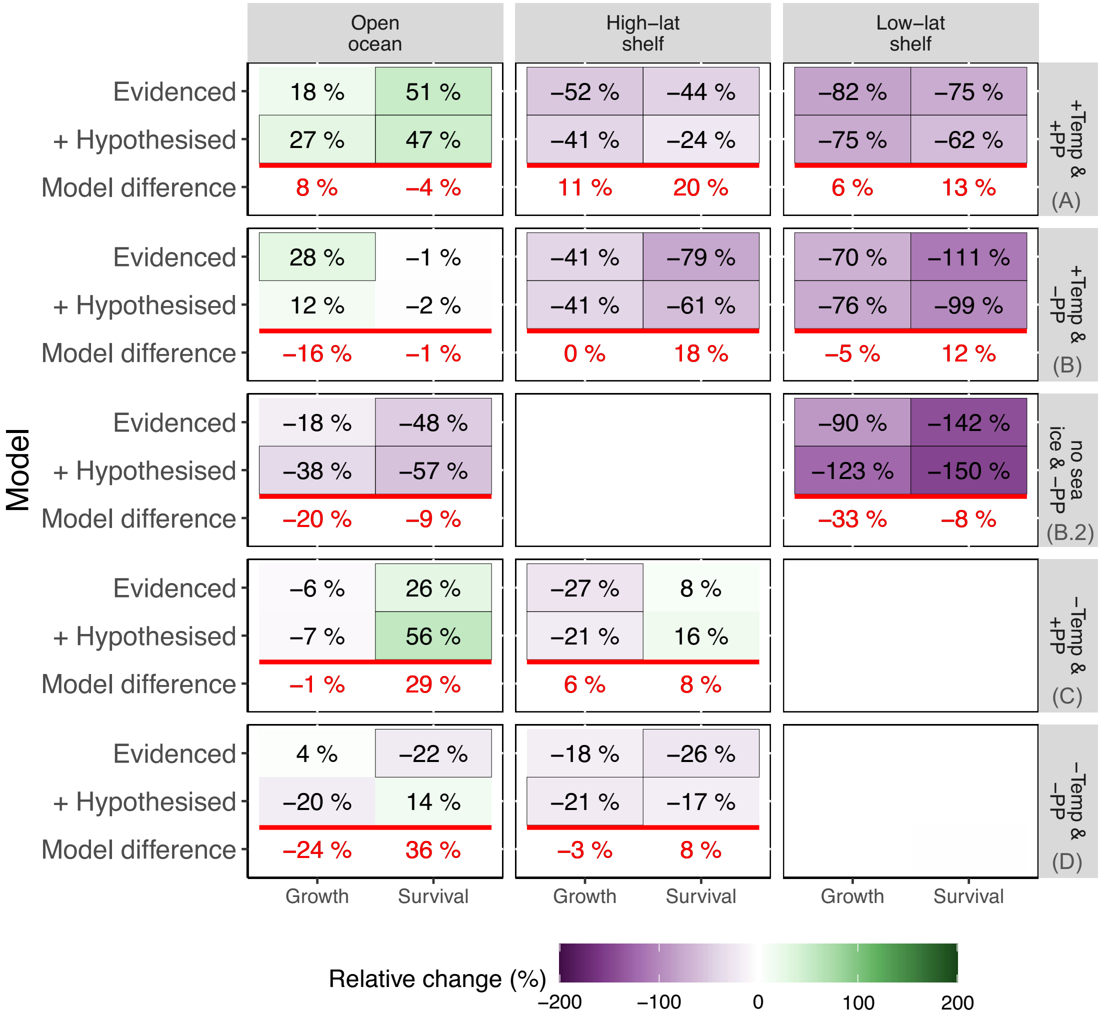


**Figure 5.** The net effects of individual drivers of climate change [autumn primary productivity (PP), ocean temperature, and wind stress] on LGS. The net response (% positive simulations–% negative simulations) of the model response nodes (growth and survival) minus the net response in the baseline habitat simulations (see Fig. 3) is shown using the colour bar. Relative differences >20% are outlined.



| Scenario | Model | Open ocean Growth | Open ocean Survival | High–lat shelf Growth | High–lat shelf Survival | Low–lat shelf Growth | Low–lat shelf Survival |
|---|---|---|---|---|---|---|---|
| +Temp & +PP (A) | Evidenced | 18 % | 51 % | −52 % | −44 % | −82 % | −75 % |
| | + Hypothesised | 27 % | 47 % | −41 % | −24 % | −75 % | −62 % |
| | Model difference | 8 % | −4 % | 11 % | 20 % | 6 % | 13 % |
| +Temp & −PP (B) | Evidenced | 28 % | −1 % | −41 % | −79 % | −70 % | −111 % |
| | + Hypothesised | 12 % | −2 % | −41 % | −61 % | −76 % | −99 % |
| | Model difference | −16 % | −1 % | 0 % | 18 % | −5 % | 12 % |
| no sea ice & −PP (B.2) | Evidenced | −18 % | −48 % | | | −90 % | −142 % |
| | + Hypothesised | −38 % | −57 % | | | −123 % | −150 % |
| | Model difference | −20 % | −9 % | | | −33 % | −8 % |
| −Temp & +PP (C) | Evidenced | −6 % | 26 % | −27 % | 8 % | | |
| | + Hypothesised | −7 % | 56 % | −21 % | 16 % | | |
| | Model difference | −1 % | 29 % | 6 % | 8 % | | |
| −Temp & −PP (D) | Evidenced | 4 % | −22 % | −18 % | −26 % | | |
| | + Hypothesised | −20 % | 14 % | −21 % | −17 % | | |
| | Model difference | −24 % | 36 % | −3 % | 8 % | | |

**Figure 6.** Impacts of climate change scenarios on LGS across all habitat zones when configuring the model to include hypothesized mechanisms. This figure is a continuation of the data presented in Fig. 4, where the coloured cells display the net response (% positive–% negative simulations) relative to baseline (Fig. 4) of krill growth and survival. In addition to the net responses using the hypothesized model structure, the difference between the net responses between the 'hypothesized' and 'evidenced' model are shown below the hypothesized net responses ('difference' = hypothesized net responses–evidenced net responses). White cells were not simulated. Climate change scenarios are listed by their short names as detailed in Table 1.

krill growth and survival responses across habitats and scenarios. The habitat baseline perturbation established strong similarities in LGS responses between the baseline results for each habitat with the main difference being a reduction in the net negative response for the open ocean habitat increasing slightly (Supplementary Fig. 3). The open ocean habitat was the only habitat that was not perturbed with glacial melt. Glacial melt was also the only habitat node with a 'hypothesized' relationship (positive relationship with nutrients, Fig. 1). Together, these results highlight the regional impact of glacial melt on nutrient variability and indicate that the nature of this relationship requires further clarification. Other than the difference between the open ocean habitat LGS net responses, the net responses for the low and high latitude habitats were within a percentage point of the baseline established without 'hypothesized' mechanisms included in the model.

The differences in relative change between the evidenced model and hypothesized model under the five climate change scenarios were mixed across LGS net responses with the majority exhibiting low magnitudes of change. While the magnitude of change is notable, the direction of the change indicates if the hypothesized mechanisms enhanced the direction of change from what was modelled in the QNM before their addition or if they invert the sign. For example, when the open-ocean habitat was perturbed using climate scenario D, net response results for survival improved by 36 percentage points from an overall negative response to a slightly positive response, and growth responses went from a net neutral result (4%) to a negative result (−24%) (Fig. 6). The magnitude of these changes is quite low when considering the possible range of possible relative change. However, the change in the direction of the response indicates that the inclusion of the hypothesized mechanisms (Fig. 7, ice terraces and predation risk) changes the model prediction to be ∼35% more suitable for survival under scenario D in the open ocean habitat. The only other result with a magnitude of change over 30% was under scenario B.2, where the relative change in net response for growth went from −90% to −123%, or a decrease of 33 percentage points, in the net growth response. In this case, these results indicate that including the hypothesized mechanisms [indirect impacts of increased nutrients, PP and particu-

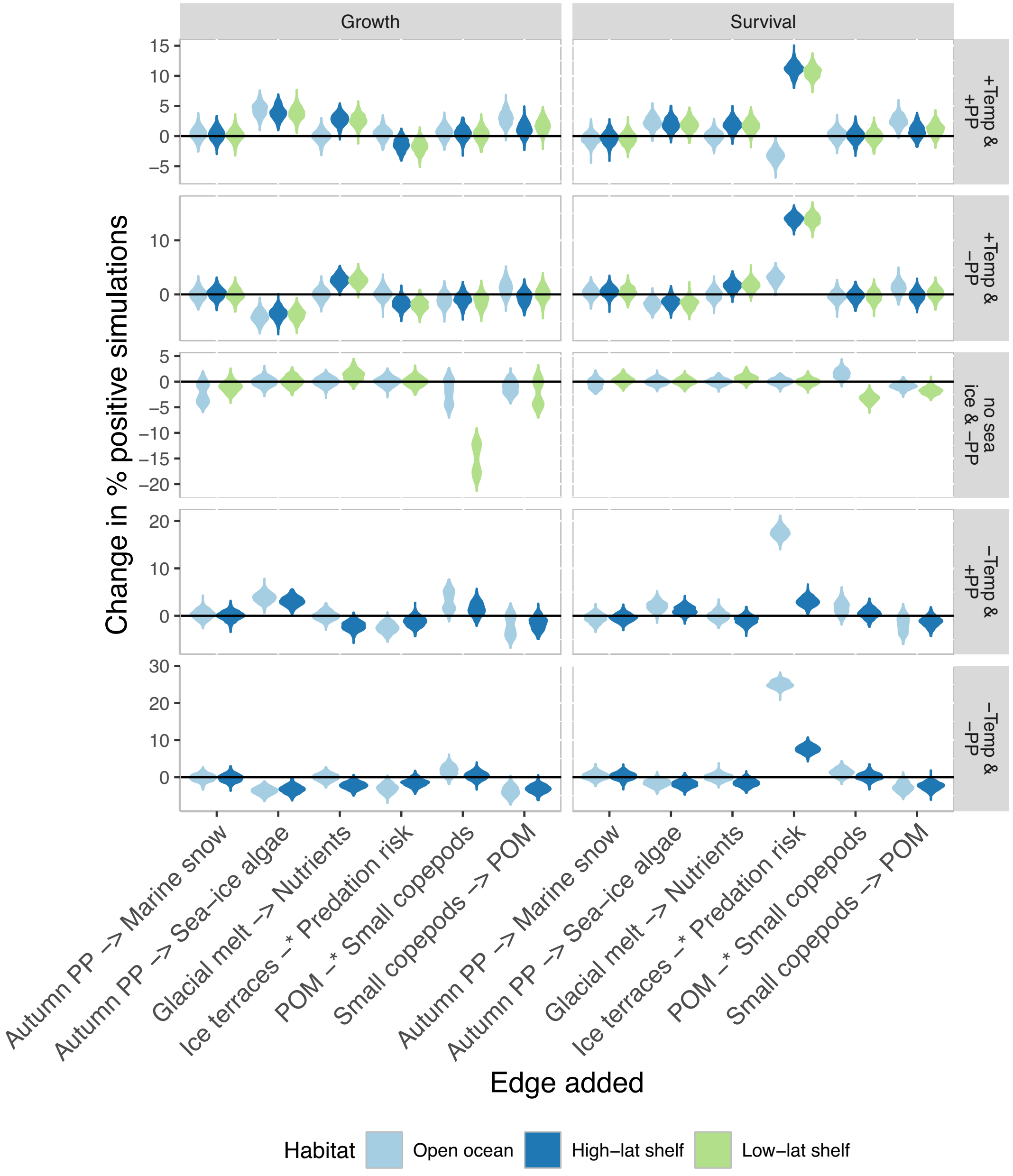


**Figure 7.** The resulting change in the % of simulations predicting positive growth or survival (columns in the multi-panel figure) when hypothesized edges were added to the model structure. The edge-adding order was permuted across all possible permutations of the hypothesized edges ($n = 6$ edges, $n = 720$ permutations). This was performed for all habitat types (represented by the colour bar) and applicable climate change scenarios (rows in the multi-panel figure). Arrows in edge names indicate positive interactions; circular markers indicate negative interactions.

late organic matter (POM) on growth] enhanced the baseline climate change results for this scenario and habitat.

The permutation analysis provided additional results to elucidate the source of the differences between configurations, quantifying the effect that the addition of an individual hypothesized relationship had on net LGS responses (Fig. 7). For the most likely climate change scenario (B: +temp and −PP) and the most significant habitat for changing LGS (low latitude shelf), this analysis revealed that the largest change in larval survival (14% increase) was related to the hypothesized negative relationship between ice terraces and predation risk. The inclusion of that refugia relationship in the model similarly accounted for 14% a increase in positive model responses for survival in the high latitude habitat (Fig. 7). The increase in positive responses from this ice terraces-refugia relationship was also notable under scenario A for both habitats and for the open ocean habitat in scenarios C and D (Fig. 7). Without the influence of sea ice in the low latitude habitat (scenario B.2), hypothesized mechanisms did not substantially impact larval survival. However, the negative relationship between POM and small copepods decreased the positive responses in growth between 10% and 20% (Fig. 7).

## Discussion

Our QNM reproduced baseline differences in LGS that are consistent with observations across our three habitat zones of interest in the southwest Atlantic sector of the Southern

Ocean. Specifically, baseline results predicted that conditions for krill LGS were most favourable in the shallow, low-latitude shelf habitat where benthic habitat is more accessible. In contrast, conditions for LGS were least favourable in open ocean habitat where the seafloor is deeper and there is no input from glacial melt. These results are consistent with current understandings of larval krill growth and survival (Perry et al. 2019) and provide confidence that the model captures realistic patterns despite its qualitative nature. By reproducing these patterns, our findings support our first research question, demonstrating that key environmental drivers—autumn PP, temperature, wind stress, and sea ice dynamics—vary regionally, shaping larval krill survival differently across habitats. This highlights how our model represents complex, real-world processes in a simplified form, allowing us to explore key mechanisms influencing LGS. As a result, the QNM serves as a reliable framework for identifying the most critical drivers and interactions under current and future environmental conditions.

Sensitivity analyses identified that decreased autumn PP had the largest impact on larval survival, particularly in the low latitude shelf habitat. The northern AP, represented by the 'low latitude shelf' habitat type, is a commercially (Nicol et al. 2012, Nicol and Foster 2016) and ecologically (Trathan and Hill 2016, Perry et al. 2019) significant habitat with the highest concentration of observational data on krill (Trathan and Hill 2016, Atkinson et al. 2017, Hendry et al. 2018, Henley et al. 2019). Critically, this habitat has undergone rapid environmental change, including periods of pronounced warming (Vaughan et al. 2003, Meredith and King 2005, Turner et al. 2016) linked to sea-ice decline (Stammerjohn et al. 2008, Turner et al. 2013, 2017) and changes in phytoplankton availability (Moline et al. 2004, Montes-Hugo et al. 2009, Mendes et al. 2013, Rozema et al. 2017). Meyer et al. (2017) identified autumn food availability as a key control on the recruitment of larval krill into adulthood, highlighting the need for better characterization of food availability during this critical season. Our findings agree and emphasize that climate-driven changes to autumnal PP—such as phenological shifts in algal blooms and changes in community composition—could have profound impacts on larval krill survival. Moreover, changes in food quality and availability interact with shifts in the predator community composition, further complicating the ecosystem response. Given the ecological and commercial importance of this region, these findings underscore the need for enhanced monitoring and research on seasonal food dynamics and their cascading effects on krill populations and dependent predators.

Under the climate change scenarios tested, both low- and high-latitude shelf habitats simulated reductions in habitat suitability for LGS when autumn PP was depressed and temperature and wind stress increased. In the low-latitude shelf habitat, all scenarios predicted negative impacts on larval krill. Decreases in autumn PP drove the largest reduction in larval survival, consistent with the reliance of larval krill on pre-winter reserves for overwintering success (Quetin et al. 2007, Meyer et al. 2009). In contrast, autumn PP had no effect on growth, reflecting the model's assumption of zero growth over winter and its limited representation of seasonal production dynamics (Meyer et al. 2009, 2017). These results are in line with similar modelling studies that identified that reduced chlorophyll-*a* availability and delayed sea-ice formation in future climate change scenarios will reduce suitable krill habitat by 80% by the end of the 21st century, including suitable spawning locations along the AP (Piñones and Fedorov 2016). However, we note that chlorophyll-*a* is not always linearly linked with phytoplankton biomass and primary production and therefore is not always a direct indicator. These results are partially due to the direct relationship between autumn PP and survival and indirect relationship between wind stress and ocean temperature within the QNM structure (Fig. 1). These indirect relationships should be considered in the future given observational evidence of a robust warming of the subsurface, subpolar deep waters (0.04 ± 0.01°C per decade) from 1992 to 2017 (Auger et al. 2021). Future research should therefore consider how temperature changes at different ocean depths might further influence larval krill in a warming climate.

Examining how uncertain interactions influenced LGS in low-latitude shelf habitat, under most climate scenarios, adding hypothesized interactions did not substantially change the predicted declines in larval krill growth and survival. However, in addressing our second and third research questions, we found that in certain scenarios, the inclusion of hypothesized mechanisms either reinforced or significantly altered baseline projections, highlighting their potential to amplify or buffer climate-driven impacts on larval krill. Two exceptions to this result warrant further discussion, as they reveal conditions under which specific hypothesized mechanisms substantially altered model outcomes and introduced additional uncertainty.

The first occurred in the low-latitude shelf habitat under scenario B.2 (no sea ice, reduced PP, increased temperature), where adding hypothesized relationships to the model led to a more than 30% decrease in what was already a significantly reduced habitat for LGS. This pattern suggests that under warmer, ice-free, and food-limited conditions, uncertain processes may reinforce negative feedback loops, particularly for larval growth. Among the hypothesized mechanisms contributing to this outcome, the relationship between small copepods and POM had the most pronounced effect. Under scenario B.2, the positive relationship between small copepods and POM, where small copepods associated with sea ice become POM when they die (Caron et al. 2016), resulted in decreased habitat suitability for LGS across simulations (Supplementary Fig. 6). When the relationship was inverted (such that small copepods were not assumed to enhance POM availability), LGS outcomes improved. This suggests that under scenario B.2, where food availability is already reduced and temperatures are elevated, the previously beneficial relationship between small copepod-derived POM and larval krill survival may break down due to food scarcity and increased metabolic demands under elevated temperatures. Warmer temperatures increase the metabolic demands of larval krill, making them more reliant on available food sources (Meyer and Teschke 2016, Ryabov et al. 2017). The reduction in primary production, combined with uncertainty in how copepod-derived POM contributes to larval feeding, may have exacerbated food limitation, intensifying the negative impacts on growth and survival. If copepod-derived POM is not an accessible or sufficient food resource under these conditions, its presence would not mitigate the effects of declining primary production. Alternatively, copepods may play a more complex role in trophic interactions, such as influencing microbial remineralization or modulating the availability of particulate versus dissolved organic matter, dynamics that are not fully captured by the model. These findings highlight the uncertainty surrounding copepod-POM interactions and their influence on food limitation, particularly in ice-free, warming scenarios where primary production is reduced. Further empirical research is needed to determine whether copepod-derived POM represents a meaningful food source for larval krill or whether alternative pathways play a greater role in overwintering survival (Moriceau et al. 2018, Manno et al. 2020)

The second exception occurred within the predictions for the open-ocean habitat under scenario D (reduced temperature and reduced PP), where adding hypothesized mechanisms substantially altered the model outcomes. Here, the relative change in larval survival shifted from an overall negative to a slightly positive response while growth moved from near neutral to negative. The permutation analysis revealed that a single hypothesized mechanism, sea ice terraces, through their potential to provide refuge from predation under conditions with greater sea ice extent, primarily drove this reversal. This highlights how a single hypothesized mechanism can invert baseline projections and underscores the importance of refining our understanding of the processes linking sea ice features, predator avoidance, and larval krill performance.

Although this result is unique to the open ocean habitat, our sensitivity analysis highlighted the broader influence of ice terraces across all habitat types. In scenarios where sea ice increased, ice terraces played a key role in shaping survival outcomes, particularly through their potential to provide refuge from predation. The simplified representation of predation risk reflects the limited understanding of predator impacts on larval krill but allows the model to qualitatively explore how predator pressures may interact with other drivers, such as habitat structure (e.g. ice terraces), to influence survival. For example, under scenario B.2, the hypothesized negative relationship between ice terraces and predation risk contributed to a 14% increase in positive simulations for survival in both the low- and high-latitude shelf habitats. Similarly, under scenarios C and D, the presence of ice terraces improved survival outcomes in the open ocean habitat. However, the extent to which ice terraces contribute to larval krill survival remains uncertain, emphasizing the need to improve confidence in these hypothesized relationships, particularly those involving sea ice convergence and predator avoidance behaviours.

These findings highlight the uncertainty surrounding key processes influencing overwinter mortality in larval krill. The role of sea ice as both a physical habitat and a driver of trophic interactions remains poorly constrained, especially in the northern AP region, where recent declines in sea-ice extent have been dramatic. When this research began, climate scenario B.2 (no sea ice) was considered plausible but unlikely. However, recent severe declines in sea ice extent (Purich and Doddridge 2023, Hobbs et al. 2024) indicate that scenario B.2 is becoming increasingly plausible, amplifying the significance of these results. Understanding how ice-free conditions alter krill recruitment dynamics is critical for predicting how Antarctic ecosystems may respond to future climate scenarios.

Ultimately, these findings reinforce the importance of resolving uncertainties in how sea-ice-dependent mechanisms, such as ice terraces, predation risk, and trophic interactions, contribute to larval krill survival. As rapid environmental change continues to shape the Antarctic ecosystem, improving our understanding of these processes will be essential for anticipating how krill populations respond to future climate scenarios. For example, although extreme sedimentation from glacial melt has been associated with larval krill mortality in both observational and laboratory experiments (Fuentes et al. 2016), adding a negative effect on growth and survival from glacial melt did not result in appreciable impacts on either outcome. We could hypothesize that scenarios where environmental extremes cause acute physiological responses resulting in mortality are not well represented by a model network which is better suited for understanding the impacts of feedback cycles between connected nodes in response to sustained perturbations.

Overall, our results highlight the importance of accurately capturing the nuances involved in larval krill survival and growth in models and provide valuable insights for directing future empirical research, prioritizing understanding the seasonal feeding patterns of larval krill and their relationship to overwinter survival via growth. For example, Bernard et al. (2019) demonstrated that larval krill in the Bransfield Strait can meet their metabolic needs over winter, regardless of the amount of sea ice present, by grazing on pelagic phytoplankton or sea-ice algae. However, many of the mechanisms linking krill and their environment remain poorly understood, and the controls on overwinter survival and recruitment involve complex processes, including seasonal sea-ice extent and internal population dynamics. Structural uncertainty, common in ecological models, can arise when deciding which interactions to include. In this study, some relationships, although supported by evidence, are not typically considered influential at the ecosystem scale. Examples include the negative effect of sea-ice thickness and DMS on light availability and the positive effect of large and small pelagic algae on DMS (detailed in Supplementary Table 1). Recognizing this uncertainty, our treatment of hypothesized relationships allowed us to explore their potential effects without committing to fixed assumptions. This approach helps address structural uncertainty as a source of indeterminacy in ecological predictions and decision-making processes (Punt and Hilborn 1997, Hosack et al. 2008).

Our model identifies areas where more clarity is needed to refine predictions of how these mechanisms impact krill population dynamics. Given the complexity and uncertainty of Southern Ocean ecosystems, it is not currently feasible to develop a detailed quantitative model that accounts for all variables and interactions. Our results serve as useful starting points for specific simulation experiments under spatially explicit frameworks such as the newly developed KRILLPODYM (Green et al. 2023). KRILLPODYM is a numerical model that can receive as inputs a suite of habitat quality indicators that modulate the growth and survival of various life stages. This highlights how computationally inexpensive qualitative simulations and more expensive quantitative simulation frameworks can be partnered to develop and test key hypotheses and ultimately inform observational strategies.

One of the key strengths of qualitative modelling is its ability to evaluate the impact of including or excluding uncertain relationships. Our findings indicate that the greatest gains in prediction precision could come from improving our understanding of key processes driving larval krill survival and growth. Specifically, priority areas for future field and laboratory studies include

(1) Seasonal food composition and larval overwintering performance: Seasonal shifts in algal blooms, sea ice algae, pelagic phytoplankton, and small copepod-associated POM impact larval krill survival. Determining how larvae utilize these resources and the importance of sea-ice dependent mechanisms in terms of feeding contributing to survival will clarify the factors driving overwinter LGS under climate-driven changes in food availability.

(2) Sea-ice terraces and predation risk: Sea-ice terraces may offer refuge and influence trophic interactions, altering larval predation pressure. Understanding how changing sea ice structure affects these predator-prey dynamics is key to predicting larval krill responses as sea ice declines.

(3) The influence of glacial melt on nutrient availability and food web dynamics: While glacial melt can alter nutrient delivery and primary production, its negative impacts on larval krill survival remain under-researched. Future studies should focus on both the longer-term effects of glacial melt on nutrient availability, phytoplankton blooms, and food quality, as well as acute impacts like sedimentation, which may not be well represented in models.

Targeting these priorities will be crucial for advancing sustainable ecosystem management in a rapidly changing environment. Our study contributes to broader efforts within the Antarctic krill research community to address uncertainties in krill population dynamics (Murphy et al. 2022). Complementary work, such as identifying critical data gaps for parameterizing krill recruitment models (Murphy et al. 2022), focuses on life history events like spawning, larval development, and overwintering. Together, these studies build a more holistic understanding of how krill respond to environmental drivers. By refining our understanding of mechanisms—such as the role of sea-ice terraces in supporting larval krill—and improving data integration, future research will be better equipped to anticipate the impacts of climate variability on krill populations and the broader Southern Ocean ecosystem.

## Glossary of terms represented by QNM nodes

### Response nodes

1. Growth (of larval krill): Increase in potential size of krill larvae (<1 year of age).
2. Survival (of larval krill): Continued life of larval krill.

### Habitat nodes (perturbed to simulate habitat changes, see Table 1)

3. Depth (of benthos): Vertical distance from the ocean surface to the seafloor within the Southwest Atlantic sector.
4. Glacial melt: Process of ice loss from glaciers due to increased temperatures, affecting sea level and ocean salinity.
5. Latitude: Geographical coordinates indicating the north-south position on Earth, with focus on the tip of the AP vs closer to the continent.

### Climate driver nodes (perturbed to simulate climate change, see Table 1)

6. Autumn primary production: Production of organic compounds by phytoplankton during the austral autumn season.
7. Ice terraces: Ice morphology features formed under the surface of sea ice by repeated cycles of melting and freezing. In this model, they represent over-rafted sea ice caused by dynamic thickening that are thought to provide refuge and a more productive feeding substrate for krill.
8. Ice thickness: Vertical measurement of sea ice.
9. Sea ice convergence: Process of sea ice floes being driven together, resulting in thickening.
10. Sea ice concentration: Fraction of a defined area covered by sea ice.
11. Temperature: Ocean temperature.
12. Wind stress: Force exerted by wind on the ocean surface.

### Biological nodes

13. DMS: Biogenic sulphur compound produced by marine phytoplankton.
14. Large pelagic algae: Algal species inhabiting the pelagic zone, characterized by their larger size and role in community structure.
15. Small pelagic algae: Small-sized algal species found in the pelagic zone, contributing to the base of the marine food web.
16. Sea ice algae: Microalgae that inhabit sea ice.
17. Small copepods: Small crustaceans that serve as prey for higher trophic levels.
18. Other grazers (competition): Species that compete for similar food resources needed by larval krill.

### Biogeochemical and ecological process nodes

19. MLD: Upper layer of the ocean where water density is uniform due to turbulent mixing, affecting heat distribution and biological processes.
20. Marine snow: Larger aggregates of organic and inorganic particles forming from the accumulation of smaller particles that descend from the upper ocean to the deep sea.
21. Nutrients: Essential elements like nitrogen, phosphorus, and silica required by marine organisms for growth.
22. POM: Organic particles suspended in the water column, ranging from microscopic to larger particles such as dead organisms, faecal pellets, and detritus.
23. Light: Solar radiation reaching the ocean, essential for photosynthesis and primary production.
24. Predation risk: Probability of an organism being preyed upon.

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## Author contributions

Zephyr T. Sylvester (Conceptualization [equal], Data curation [equal], Formal analysis [equal], Funding acquisition [equal], Investigation [equal], Methodology [equal], Project administration [lead], Resources [equal], Software [equal], Supervision [lead], Validation [equal], Visualization [equal], Writing – original draft [lead], Writing – review & editing [lead]), D. Veytia (Conceptualization [equal], Data curation [equal], Formal analysis [lead], Investigation [equal], Methodology [equal], Project administration [equal], Resources [equal], Software [equal], Supervision [equal], Validation [equal], Visualization [equal], Writing – original draft [equal], Writing – review & editing [equal]), A. A. Bahl (Conceptualization [supporting], Investigation [supporting], Validation [supporting], Writing – review & editing [supporting]), D. Bahlburg (Conceptualization [supporting], Investigation [supporting], Validation [supporting], Writing – review & editing [supporting]), D. Benkort (Conceptualization [equal], Data curation [equal], Investigation [equal], Validation [equal], Writing – review & editing [equal]), S. Bestley (Investigation [equal], Validation [equal], Writing – review & editing [equal]), B. Cagdas (Investigation [equal], Writing – review & editing [supporting]), A. C. Cleary (Conceptualization [equal], Data curation [equal], Investigation [equal], Validation [equal], Writing – review & editing [equal]), A. Constable (Conceptualization [equal], Resources [supporting], Writing – review & editing [supporting]), S. Corney (Conceptualization [equal], Data curation [equal], Formal analysis [equal], Funding acquisition [equal], Investigation [equal], Methodology [equal], Project administration [equal], Resources [equal], Software [equal], Supervision [equal], Validation [equal], Writing – review & editing [equal]), B. A. Fach (Conceptualization [equal], Data curation [equal], Investigation [equal], Validation [equal], Writing – review & editing [equal]), N. Hellessey (Conceptualization [equal], Data curation [equal], Investigation [equal], Validation [equal], Writing – original draft [supporting], Writing – review & editing [equal]), S. L. Hill (Conceptualization [equal], Data curation [equal], Methodology [equal], Validation [equal], Writing – review & editing [equal]), N. M. Johnston (Conceptualization [equal], Funding acquisition [lead], Investigation [equal], Resources [equal], Supervision [supporting], Validation [equal], Writing – review & editing [equal]), S. Labrousse (Conceptualization [equal], Data curation [equal], Investigation [equal], Methodology [equal], Validation [equal], Visualization [equal], Writing – original draft [supporting], Writing – review & editing [equal]), B. Merkel (Conceptualization [equal], Data curation [equal], Investigation [equal], Methodology [equal], Validation [equal], Writing – review & editing [equal]), E. J. Murphy (Conceptualization [equal], Data curation [equal], Funding acquisition [equal], Investigation [equal], Resources [equal], Supervision [supporting], Validation [equal], Writing – review & editing [equal]), R. C. Subramaniam (Conceptualization [equal], Data curation [equal], Formal analysis [equal], Investigation [equal], Methodology [equal], Software [equal], Validation [equal], Visualization [equal], Writing – original draft [supporting], Writing – review & editing [equal]), S. Thorpe (Conceptualization [equal], Data curation [equal], Investigation [equal], Validation [equal], Writing – review & editing [equal]), and B. Raymond (Conceptualization [equal], Data curation [equal], Formal analysis [equal], Funding acquisition [equal], Investigation [equal], Methodology [equal], Project administration [equal], Resources [equal], Software [equal], Supervision [equal], Validation [equal], Visualization [equal], Writing – original draft [equal], Writing – review & editing [equal])

## Supplementary material

Supplementary data is available at *ICES Journal of Marine Science* online.

Supplementary Table 1 details the qualitative model interactions, classifications, mechanisms, and references used to build to model. A full reference list is provided for the table as well as a codebook of metadata.

Supplementary Material 1 details the 'community matrix process'

Supplementary Figs. 1–6 provide additional context for specific results. All figures are referenced within the main text.

*Conflict of interest*: None declared.

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## Data availability

The data and code used to build the models and generate predictions are available on GitHub and can be publicly accessed at https://github.com/SCAR/ICED-krill-modelling upon publication.

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