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How biological clocks and changing environmental conditions determine local population growth and species distribution in Antarctic krill (*Euphausia superba*): a conceptual model

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ABSTRACT

The Southern Ocean ecosystem is characterized by extreme seasonal changes in environmental factors such as day length, sea ice extent and food availability. The key species Antarctic krill (*Euphausia superba*) has evolved metabolic and behavioural seasonal rhythms to cope with these seasonal changes. We investigate the switch between a physiological less active and active period for adult krill, a rhythm which seems to be controlled by internal biological clocks. These biological clocks can be synchronized by environmental triggers such as day length and food availability. They have evolved for particular environmental regimes to synchronize predictable seasonal environmental changes with important life cycle functions of the species. In a changing environment the time when krill is metabolically active and the time of peak food availability may not overlap if krill's seasonal activity is solely determined by photoperiod (day length). This is especially true for the Atlantic sector of the Southern Ocean where the spatio-temporal ice cover dynamics are changing substantially with rising average temperatures. We developed an individual-based model for krill to explore the impact of photoperiod and food availability on the growth and demographics of krill. We simulated dynamics of local krill populations (with no movement of krill assumed) along a south-north gradient for different triggers of metabolic activity and different levels of food availability below the ice. We also observed the fate of larval krill which cannot switch to low metabolism and therefore are likely to overwinter under ice. Krill could only occupy the southern end of the gradient, where algae bloom only lasts for a short time, when alternative food supply under the ice was high and metabolic activity was triggered by photoperiod. The northern distribution was limited by lack of overwintering habitat for krill larvae due to short duration of sea ice cover even for high food content under the ice. The variability of the krill's length-frequency distributions varied for different triggers of metabolic activity, but did not depend on the sea ice extent. Our findings suggest a southward shift of krill populations due to reduction in the spatial sea ice extent, which is consistent with field observations. Overall, our results highlight the importance of the explicit consideration of spatio-temporal sea ice dynamics especially for larval krill together with temporal synchronization through internal clocks, triggered by environmental factors (photoperiod and food) in adult krill for the population modelling of krill.

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1. Introduction

Environmental conditions such as air temperature, water temperature, and sea ice dynamics are changing at an unprecedented rate in the Atlantic sector of the Southern Ocean ecosystem (Skvarca et al., 1999, Vaughan et al., 2003). Globally (Walther et al., 2002) and for both polar regions (Montes-Hugo et al., 2009, Schofield et al., 2010, Nielsen et al., 2013) species are already responding to climate change. The response of Antarctic krill (*Euphausia superba* – from here on called krill) is of special interest due to its central role in the food web of the Southern Ocean (Loeb et al., 1997) and its growing importance for the fishery (Everson, 2000). Therefore the findings of recent studies regarding responses of krill to climate change, ocean acidification, and habitat change in krill are of public concern (Atkinson et al., 2004, Hill et al., 2013, Kawaguchi et al., 2013). At the same time krill is also known for its physiological plasticity and its ability to adapt to a wide range of environmental conditions as well as their seasonal fluctuation, allowing for krill's wide latitudinal distribution between 50°S (e.g. South Georgia) and 70°S (e.g. Amundsen Sea) (Atkinson et al., 2004).

One of the overwintering strategies for adult krill is to reduce metabolic activity during winter when there is not much food available compared to summer period when massive algae blooms occur (Kawaguchi et al., 2007, Meyer 2012, Meyer et al., 2009, 2010). This reduced metabolic activity is hypothesized to be not only a response to reduced food availability but also driven by an endogenous timing system synchronized by the environmental 'Zeitgeber' photoperiod (Teschke et al., 2007, 2008, 2011, Meyer et al., 2010). It is crucial to understand the details of this endogenous timing mechanism to assess krill's capacity to adapt to climate change because the metabolic activity of krill and favourable environmental conditions could go out of phase in the future with unknown consequences. The impact of an internal timing mechanisms on krill's spatial distribution and population-level patterns such as demographic growth rate and size structure is so far unknown as well as which environmental factors (photoperiod or food, or both) act as 'Zeitgeber' to initiate the increasing metabolic activity in adult krill after the winter period. An additional important aspect of environmental conditions on the population dynamics of krill is the survival of krill larvae during winter. Krill larvae cannot reduce their metabolic activity and have to forage throughout the winter. Therefore sea ice has been suggested as overwintering habitat for krill larvae providing both shelter and food (Daly, 1990, Meyer et al., 2009). Being under the ice can be beneficial since retreating ice in spring, a stable surface layer due to low salinity, as well as sufficient light and nutrients promotes an algae bloom and hence favourable food conditions for both larvae and adults (Meyer et al., 2010). Furthermore, both larvae and adult krill may directly forage for algae growing underneath the sea ice (Daly, 1990).

There is a rich history of krill models investigating the growth of krill (see Candy and Kawaguchi, 2006 for an overview, Lowe et al., 2012 for a simulation model for krill larvae) and on the role of krill in food webs (e.g. Hill et al., 2012). There are fewer mechanistic models that allow simulating the physiological or behavioural response of krill to environmental changes. Stage-structured models considering energy budgets have been used to assess whether certain movement pathways from the Western Antarctic Peninsula to South Georgia are possible (Fach et al., 2002) and a "dynamic state-variable model", which is based on an optimization algorithm, has been used to explain shrinkage in individual krill size in response to predators (Alonzo and Mangel, 2001). Thus, to investigate the link between potential environmental triggers (i.e. day length and food availability), environmental change (sea ice coverage), internal biological clocks, and population structure and species distribution, we constructed a new individual-based model for krill, where we model 33 separate populations along a south-north gradient. We aimed to understand in which way environmental factors such as ice cover and metabolic shift affect local population growth and size structure. We specifically tested the impact of five environmental 'trigger' scenarios for krill, two different scenarios of the spatio-temporal ice cover dynamics, and different levels of food availability under the sea ice.

Our model includes a realistic description of krill growth, that is based on a recent version of Dynamic Energy Budget theory (DEBKiss; Jager et al., 2013), but the environmental settings and the assumption that krill does not move reflect that our purpose here was conceptual understanding, not a realistic representation of spatio-temporal dynamics of krill populations. Our 33 local krill populations represent 'probes' that translate assumptions about environmental triggers into assessments of local habitat quality for krill. We then take local habitat quality as a proxy for the potential distribution of krill.

2. Methods

2.1. The model

We developed an individual based model for krill that is available in the electronic supplementary material as appendix 1. The model was implemented using the software platform NetLogo 5.0.2 (Wilensky, 1999). The model description below follows the ODD protocol (Overview, Design, and Details protocol, Grimm et al., 2006, 2010).

2.1.1. Purpose

We investigate the effect of climate change (in terms of changing ice cover dynamics), and the nature of the trigger of krill to switch metabolic activity (day length, food availability) on its individual growth in body length, frequency distribution of body length and age in the population, and species distribution.

2.1.2. Entities, state variables and scales

The model entities are krill individuals and spatial units. Krill individuals have the following state variables: body length [continuous, cm], age [integer, days], larval status [yes, no], maturity [continuous value], shrinkage [continuous, cm], day length when metabolic activity changes depending on the scenario [continuous, hours], metabolic state [active, reduced], reproductive events [integer, dimensionless].

Krill are assumed stationary with no latitudinal directions movements, i.e. they stay their whole life at their position along the south-north gradient.

Spatial units, or grid cells (called patches in NetLogo), are arranged in a one-dimensional array along a south-north gradient (Fig. 1). Grid cells have the following state variables: food availability [continuous value >0], ice cover [covered or free], duration of algae bloom [integer, days], day length [continuous, hours].

Simulations run in daily time steps for 15 years. Before every simulation the model is run for one initialisation year without krill to initialize the environmental conditions such as food content. The spatial extent of the one-dimensional array of grid cells represents a latitudinal gradient, defined by the temporal ice cover dynamics and day length (maximum and minimum day length 16.8 h and 7.2 h for the top grid cell, respectively, and 24 h and 0 h for the bottom grid cell, corresponding to a latitudinal range between 50°S and 70°S).

2.1.3. Process overview and scheduling

The following processes are performed each day in the given order (Fig. 2); entities are processed in a randomized sequence and state variables are updated immediately (all processes are