RESEARCH

The impact of salps (*Salpa thompsoni*) on the Antarctic krill population (*Euphausia superba*): an individual-based modelling study

Bruno Walter Pietzsch[1*] , Aaron Schmidt[1], Jürgen Groeneveld[2], Dominik Bahlburg[1,2], Bettina Meyer[3,4,5] and Uta Berger[1]

Abstract

Background Krill (*Euphausia superba*) and salps (*Salpa thompsoni*) are key macrozooplankton grazers in the Southern Ocean ecosystem. However, due to differing habitat requirements, both species previously exhibited little spatial overlap. With ongoing climate change-induced seawater temperature increase and regional sea ice loss, salps can now extend their spatial distribution into historically krill-dominated areas and increase rapidly due to asexual reproduction when environmental conditions are favorable. Understanding the potential effects on krill is crucial, since krill is a species of exceptional trophic significance in the Southern Ocean food web. Negative impacts on krill could trigger cascading effects on its predators and prey. To address this question, we combined two individual-based models on salps and krill, which describe the whole life cycle of salp individuals and the dynamic energy budget of individual krill. The resulting new model PEKRIS (*PErformance of KRIll vs. Salps*) simulates a krill population for 100 years under varying chlorophyll-a concentrations in the presence or absence of salps.

Results All of the investigated krill population properties (abundance, mean length, and yearly egg production) were significantly impacted by the presence of salps. On the other hand, salp density was not impacted if krill were present. The medians of krill population properties deviated during variable maximum chlorophyll-a density per year when salps were introduced by -99.9% (-234 individuals per 1000 m^3) for krill density, -100% ($-22{,}062$ eggs per 1000 m^3) for krill eggs and -0.9% (-0.3 mm) for mean length of krill.

Conclusions If both species compete for the same food resource in a closed space, salps seem to inhibit krill populations. Further simulation studies should investigate whether this effect prevails if different phytoplankton sizes and consumption preferences of krill are implemented. Furthermore, direct predation of the two species or consumption of krill fecal pellets by salps could change the impact size of the food competition.

Keywords *Euphausia superba*, *Salpa thompsoni*, Individual-based model, Food competition, Population dynamics, DEB theory

*Correspondence:
Bruno Walter Pietzsch
bruno_walter.pietzsch@tu-dresden.de
Full list of author information is available at the end of the article

Pietzsch *et al. Ecological Processes*   (2023) 12:50

Page 2 of 16

Background

Antarctic krill (*Euphausia superba* Danna, 1850—hereafter krill) are large euphausiids with a maximum length of six centimeters, with a lifespan of up to 7 or 8 years (Ross and Quetin 1991; Siegel 2017) and a circumpolar distribution, bordered by the Southern Polar Front in the North and by the ice-covered Antarctic continent in the South (Siegel 2005). In contrast, the pelagic tunicate (*Salpa thompsoni* Foxton, 1961—hereafter salps) grows up to 16 cm, reaching a lifespan of up to 15 months (Loeb and Santora 2012; Siegel 2017; Pakhomov et al. 2018). Typically, salps are found in warmer, ice-free waters (Foxton 1966; Pakhomov and Hunt 2017).

Both species are considered key macrozooplankton grazers in the Southern Ocean ecosystem, possibly competing for the same food source, phytoplankton, and having enormous impacts on biogeochemical cycling, such as carbon sequestration (Gleiber et al. 2012; Cavan et al. 2019; Pauli et al. 2021b). For example, krill and salp fecal pellets account for 75% of total carbon at 300 m at the Antarctic Peninsula (Pauli et al. 2021a). Former studies concluded that the core habitats of salps and krill are spatially separated due to their different habitat demands for optimal fitness (Torres et al. 1984; Hempel 1985; Siegel et al. 1992; Pakhomov et al. 2002). Due to the increasing anthropogenic warming trend in the Western Antarctic Peninsula region, the distribution of both species increasingly overlaps (Fransz and Gonzalez 1997; Loeb et al. 1997; Pakhomov and Froneman 2000; Plum et al. 2020). While salps can expand their range further South through the rising seawater temperatures and changing sea ice dynamics (Atkinson et al. 2004), the local krill population is possibly shrinking and contracting southwards along the Antarctic Peninsula (Atkinson et al. 2019). As a result of this process, krill can be replaced by salps (Plum et al. 2020). With the continuing warming trend, it has been debated whether salps might play an increasing role in the local food web, implicating a change in the web's pathways. This change could affect the populations of apex predators and other organisms, which again could influence the regional carbon flux due to altering the biogeochemical cycling (Perissinotto and Pakhomov 1998; Pakhomov 2004; Siegel 2005; Loeb and Santora 2012). This is especially important, as the reproductive strategy of salps, consisting of alternations between chain-forming sexual and solitary asexual life stages, allows rapid growth to very high densities in short amounts of time (Loeb and Santora 2012). These so-called blooms are known to reduce primary producer biomass substantially and, thus, the food source for salps and krill (Dubischar and Bathmann 1997).

Therefore, it is crucial to understand how an increasing salp population might affect krill populations under different environmental conditions. Here, we linked two existing individual-based models that simulate the life cycle and metabolism of a salp population (Henschke et al. 2018; Groeneveld et al. 2020) and the energy budget of krill (Jager and Ravagnan 2015; Bahlburg et al. 2021). Individual-based models describe individuals as singular entities with sensing, decision-making capabilities, and interaction, where emerging model results and patterns arise primarily from the simulated individuals' traits (Railsback and Grimm 2011). Therefore, individual-based models on krill and salps display population growth and trajectories as a direct result of individual food consumption, reproduction fitness, and mortality (Groeneveld et al. 2020; Bahlburg et al. 2021). Dynamic Energy Budget (DEB) theory, on the other hand, describes how an organism acquires and uses energy and essential elements for physiological processes (Nisbet et al. 2012). It also explains how physiological performance is influenced by environmental variables, such as food density and temperature (Nisbet et al. 2012). A standard DEB model describes the performance of all life stages of an animal and predicts both intraspecific and interspecific variation in physiological rates (Nisbet et al. 2012). Jager and Ravagnan (2015) developed and parameterized, such as the DEB model for krill, which was later incorporated into an individual-based model by Bahlburg et al. (2021) and which we implemented into the individual-based salp model from Groeneveld et al. (2020). The ultimate purpose of the combined individual-based model is to compare the amount, size, and reproduction of a krill population in the absence and presence of salps. The name of the combined model PEKRIS stands for PErformance of KRIll *vs.* Salp. In this study, we (1) present this model and its behavior in detail; and (2) assess through simulation experiments how the presence of salps and temporal variability of food availability affect the performance of krill individuals and the subsequent population dynamics of krill. We hypothesize that given competition with salps for food, the following life-history traits of krill decrease:

1) The density.
2) The mean body length.
3) The number of eggs released.
4) Furthermore, a fluctuation in food availability leads to asynchronous reactions of salp and krill populations.

Methods

Model description

Preamble

The individual-based model PEKRIS was implemented in NetLogo (Wilensky and Rand 2015) version 6.2 and

builds on existing salp population dynamics models (Henschke et al. 2018; Groeneveld et al. 2020). We extended this model by implementing krill individuals following a simplified dynamic energy budget theory (Sousa et al. 2010; Jager et al. 2013; Bahlburg et al. 2021). The PEKRIS model description follows the Overview, Design, and Details (ODD) protocol (Grimm et al. 2006, 2020) and is presented in the following sections. To improve the readability and to shorten the manuscript, we provided the last part of the protocol about the Details on model initialization and sub-models as Additional file 1: S1.

Purpose and patterns

The proximate purpose of PEKRIS (Performance of KRIll vs. Salps) is to predict the growth, abundance, and reproduction events of krill (*Euphausia superba* Danna, 1850) and salps (*Salpa thompsoni* Foxton, 1961) as a function of temperature, individual energy budget and chlorophyll-a availability as a proxy of food availability in the region of the Antarctic Peninsula. The ultimate purpose of the model is to compare the amount, size, and reproduction of a krill population in the absence and presence of salps.

Patterns used for validating the model results against empirical and simulated data are trajectories for maximum sizes, metabolic activities, or reproductive outputs and ranged, therefore, from the individual krill or salp to the population level known from the literature (Ikeda 1981; Ikeda and Mitchell 1982; Quetin and Ross 1991; Ross and Quetin 1991; Nicol et al. 1995; Iguchi and Ikeda 2004; Atkinson et al. 2006; Dubischar et al. 2006; Siegel 2016; Pakhomov and Hunt 2017; Pakhomov et al. 2018) and other simulation studies (Hofmann and Lascara 2000; Groeneveld et al. 2020; Bahlburg et al. 2021). The usage of these references for model validation is highlighted in the following section on the state variables of each simulated entity and the corresponding sections of the PEKRIS model code itself.

Entities, state variables, and scales

The following entities are included in the model: cubic grid cells that contain chlorophyll-a, krill individuals (juveniles and adults), clutches (krill egg packages), and the life cycle stages of salps: solitary oozoids (asexual), chain-forming blastozooids (female) and solitary blastozooids (male). We decided to differentiate the life stages of both krill and salps as separate entities to decrease the computational cost of the model. The state variables, the possible value ranges, and the units of these entities are documented in Table 1.

Time steps define the temporal scale of the model, where each time step resembles 1 day in the real world. Model dynamics are usually simulated for 100 years but

can be varied. The spatial scale of the model is defined by cubic grid cells, each representing 16 cubic meters of water. The model landscape consists of 51 times 51 such cells, which represent 2,601 cubes and result in a total modeled domain size of 41,616 cubic meters of water (see Sect. 1.2 initialization of Additional file 1: S1 for more details).

Process overview and scheduling

The model is developed to cover the whole life cycle of multiple krill and salp generations over several years. It is structured into nine processes (see Sect. 1.4 submodels of Additional file 1: S1): one related to the environment (update chlorophyll-a content of each patch), six concerning krill and salp individuals (growth, asexual and sexual reproduction, mortality, immigration, and movement) and two governing model results (calculation of global results and updating the plots in the model's interface). The patches update their state variables once during the model setup and every time step of the simulation. All processes concerning krill and salps, such as growth, reproduction, mortality, immigration, and movement, occur on each time step of the model run. Calculating global model results and drawing and updating the plots in the model interface are also performed each time step.

The simulation starts with creating the modeled domain, where each patch is assigned the maximum possible chlorophyll-a concentration depending on the chosen scenario (see Sect. 1.2 Initialization of Additional file 1: S1 for details). The setup of the modeled world is followed by the creation of krill and salp individuals, respectively (Fig. 1). A model run starts with the individual growth of krill and salps. This is scheduled first as subsequent processes, such as asexual and sexual reproduction, depend on the individual's size and carbon storage. The reproduction of krill and salps is scheduled next as it is directly related to the individual size and has to be performed before immigration or mortality takes place. Immigration of krill and salp individuals takes place after the mortality routine to ensure immigrating individuals live at least one time-step. The order of updating the environment and the movement of krill and salps are interchangeable. It is essential to perform the update environment procedure before global results are calculated (second last step), and the plots are updated (last step).

Basic principles

In the PEKRIS model, the growth in body length of both krill and salp individuals depends on the temperature, current body length, and food availability (see Sect. 1.4.2 of Additional file 1: S1). The temperature dependency of

Pietzsch *et al. Ecological Processes*   (2023) 12:50

Page 4 of 16

Table 1 State variables with their values (ranges), units, and references of origin or validation, respectively, for the entities of the PEKRIS model

Entity	State variable	Label	Value (range)	Unit	References
Krill	Structural body weight (cubed physical body length)	W_V	0.01–197.98	mg DW	Ikeda and Mitchell (1982)
	Mass of reproduction buffer	W_R	0.00–118.33	mg	Nicol et al. (1995)
	Structural body length	structural_length	0.34–9.65	mm	Quetin and Ross (1991); Hofmann and Lascara (2000); Reiss et al. (2008); Siegel (2017)
	Assimilation	J_A	0.00–3.71	mg d^{-1}	Jager and Ravagnan (2015)
	Somatic maintenance	J_M	0.00–2.80	mg d^{-1}	Jager and Ravagnan 2015
	Structural growth	J_V	0.00–0.41	mg d^{-1}	Hofmann and Lascara (2000); Reiss et al. (2008)
	Investment reproduction buffer	J_R	0.00–0.74	mg d^{-1}	Jager and Ravagnan (2015)
	Number of spawning events	number_of_spawnings	0–3	n	Siegel (2016)
	Age	age	0–2190	d	Quetin and Ross (1991); Reiss et al. (2008); Siegel (2017)
	Age of first reproduction	age_of_first_reproduction	471–1372	d	Siegel (2017)
	Number of eggs released	number_of_eggs	0–4020	n	Bahlburg et al. (2021)
	Days of starvation	days_of_starvation	0–186	d	Quetin and Ross (1991)
Clutch	Structural body weight (cubed physical body length)	W_V	0.01–5.22	mg DW	–
	Mass of reproduction buffer	W_R	0.00–1.19	mg	Ikeda (1981); Jager and Ravagnan (2015)
	Structural body length	structural_length	0.34–2.87	mm	–
	Assimilation	J_A	0.00–0.30	mg d^{-1}	Jager and Ravagnan (2015)
	Somatic maintenance	J_M	0.00–0.07	mg d^{-1}	Jager and Ravagnan (2015)
	Structural growth	J_V	0.00–0.14	mg d^{-1}	Jager and Ravagnan (2015)
	Age	age	0–117	d	–
	Days without food	days_of_starvation	0–23	d	Ross and Quetin (1991)
	Number of eggs in the clutch	number	10–4020	n	Bahlburg et al. (2021)
Oozoid	Body length	body_length	0.40–10.50	cm	Harbou (2009); Pakhomov and Hunt (2017); Pakhomov et al. (2018)
	Age	age	0–450	d	Loeb and Santora (2012)
	Number of chain releases	number_of_chain_releases	0–3	n	Harbou (2009); Groeneveld et al. (2020)
	Days with food uptake below the maintenance cost	days_of_starvation	0–30	d	Groeneveld et al. (2020)
	Generation number	number_of_generation_season	0–4	n	Groeneveld et al. (2020)
	Time from first to last chain release	regeneration_time	0–185	d	Groeneveld et al. (2020)
	Carbon weight	carbon_weight	0.03–94.81	mg	Dubischar et al. (2006); Harbou (2009)
	Carbon storage for reproduction	carbon_reproduction	1.01–7.38	mg	Groeneveld et al. (2020)
Blastozooid	Body length	body_length	2.50–6.85	cm	Harbou (2009)
	Age	age	0–150	d	Loeb and Santora (2012)
	Days without food	days_of_starvation	0–30	d	Groeneveld et al. (2020)
	Generation number	number_of_generation_season	0–3	n	Groeneveld et al. (2020)
	Carbon weight	carbon_weight	2.62–32.60	mg	Groeneveld et al. (2020)
	Carbon storage for reproduction	carbon_reproduction	0.00–7.28	mg	Groeneveld et al. (2020)
Chain	Number of individuals	number	1–213	n	Harbou (2009)
	Body length	body_length	0.50–2.50	cm	Harbou (2009); Pakhomov and Hunt (2017)
	Age	age	0–150	d	Loeb and Santora (2012)
	Days with a lack of food	days_of_starvation	0–30	d	Groeneveld et al. (2020)
	Generation number	number_of_generation_season	0–5	n	Groeneveld et al. (2020)
	Carbon weight	carbon_weight	0.05–2.62	mg	Dubischar et al. (2006); Harbou (2009)
	Carbon storage for reproduction	carbon_reproduction	0.00–0.46	mg	Groeneveld et al. (2020)
Patch	Food (chlorophyll-a) concentration	chla	0.08–27.02	mg m^{-3}	Groeneveld et al. (2020)

Pietzsch *et al. Ecological Processes*   (2023) 12:50

Page 5 of 16

Table 1 (continued)

The value ranges were determined by simulating the model for 6 years under varying chlorophyll-a concentrations and performing 30 repetitions. The structural body length of krill has to be multiplied by five to get the actual length

DW dry weight

food intake and respiration processes was implemented as an Arrhenius function previously introduced and parameterized for krill (Bahlburg et al. 2021) and salps (Groeneveld et al. 2020). Food uptake is modeled using species-specific Holling type II functional responses. Processes governing the distribution, storage, and consumption of energy originating from food intake follow the dynamic energy budget model theory (Sousa et al. 2010), which was simplified (Jager et al. 2013) and parameterized for krill (Jager and Ravagnan 2015).

Birth and death are other fundamental processes of population dynamics included in the model. Immigration is included for salps and krill (see Sect. 1.4.6 of Additional file 1: S1). At the same time, the emigration of both species is not explicitly modeled (or it is assumed that the "normal" immigration and emigration are outbalanced). The processes above concerning salps originate from the individual-based model introduced by Groeneveld et al. (2020). For krill, some of these processes are based on the works of Jager and Ravagnan (2015) and, Bahlburg et al. (2021), which will be explained in more detail in the corresponding submodel section of this ODD protocol (Overview, Design, and Details). Examples are the size-dependent number of eggs released by each krill individual (Bahlburg et al. 2021) in Sect. 1.4.4 of Additional file 1: S1 and the ratio of energy allocation for growth and reproduction (Jager and Ravagnan 2015) in Sect. 1.4.2 of Additional file 1: S1.

Emergence
The model's primary results—abundances, growth, and reproductive activity of krill and salps—emerge from the seasonal course of temperature and chlorophyll-a availability as well as direct competition for food between individuals from one species and individuals from different species.

Interaction
Direct interactions between salp and krill individuals happen via feeding on the same food resource when individuals occupy the same patch. The model does not implement direct feeding of salps on krill eggs or adults.

Stochasticity
Stochasticity is considered in most processes, e.g., movement, mortality, immigration, and reproduction

(Table 2). More implementation details are described in Sects. 1.2 and 1.4 of the Additional file 1: S1, respectively.

Observation
For krill, the density of post-larvae krill in individuals per 1000 m^3, the post-larvae krill mean body size in mm, and the annual number of eggs the population releases are stored. For salps, the maximum annual peak density in individuals per 1000 m^3 and the median of seasonal peak abundances is stored on the 180th day of each year.

Model sensitivity
We conducted a global sensitivity analysis relying on random sampling and applying an analysis of variance (ANOVA) to quantify the influence of parameters and interactions on the model outputs. As response variables for measuring the model's sensitivity, we used population properties such as abundance for both species and mean length and eggs released per year for krill only. These are the same model outputs we investigated during our simulation experiments in the following section. In conclusion, the presence of salps, chlorophyll-a growth, and decay as well as the half saturation constant of krill turn out to be the most influential parameters for response variables concerning krill. For salps, parameters such as the daily mortality, chlorophyll-a scenario, and chlorophyll-a growth exert moderate-to-high influences. The detailed sensitivity analysis can be found in Additional file 2: S2.

Simulation experiments
To investigate the possible influence of increased salp presence on the population dynamics of krill, we simulated a time series of krill and salp population dynamics for 100 years. In scenario one, salp individuals could immigrate into the modeled domain and could perform rapid population growth. In scenario number two, only krill individuals were simulated, and no salp immigration was allowed. In a third scenario, we only simulated salps to validate our model results with a previous simulation study on salps (Groeneveld et al. 2020). To account for the impact of food availability on the krill and salp population dynamics, two scenarios concerning the chlorophyll-a availability were also investigated: (1) the maximum possible chlorophyll-a density was fixed to 0.54 mg per m^3, which reflects the mean of AMLR data (Southeast Fisheries Science Center
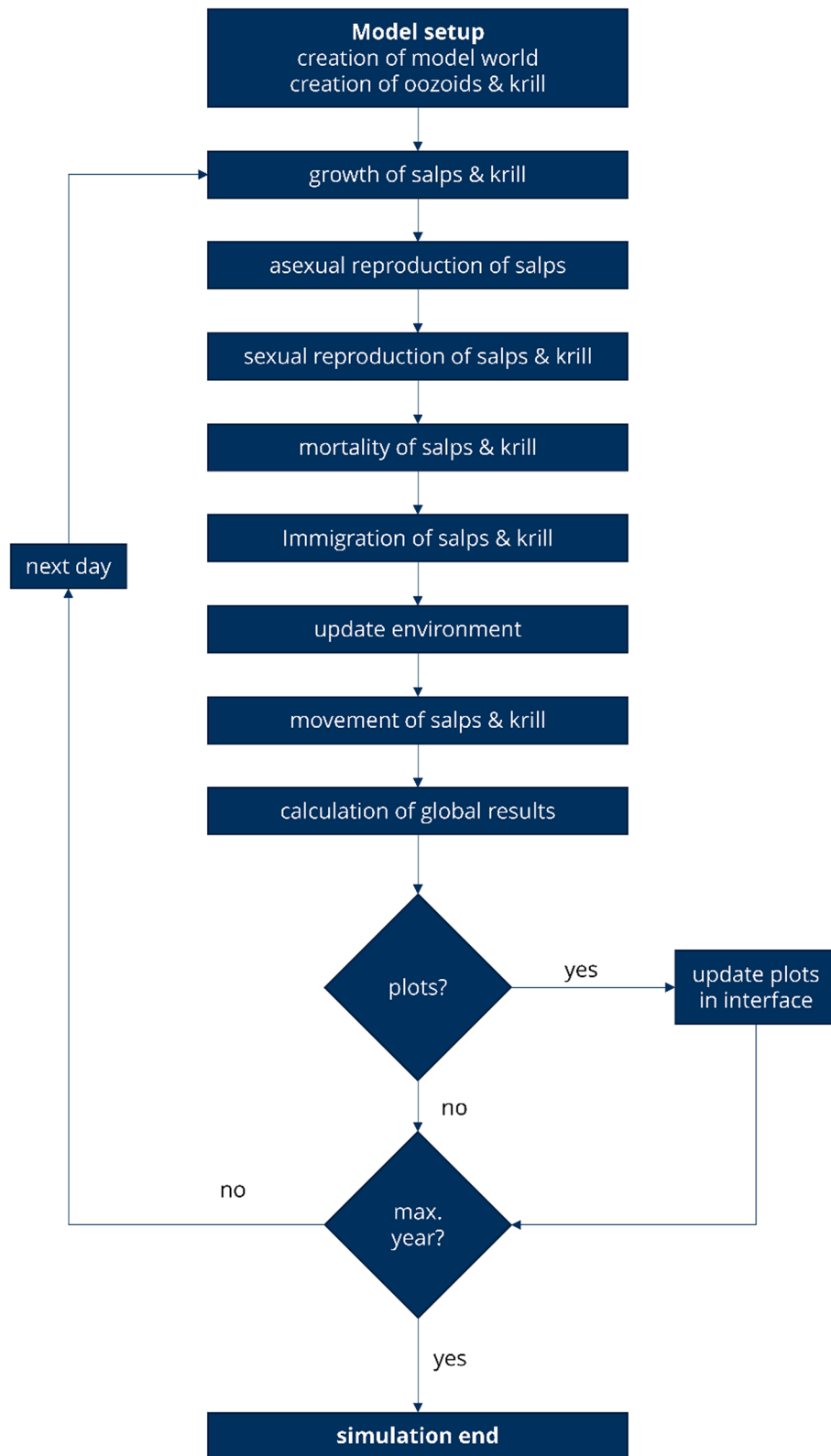
Fig. 1 Flow chart showing the schedule of processes performed during a simulation run of PEKRIS. The simulation starts by setting up the environment and randomly placing salps and krill individuals in the modeled domain. After that, and for each time step, the growth, mortality, immigration, and movement of krill and salps are simulated, updating the environment and calculating the model results. The simulation ends if the predefined amount of years is simulated

Table 2 Subjects and timing of stochasticity in the PEKRIS model with a short explanation

Subject	Timing	Explanation
Placement	(1) Model setup and; (2) each time step	Individuals are distributed randomly over the modeled domain during the creation of krill and salps in the model setup, during the immigration of salp and krill individuals, and during the birth of clutches (sexual reproduction of krill). See Sects. 1.2 and 1.4.6 of Additional file 1: S1
Movement	Each time step	Each salp and krill individual moves to a randomly chosen neighboring grid cell at each time step. The probability of each of the eight neighboring grid cells being chosen as the new position is equal. See Sect. 1.4.8 of Additional file 1: S1
Mortality	Each time step	Death is simulated by drawing random numbers for each krill and salp individual separately. If the drawn number is below the predefined threshold, the individual dies. Thresholds for all entities are 2.5% for salps, 0.07% for krill, and 5.0% for clutches. See Sect. 1.4.5 of Additional file 1: S1
Immigration	Each time step	Immigration of salps during the spring, summer, and autumn is simulated by drawing a random number each day as long as no salps are present. If this number is below the threshold of 0.85%, ten salp individuals are created within the modeled domain. See Sect. 1.4.6 of Additional file 1: S1
Chlorophyll-a availability	(1) Model setup and; (2) each year	Suppose chlorophyll-a supply is set to follow a lognormal distribution during the simulation. These parameters were derived from the US Antarctic Marine Living Resource (AMLR) program run by the National Oceanic and Atmospheric Administration (NOAA), as described in Groeneveld et al. (2020). See Sects. 1.2 and 1.4.7 of Additional file 1: S1
Reproduction	Each time step	A random number is drawn during each salp's reproduction event. With a probability of 70%, blastozooids and oozoids are produced. In 30% of all cases, only blastozooids are generated by the individual salp for the given reproduction event. See Sects. 1.4.3 and 1.4.4 of Additional file 1: S1

Stochasticity occurs during the model setup (placing the krill and salp individuals) and during the movement, mortality, immigration, and reproduction of both species

More details on each process listed here are described in the corresponding Details in Sects. 1.2 and 1.4 of Additional file 1: S1

**Table 3** Properties of krill and salp population dynamics investigated during the experiments

Property	Unit
The density of post-larvae krill	$n/1000\ m^3$
The mean length of post-larvae krill	mm
The density of krill eggs released	$n/1000\ m^3$
The density of salps	$n/1000\ m^3$

The main outputs of the PEKRIS model are the abundance of post-larvae krill concerning the water body of the modeled domain ($n/1000\ m^3$), the mean length of post-larvae krill individuals present, the number of eggs released per year related to the modeled water body ($n/1000\ m^3$) and, the maximum abundance of salps during the year related to the modeled water body ($n/1000\ m^3$)

2020) as implemented by Groeneveld et al. (2020); and (2) the maximum possible chlorophyll-a density varied between years following a lognormal distribution with a mean log of 3.83 and an sd log of 0.58 as derived from long-term AMLR data (Southeast Fisheries Science Center 2020) by Groeneveld et al. (2020). Cross-combining the two chlorophyll scenarios (fixed, stochastic) and the three species scenarios (only krill, both species, and only salps) resulted in six simulation experiments. To account for the stochasticity of the individual-based models, we repeated each combination 30 times. The model outputs were measured each day and consisted of three krill population properties and one salp abundance measure (Table 3).

To analyze the possible impact of competition of both species and the maximum chlorophyll-a availability on the population dynamics of krill and salps, we generated a time series over the simulated 100 years using the mean of the 30 repetitions of each simulated year. This was done for each of the four model outputs separated by the chlorophyll-a availability scenario, assigning a different line type for the scenario salps only, krill only, or both species (Fig. 2). Furthermore, boxplots were generated using the data of years 31 to 100 to compare the model results between the four simulation experiments (Fig. 3). To detect possible significant differences, we performed an analysis of variance (ANOVA) (Chambers and Hastie 2017) after determining if a normal distribution of the output data could be verified by a Shapiro–Wilk test (Royston 1995). Otherwise, a Scheirer–Ray–Hare test was applied using rank transformation (Dytham 2011). For data processing, the free statistical software R (R Core Team 2020) in version 4.0.4 was used along with the packages *tidyr* (Wickham 2021) in version 1.1.4 to process the data and *ggplot2* (Wickham 2016) in version 3.3.5 to visualize the results.

Pietzsch *et al. Ecological Processes* (2023) 12:50

Page 8 of 16
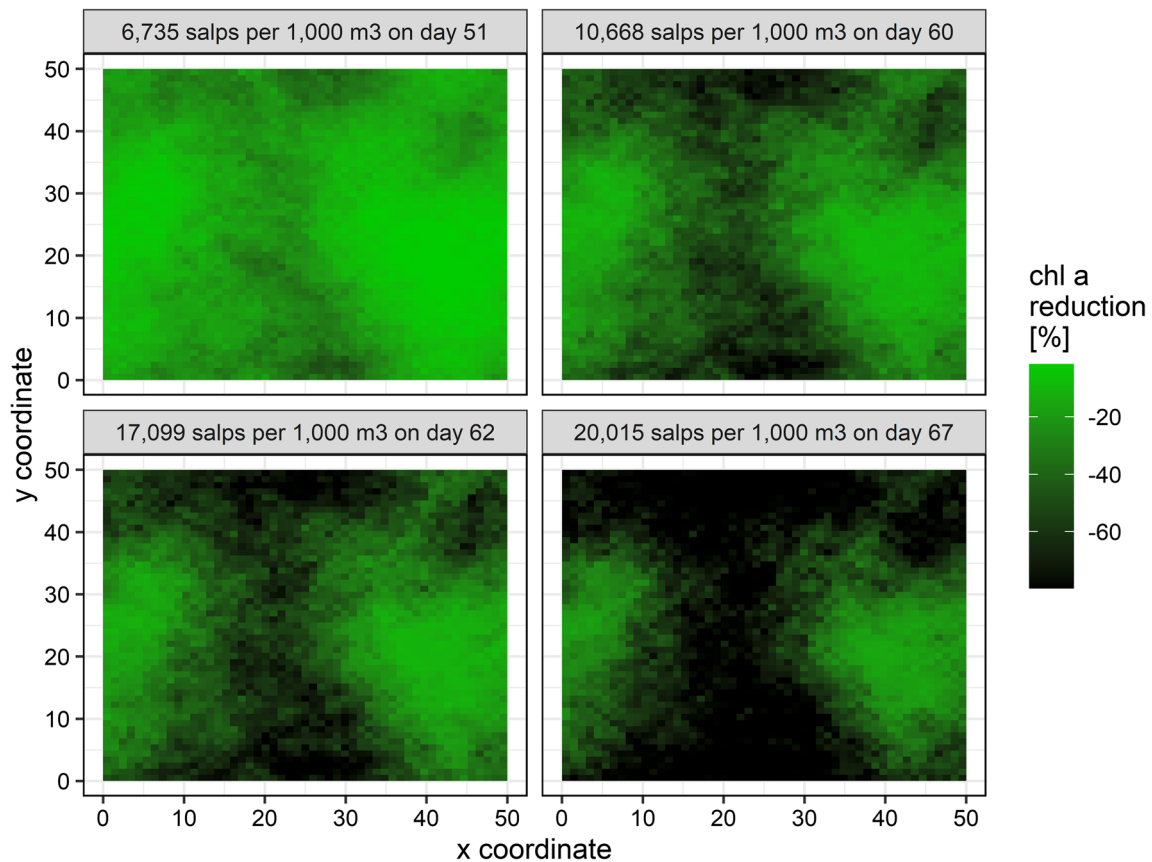
Fig. 2 Impact of growing salp densities [individuals per 1000 m³] on the chlorophyll-a concentration of the modeled domain throughout 2 weeks of a simulation run in the PEKRIS model. Each panel displays the modeled domain within PEKRIS consisting of 51×51 cells of 16 cubic meters for different days throughout one simulated season. Chlorophyll-a reduction is shown as a color gradient from green (theoretical maximum of chlorophyll-a concentration at the given time of year) to black (minimum chlorophyll-a concentration recorded during the simulation run)

Results

Impact of salp blooms on chlorophyll-a availability

The model describes a virtual domain of two-dimensional grid cells displaying 41,646 cubic meters of seawater, where krill and salp individuals move. During the simulation experiments, snapshots of the cells' chlorophyll-a content were extracted to display the effect of growing salp densities throughout 2 weeks of a simulation run on the available food (Fig. 2). It can be seen that increasing salp densities led to a higher chlorophyll-a reduction and extended areas depleted of chlorophyll-a. Blooms with 20,000 individuals per 1000 m³ reduced chlorophyll-a concentration in large areas of the modeled domain by more than 60%. Lower densities still locally reduced chlorophyll-a by up to 40% and up to 20% in broader areas.

Time series of krill and salp population dynamics in the absence and presence of salps

Stochastic fluctuations of maximum chlorophyll-a concentration led to more substantial annual variability in density, mean length, and the yearly number of eggs released by krill during a hundred years (Fig. 3). The modeled krill could release up to 189,000 eggs per 1000 m³ in 1 year if the maximum chlorophyll-a concentration reached or exceeded 1.00 mg per m³. While mean length increased in years with chlorophyll-a concentration

(See figure on next page.)

Fig. 3 Time series of krill and salp population dynamics. Time series for the mean of 30 repetitions of the density of post-larvae krill (first row), mean length of post-larvae krill (second row), the density of eggs released by krill per year (third row), and max annual density of salps (fourth row) separated by chlorophyll-a scenario (columns). The left column depicts the simulations with a fixed maximum chlorophyll-a concentration per year of 0.54 mg per m³. In comparison, the right column shows the model results during lognormal maximum chlorophyll-a concentration (mean log = 3.83 mg per m³ and sd log = 0.58 mg per m³). The possible maximum chlorophyll-a concentration in each year is shown as green coloring

Pietzsch *et al. Ecological Processes*   (2023) 12:50

Page 9 of 16
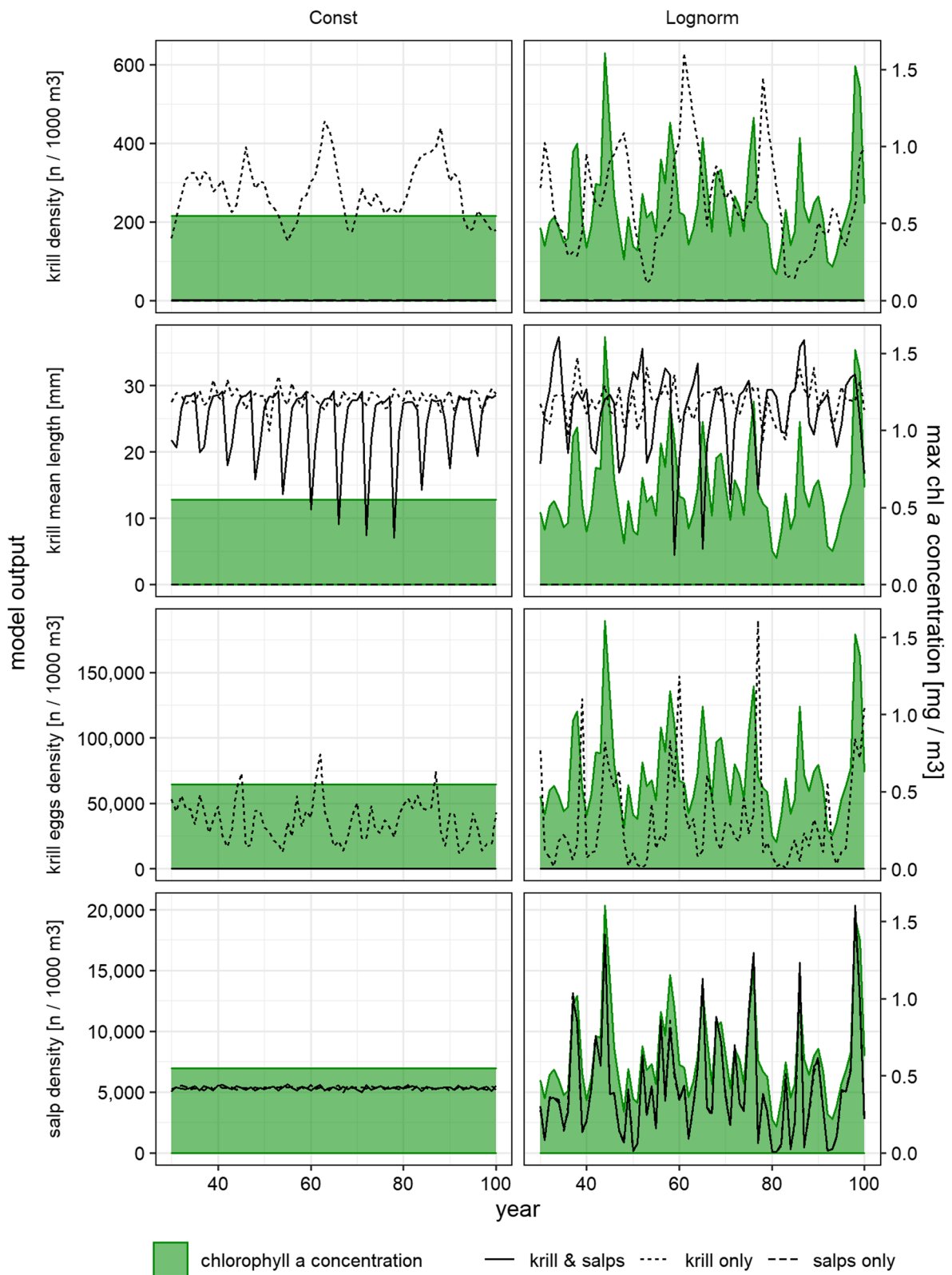
Fig. 3 (See legend on previous page.)

Pietzsch *et al. Ecological Processes*   (2023) 12:50

Page 10 of 16

surpassing 0.54 mg per m^3, the density increased after such years. Differences in krill population dynamics due to the presence of salps could be detected for all three population properties: with salps present no reproduction in krill took place and the population shrunk and eventually deceased. The maximum densities of salps were strongly influenced by food availability, in terms of chlorophyll-a concentration, throughout the simulated time series of 100 years (Fig. 3). High salp peak densities were related to high annual chlorophyll-a concentration. In contrast, if the annual maximum chlorophyll-a concentration was below the average of 0.54 mg per m^3, salps could not grow to densities above 6000 individuals per 1000 m^3. The presence of krill had no impact on the density of salps regardless of the chlorophyll-a configuration.

Differences in population dynamics due to competition with the other species

Comparing the distribution of model outputs over the hundred-year time series revealed a significant difference if salps were introduced for the density of krill (p value < 2e−16), krill mean length (p value of 0.0003) and in eggs released by krill (p value < 2e−16) (Table 4). Furthermore, the post-larvae length of krill was significantly impacted by the interaction of salp presence and chosen chlorophyll-a configuration (p value of 0.033). For salps,

significant effects due to the chosen chlorophyll-a configuration were detectable (p value of 6.655e−05).

To emphasize the differences in population properties due to the presence and absence of the other species as well as the chosen chlorophyll-a configuration, boxplots were generated (Fig. 4). The displayed median of krill density decreased by 99.9% when salps were introduced (271 individuals per 1000 m^3 during constant and 234 individuals per 1000 m^3 during lognormal chlorophyll-a configuration). In addition, the median amount of eggs released by krill per year declined by 100% when salps were present (22,062 eggs per 1000 m^3 under varying chlorophyll-a and 37,096 eggs per 1000 m^3 under constant chlorophyll-a configuration). The mean length of krill post-larvae stages declined by 2.8% (0.8 mm) during constant and by 0.9% (0.3 mm) during lognormal configuration. Tha abundance of salps (individuals per 1000 m^3) deviated by 0.1% (3 individual) during variable and by 0.2% (7%) during constant chlorophyll-a configuration when krill were introduced (Table 5).

Discussion

In this study, and for the first time, we linked an individual-based energy budget model of krill (*Euphausia superba*) (Jager and Ravagnan 2015; Bahlburg et al. 2021) with an individual-based model simulating the life history of salps (*Salpa thompsoni*) (Groeneveld et al. 2020). We investigated the effect of food competition between

Table 4 Results of the Scheirer–Ray–Hare test investigating significant impacts of competition with the other species, chlorophyll-a configuration, and their interaction on the investigated model outputs (responses)

Response	Source	Df	Sum Sq	Mean Sq	*F* value	*p* value	Sig
Post larvae krill density [n/1000 m^3]	Species	1	1,431,644	1,431,644	212.252	0.000	***
	Chlorophyll config	1	220	220	0.033	0.857	
	Species:chla_config	1	8657	8657	1.284	0.257	
	Residuals	280	468,314	1673	–	–	
Post larvae krill mean length [mm]	Species	1	87,958	87,958	13.040	0.000	***
	Chlorophyll config	1	6323	6323	0.937	0.333	
	Species:chla_config	1	30,601	30,601	4.537	0.033	*
	Residuals	280	1,783,954	6371	–	–	
Krill egg density [n/a]	Species	1	1,431,644	1,431,644	235.942	0.000	***
	Chlorophyll config	1	828	828	0.137	0.137	
	Species:chla_config	1	12,778	12,778	2.106	2.106	
	Residuals	280	271,931	971	–	–	
Salp density [n/1000 m^3]	Species	1	46	46	0.007	0.934	
	Chlorophyll config	1	107,290	107,290	15.907	0.000	***
	Species:chla_config	1	0	0	0.000	0.996	
	Residuals	280	1,801,499	6434	–	–	

The tests were applied for the yearly medians in the years 30–100

Competition with the other species is coded as 'species' and chlorophyll-a configuration as 'chla_config'

Significance levels were coded as '***'—0.001, '**'—0.01, '*'—0.05

Pietzsch *et al. Ecological Processes*   (2023) 12:50

Page 11 of 16
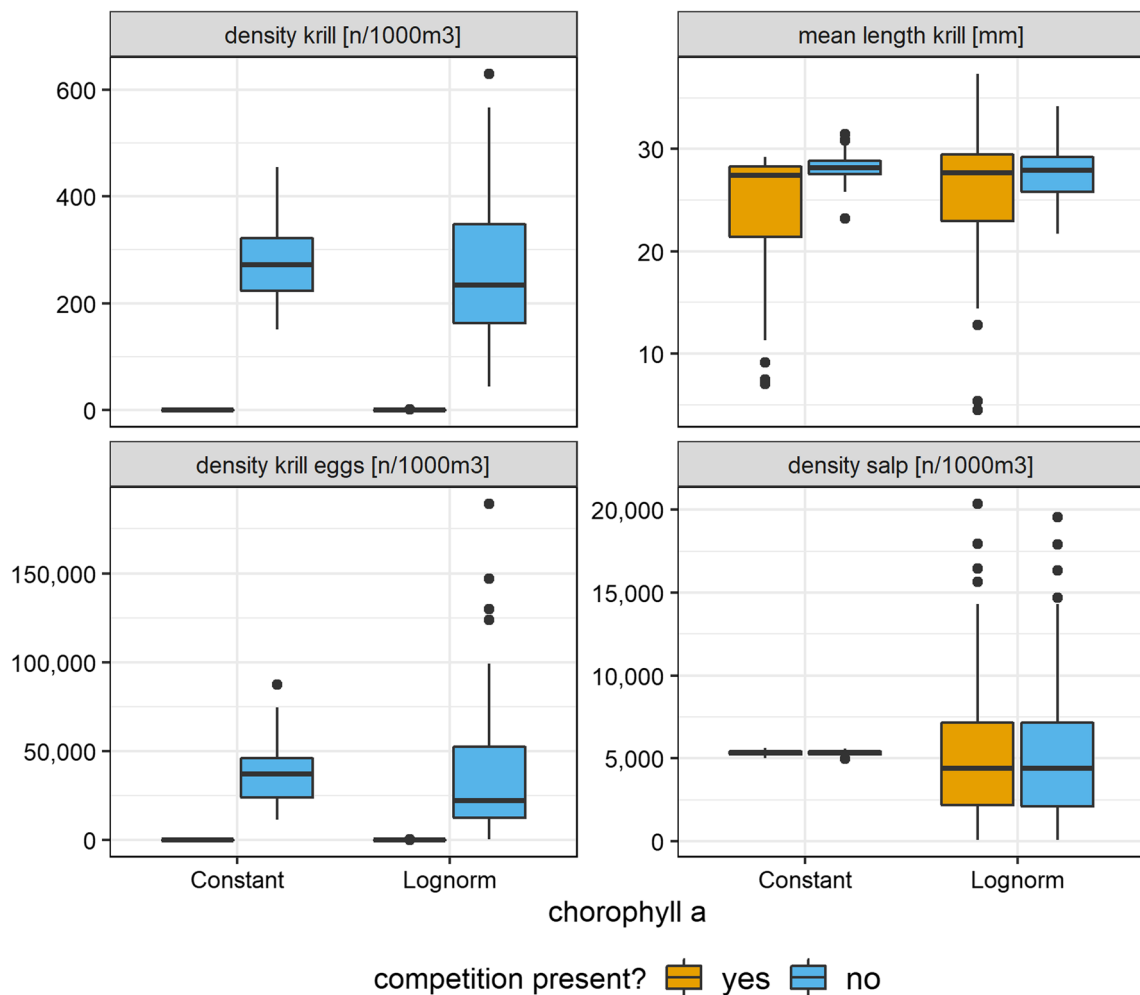
Fig. 4 Krill population dynamics in the presence and absence of salps. Boxplots displaying the distribution of post-larvae krill density (top left panel), mean post-larvae krill length (top right panel), number of eggs released by krill per year (bottom left panel), and salp density (bottom right panel) for the model runs and the years 30–100. The boxplots are separated by chlorophyll-a scenario (*x*-axis of each plot) and competition with the other species, respectively (coloring of boxplots)

Table 5 Absolute and relative differences in medians of 100 years for population properties of krill and salps due to the introduction of competition with the other species

Output	Chlorophyll-a scenario	Other species present	No other species present	The absolute difference [*n*]	The relative difference [%]
Krill density [n/1000 m³]	Constant	0.28	271.65	− 271.4	− 99.9
	Lognormal	0.34	234.23	− 233.9	− 99.9
Mean length [mm]	Constant	27.40	28.18	− 0.8	− 2.8
	Lognormal	27.69	27.95	− 0.3	− 0.9
Krill egg density [n/1000 m³]	Constant	0.00	37,096.01	− 37,096.0	− 100.0
	Lognormal	0.00	22,061.90	− 22,061.9	− 100.0
Salp density [n/1000 m³]	Constant	5351.19	5348.11	3.1	0.1
	Lognormal	4405.87	4398.72	7.1	0.2

The chosen chlorophyll-a scenario separated the results (constant low concentration of 0.54 mg per m³ or lognormal distribution with mean log = 3.83 mg per m³ and sd log = 0.58 mg per m³)

The density and mean length of krill were calculated for the post-larvae krill stages only

Pietzsch *et al. Ecological Processes*   (2023) 12:50

Page 12 of 16

krill and salps and the influence of varying chlorophyll-a concentration on the population dynamics of krill over 100 years. In the following paragraphs, the results of the model application are discussed.

The 100-year simulations highlight the strong impact of a stochastic environment on the minimum, maximum, and annual fluctuations of abundance, mean length, and the number of eggs released by krill per year. The median of simulated krill densities ranges from 234 to 272 individuals per 1000 m^3 dependent on chlorophyll-a scenario and the presence of salps. These values are at the lower end of reported ranges such as 306.9 individuals per 1000 m^3 converted from 89 individuals per m^2 and 290 m water depth (Nordhausen 1994), 346.1 individuals per 1000 m^3 calculated as mean (Hosie et al. 1988) or 510.9 individuals per 1000 m^3 calculated as stratified mean (Siegel et al. 2002). Our model showed that increases in post-larvae krill density happen in or directly after years of high maximum chlorophyll-a densities and are following other studies that found correlations between krill abundance or density with phytoplankton biomass or chlorophyll-a (Atkinson et al. 2004). Similar findings related high krill abundance to low temperatures (Trathan et al. 2003; Lee et al. 2010), an alias for food availability besides other factors. Years with higher food availability resulted in more eggs released by adult krill per year, following several other studies that linked food availability with successful recruitment (Loeb et al. 1997; Ross et al. 2000; Siegel 2000; Quetin and Ross 2001, 2003; Fraser and Hofmann 2003). Furthermore, the new model showed a population cycle of krill regardless of the chosen chlorophyll-a scenario and the presence or absence of salps. This follows the findings of Ryabov et al. (2017), who described a 5–6-year population cycle of krill, which they primarily linked to intraspecific competition for food. One contributing factor facilitating these population cycles is the nature of our and Ryabov et al.'s (2017) modeling environments. Both systems are closed and do not allow for the emigration of krill individuals, which would otherwise decrease intraspecific competition. Furthermore, our model did not include seasonal stage-specific spatial separation of krill populations observed in the field (Siegel 1988; Lascara et al. 1999; Perry et al. 2019). The seasonal spatial separation of krill life stages reduces resource competition between adults and recruits during periods of low productivity and has been hypothesized as an effective evolutionary adaptation maximizing krill population growth (Nicol 2006).

Our simulation results showed that during the low and constant chlorophyll-a scenario (maximum concentration of 0.54 mg per m^3), salp densities did not exceed 5000 individuals per 1000 m^3. This follows the findings of Groeneveld et al. (2020), which present the baseline salp model used in our study. They concluded that salp abundance under the scenario of fixed primary production "is mainly driven by immigration (or population survival during overwintering) of small seeding populations". On the other hand, in years with high chlorophyll-a concentration in the non-constant scenario, our results showed peak salp densities of up to 29,669 individuals per 1000 m^3 which are close to the densities reported by the observations from the AMLR data set, which showed a maximum of 42,000 individuals per 1000 m^3 (Southeast Fisheries Science Center 2020). This high peak abundance in years with high chlorophyll-a availability was also reported by Groeneveld et al. (2020), where salp blooms were mainly driven by varying chlorophyll-a concentrations and averted during years with low densities. *Salpa thompsoni* is known for its ability to quickly respond to changing environmental conditions (Henschke and Pakhomov 2019) due to its short life cycles and explosive population growth capabilities originating from its capability to reproduce asexually (Foxton 1966; Pakhomov et al. 2002), which in turn results in high fluctuations between years (Siegel 2017). Under favorable conditions, *S. thompsoni* can exhibit exponential population growth due to their exceptionally high growth and filtration rates (Alldredge and Madin 1982; Perissinotto and Pakhomov 1997; Dubischar et al. 2006). In another modeling study, chlorophyll-a and temperature were detected as the main drivers for the recreation of seasonal and inter-annual salp population dynamics (Henschke et al. 2018). In contrast, Pakhomov et al. (2006) did not find a relation between salp densities and chlorophyll-a concentrations. One reason for this difference may lie within the possible clogging of the salp filtering apparatus at high particle concentrations, which can lead to the collapse of the whole population (Perissinotto and Pakhomov 1997, 1998; Kawaguchi et al. 2004). A primary driver for salp population success seems connected to blastozooid reproductive fitness, which is limited by shallow temperatures and low food conditions (Henschke and Pakhomov 2019).

Our simulation results showed a significant effect of food competition with salps on the abundance of krill per 1000 m^3, the amount of eggs released per 1000 m^3, and the mean length of krill. This strong effect of food competition on the krill population by salps could be linked to the depletion of chlorophyll-a in large areas during blooms and might be further amplified by our model assumptions which did not provide the possibility for krill to emigrate or to differentiate different algae sizes which could be preferably consumed by one species or the other (Alldredge and Madin 1982; Moline et al. 2004). These findings contrast Siegel and Loeb (1995), who found no meaningful correlation between

Pietzsch *et al. Ecological Processes*   (2023) 12:50

Page 13 of 16

median salp abundance and mean krill stock density. As the relationship was non-linear, the authors hypothesized that there could be "a salp density threshold level above which the krill distributional attributes are negatively affected" (Siegel and Loeb 1995). Their finding further emphasizes that recruitment indices had a "fairly strong" negative correlation with the salp abundance (Siegel and Loeb 1995). Our study's results support this hypothesis regarding krill recruitment under varying chlorophyll-a scenarios, as the median of the 100 years showed a reduction of 100% in eggs released per year and 1000 m^3. In addition, the 100-year median of krill densities decreased by nearly 100% during varying chlorophyll-a density when salps were introduced. Snapshots of the chlorophyll-a amount of the modeled domain during the simulation experiments revealed an areal reduction of chlorophyll-a content of up to 60% if salp density exceeded 10,000 individuals per 1000 m^3, which supports the threshold hypothesis of Siegel and Loeb (1995). In general, the food competition between salps and krill is hypothesized to be an essential factor for krill abundance (Perissinotto and Pakhomov 1998). Particularly salps' ability for explosive reproduction events is seen as a possibility to act as a competitor for food (Siegel and Loeb 1995; Chiba et al. 1998). Another study suggests no or little competition for phytoplankton between *Euphausia superba* and *Salpa thompsoni* (Kawaguchi and Mare 1998). A possible explanation for this lack of competition is seen in different food particle size preferences by salps and krill (Alldredge and Madin 1982; Moline et al. 2004), although this hypothesis has recently been challenged (Pauli et al. 2021b). Another possibility for competition between salps and krill is the direct predation of the two species. Some findings indicate direct predation of salps by krill (Kawaguchi and Takahashi 1996) as well as of krill eggs and larvae by salps (Huntley et al. 1989; Nishikawa et al. 1995; Perissinotto and Pakhomov 1998; Pakhomov 2004) is possible. For further simulation studies with the proposed PEKRIS model, it is emphasized to investigate whether this strong competition prevails if phytoplankton sizes and consumption preferences of krill are modeled. In addition, the direct predation of the two species and the consumption of krill fecal pellets by salps might further change the impact size of the competition.

Conclusions

In conclusion, we can answer our research hypotheses as follows:

1) The density of krill decreases with existing food competition with salps

   It was possible to detect a significant impact of competition with salps on the density of krill. The median abundance of the 100 years showed a reduction of 99.9% or 234 individuals per 1000 m^3 in the case of varying chlorophyll-a concentration and of 99.9% or 271 individuals per 1000 m^3 during constant concentration.

2) The mean body size of krill decreases with existing food competition with salps

   A significant but marginal deviation of the mean length could be detected by introducing salps. The median of the mean body length of krill throughout the 100 years showed a decrease of 2.8% (0.8 mm) during constant and of 0.9% (0.3 mm) during varying chlorophyll-a concentration.

3) The number of eggs krill releases yearly decreases when salps are present

   Due to the presence of salps, a significant reduction was detectable. The median yearly number of eggs released by krill showed a decrease of 100.0% or 22,062 eggs per 1000 m^3 during varying and of 100.0% or 37,096 eggs per 1000 m^3 during constant chlorophyll-a concentration.

4) A fluctuation in food availability leads to asynchronous reactions of salp and krill populations

   The reactions of salps to annual fluctuations of chlorophyll-a usually happen within the same year (for maximum peak density). For krill, density, and amount of eggs released per year were predominantly driven by the maximum chlorophyll-a density of the previous years.

In the future, the newly developed individual-based model PEKRIS could be used to investigate whether this strong competition prevails if phytoplankton sizes and consumption preferences of krill are modeled. In addition, the direct predation of the two species and the consumption of krill fecal pellets by salps might further change the impact size of the competition. Another important research direction could be to investigate the impact of climate change and the corresponding warming oceans on the energy budgeting, food consumption, and metabolism maintenance of Antarctic krill (*Euphausia superba*) as well as the competition for food with salps (*Salpa thompsoni*). Warmer temperatures are expected to alter sea ice and ice shelf dynamics, leading to decreases in krill abundance (Vaughan and Doake 1996; Quetin et al. 2007). At the same time, salps may be favored by the warming trend (Pakhomov 2004), further intensifying the pressure on krill populations. Another possible application scenario of PEKRIS is investigating predation and fishery on the krill population dynamics.

Pietzsch *et al. Ecological Processes*   (2023) 12:50

Page 14 of 16

Abbreviations

AMLR   US Antarctic Marine Living Resource program
ANOVA   Analysis of variance
DEB   Dynamic energy budget theory
IBM   Individual-based model
PEKRIS   PErfromance of KRIll vs. Salps

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s13717-023-00462-9.

> **Additional file 1: S1 Appendix.** Details of the model description following the ODD protocol.
>
> **Additional file 2: S2 Appendix.** Sensitivity analysis of PEKRIS.

Author contributions

BWP developed, tested, and analyzed the model, processed and visualized the results, and wrote the first draft of the manuscript. AS worked on the model development, testing, and analysis and wrote parts of the first draft of the manuscript. JG conceptualized and developed the model and reviewed and edited the manuscript. DB reviewed the model and edited the manuscript. BM conceptualized the project, reviewed and edited the manuscript, and acquired the project funding. UB conceptualized the project, reviewed and edited the manuscript, and supervised the study. All authors have read and approved the submitted version.

Availability of data and materials

The model code, all R scripts, and, model outputs generated for this study are available at https://github.com/bwpietzsch/PEKRIS/releases/tag/1.2.

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
The authors declare that they have no competing interests.

Author details

[1]Faculty of Environmental Sciences, Institute of Forest Growth and Forest Computer Sciences, Technische Universität Dresden, 01062 Dresden, Germany. [2]Department of Ecological Modelling, Helmholtz Centre for Environmental Research - UFZ, Leipzig, Germany. [3]Section Polar Biological Oceanography, Alfred Wegener Institute Helmholtz Centre for Polar and Marine Research, Bremerhaven, Germany. [4]Institute for Chemistry and Biology of the Marine Environment (ICBM), Carl-Von-Ossietzky University, Oldenburg, Germany. [5]Helmholtz Institute for Marine Functional Biodiversity (HIFMB), Oldenburg, Germany.

References

Alldredge AL, Madin LP (1982) Pelagic tunicates: unique herbivores in the marine plankton. Bioscience 32:655–663. https://doi.org/10.2307/1308815

Atkinson A, Siegel V, Pakhomov E, Rothery P (2004) Long-term decline in krill stock and increase in salps within the Southern Ocean. Nature 432:100–103. https://doi.org/10.1038/nature02996

Atkinson A, Shreeve RS, Hirst AG et al (2006) Natural growth rates in Antarctic krill (*Euphausia superba*): II. Predictive models based on food, temperature, body length, sex, and maturity stage. Limnol Oceanogr 51:973–987. https://doi.org/10.4319/lo.2006.51.2.0973

Atkinson A, Hill SL, Pakhomov EA et al (2019) Krill (*Euphausia superba*) distribution contracts southward during rapid regional warming. Nat Clim Change 9:142–147. https://doi.org/10.1038/s41558-018-0370-z

Bahlburg D, Meyer B, Berger U (2021) The impact of seasonal regulation of metabolism on the life history of Antarctic krill. Ecol Model 442:109427. https://doi.org/10.1016/j.ecolmodel.2021.109427

Cavan EL, Belcher A, Atkinson A et al (2019) The importance of Antarctic krill in biogeochemical cycles. Nat Commun 10:4742. https://doi.org/10.1038/s41467-019-12668-7

Chambers JM, Hastie TJ (2017) Statistical Models in S. Routledge, Milton Park

Chiba S, Horimoto N, Satoh R et al (1998) Macrozooplankton distribution around the Antarctic divergence off Wilkes Land in the 1996 austral summer : with reference to high abundance of *Salpa thompsoni*. Polar Biol 11:33–50

Dubischar CD, Bathmann UV (1997) Grazing impact of copepods and salps on phytoplankton in the Atlantic sector of the Southern Ocean. Deep Sea Res Part II Top Stud Oceanogr 44:415–433. https://doi.org/10.1016/S0967-0645(96)00064-1

Dubischar CD, Pakhomov EA, Bathmann UV (2006) The tunicate *Salpa thompsoni* ecology in the Southern Ocean. II. Proximate and elemental composition. Mar Biol 149:625–632. https://doi.org/10.1007/s00227-005-0226-8

Dytham C (2011) Choosing and using statistics: a biologist's guide, 3rd edn. Hoboken, Wiley

Foxton P (1966) The distribution and life-history of *Salpa thompsoni* Foxton with observations on a related species *Salpa gerlachei* Foxton. Cambridge University Press, Cambridge

Fransz HG, Gonzalez SR (1997) Latitudinal metazoan plankton zones in the antarctic circumpolar current along 6°W during austral spring 1992. Deep Sea Res Part II Top Stud Oceanogr 44:395–414. https://doi.org/10.1016/S0967-0645(96)00065-3

Fraser WR, Hofmann EE (2003) A predator's perspective on causal links between climate change, physical forcing and ecosystem response. Mar Ecol Prog Ser 265:1–15. https://doi.org/10.3354/meps265001

Gleiber M, Steinberg D, Ducklow H (2012) Time series of vertical flux of zooplankton fecal pellets on the continental shelf of the Western Antarctic Peninsula. Mar Ecol Prog Ser 471:23–36. https://doi.org/10.3354/meps10021

Grimm V, Berger U, Bastiansen F et al (2006) A standard protocol for describing individual-based and agent-based models. Ecol Model 198:115–126. https://doi.org/10.1016/j.ecolmodel.2006.04.023

Grimm V, Railsback SF, Vincenot CE et al (2020) The ODD protocol for describing agent-based and other simulation models: a second update to improve clarity, replication, and structural realism. J Artif Soc Soc Simul 23:7. https://doi.org/10.18564/jasss.4259

Groeneveld J, Berger U, Henschke N et al (2020) Blooms of a key grazer in the Southern Ocean—an individual-based model of *Salpa thompsoni*. Prog Oceanogr 185:102339. https://doi.org/10.1016/j.pocean.2020.102339

Harbou LV (2009) Trophodynamics of Salps in the Atlantic Southern Ocean. Universitaet Bremen

Hempel G (1985) On the biology of polar seas, particularly the Southern Ocean. Wiley, Chichester

Henschke N, Pakhomov EA (2019) Latitudinal variations in *Salpa thompsoni* reproductive fitness. Limnol Oceanogr 64:575–584. https://doi.org/10.1002/lno.11061

Henschke N, Pakhomov EA, Groeneveld J, Meyer B (2018) Modelling the life cycle of *Salpa thompsoni*. Ecol Model 387:17–26. https://doi.org/10.1016/j.ecolmodel.2018.08.017

Pietzsch *et al. Ecological Processes*   (2023) 12:50

Page 15 of 16

Hofmann EE, Lascara CM (2000) Modeling the growth dynamics of Antarctic krill *Euphausia superba*. Mar Ecol Prog Ser 194:219–231. https://doi.org/10.3354/meps194219

Hosie GW, Ikeda T, Stolp M (1988) Distribution, abundance and population structure of the Antarctic krill (*Euphausia superba* Dana) in the Prydz Bay region, Antarctica. Polar Biol 8:213–224. https://doi.org/10.1007/BF00443453

Huntley M, Sykes P, Marin V (1989) Biometry and trophodynamics of *Salpa thompsoni* Foxton (Tunicata: Thaliacea) near the Antarctic Peninsula in austral summer, 1983–1984. Polar Biol. https://doi.org/10.1007/BF00238291

Iguchi N, Ikeda T (2004) Metabolism and elemental composition of aggregate and solitary forms of *Salpa thompsoni* (Tunicata: Thaliacea) in waters off the Antarctic Peninsula during austral summer 1999. J Plankton Res 26:1025–1037. https://doi.org/10.1093/plankt/fbh093

Ikeda T (1981) Metabolic activity of larval stages of antarctic krill. Antarct J 16:161

Ikeda T, Mitchell AW (1982) Oxygen uptake, ammonia excretion and phosphate excretion by krill and other Antarctic zooplankton in relation to their body size and chemical composition. Mar Biol 71:283–298. https://doi.org/10.1007/BF00397045

Jager T, Ravagnan E (2015) Parameterising a generic model for the dynamic energy budget of Antarctic krill *Euphausia superba*. Mar Ecol Prog Ser 519:115–128. https://doi.org/10.3354/meps11098

Jager T, Martin BT, Zimmer EI (2013) DEBkiss or the quest for the simplest generic model of animal life history. J Theor Biol 328:9–18. https://doi.org/10.1016/j.jtbi.2013.03.011

Kawaguchi S, de la Mare WK (1998) Do krill and salps compete? Contrary evidence from the krill fisheries. CCAMLR Sci 5:205–216

Kawaguchi S, Takahashi Y (1996) Antarctic krill (*Euphausia superba* Dana) eat salps. Springer-Verlag, Berlin

Kawaguchi S, Siegel V, Litvinov F et al (2004) Salp distribution and size composition in the Atlantic sector of the Southern Ocean. Deep Sea Res Part II Top Stud Oceanogr 51:1369–1381. https://doi.org/10.1016/j.dsr2.2004.06.017

Lascara CM, Hofmann EE, Ross RM, Quetin LB (1999) Seasonal variability in the distribution of Antarctic krill, *Euphausia superba*, west of the Antarctic Peninsula. Deep Sea Res Part Oceanogr Res Pap 46:951–984. https://doi.org/10.1016/S0967-0637(98)00099-5

Lee CI, Pakhomov E, Atkinson A, Siegel V (2010) Long-term relationships between the marine environment, krill and salps in the Southern Ocean. J Mar Biol 2010:1–18. https://doi.org/10.1155/2010/410129

Loeb VJ, Santora JA (2012) Population dynamics of *Salpa thompsoni* near the Antarctic Peninsula: growth rates and interannual variations in reproductive activity (1993–2009). Prog Oceanogr 96:93–107. https://doi.org/10.1016/j.pocean.2011.11.001

Loeb V, Siegel V, Holm-Hansen O et al (1997) Effects of sea-ice extent and krill or salp dominance on the Antarctic food web. Nature 387:897–900. https://doi.org/10.1038/43174

Moline MA, Claustre H, Frazer TK et al (2004) Alteration of the food web along the Antarctic Peninsula in response to a regional warming trend. Glob Change Biol 10:1973–1980. https://doi.org/10.1111/j.1365-2486.2004.00825.x

Nicol S (2006) Krill, currents, and sea ice: *Euphausia superba* and its changing environment. Bioscience 56:111–120. https://doi.org/10.1641/0006-3568(2006)056[0111:KCASIE]2.0.CO;2

Nicol S, de Mare WK, Stolp M (1995) The energetic cost of egg production in Antarctic krill (*Euphausia superba* Dana). Antarct Sci 7:25–30. https://doi.org/10.1017/S0954102095000058

Nisbet RM, Jusup M, Klanjscek T, Pecquerie L (2012) Integrating dynamic energy budget (DEB) theory with traditional bioenergetic models. J Exp Biol 215:892–902. https://doi.org/10.1242/jeb.059675

Nishikawa J, Naganobu M, Ichii T et al (1995) Distribution of salps near the South Shetland Islands during austral summer, 1990–1991 with special reference to krill distribution. Polar Biol 15:31–39. https://doi.org/10.1007/BF00236121

Nordhausen W (1994) Winter abundance and distribution of *Euphausia superba*, *E. crystalorophias*, and *Thysanoessa macrura* in Gerlache Strait and Crystal Sound, Antarctica. Mar Ecol Prog Ser 109:131–142

Pakhomov EA (2004) Salp/krill interactions in the eastern Atlantic sector of the Southern Ocean. Deep Sea Res Part II Top Stud Oceanogr 51:2645–2660. https://doi.org/10.1016/j.dsr2.2001.03.001

Pakhomov EA, Froneman PW (2000) Composition and spatial variability of macroplankton and micronekton within the Antarctic Polar Frontal Zone of the Indian Ocean during austral autumn 1997. Polar Biol 23:410–419. https://doi.org/10.1007/s003000050462

Pakhomov EA, Hunt BPV (2017) Trans-Atlantic variability in the ecology of the pelagic tunicate *Salpa thompsoni* near the Antarctic Polar Front. Deep Sea Res Part II Top Stud Oceanogr 138:126–140. https://doi.org/10.1016/j.dsr2.2017.03.001

Pakhomov EA, Froneman PW, Perissinotto R (2002) Salp/krill interactions in the Southern Ocean: spatial segregation and implications for the carbon flux. Deep Sea Res Part II Top Stud Oceanogr 49:1881–1907. https://doi.org/10.1016/S0967-0645(02)00017-6

Pakhomov EA, Dubischar CD, Strass V et al (2006) The tunicate *Salpa thompsoni* ecology in the Southern Ocean. I. Distribution, biomass, demography, and feeding ecophysiology. Mar Biol 149:609–623. https://doi.org/10.1007/s00227-005-0225-9

Pakhomov E, Pakhomova L, Iversen M et al (2018) Biology of the Pelagic Tunicate, *Salpa thompsoni*, in the Western Atlantic Sector of the Southern Ocean during March–May 2018. In: Reports on polar and marine research, pp 28–33

Pauli N-C, Flintrop CM, Konrad C et al (2021a) Krill and salp faecal pellets contribute equally to the carbon flux at the Antarctic Peninsula. Nat Commun 12:7168. https://doi.org/10.1038/s41467-021-27436-9

Pauli N-C, Metfies K, Pakhomov EA et al (2021b) Selective feeding in Southern Ocean key grazers—diet composition of krill and salps. Commun Biol 4:1061. https://doi.org/10.1038/s42003-021-02581-5

Perissinotto R, Pakhomov EA (1997) Feeding association of the copepod *Rhincalanus gigas* with the tunicate salp *Salpa thompsoni* in the southern ocean. Mar Biol 127:479–483. https://doi.org/10.1007/s002270050036

Perissinotto R, Pakhomov EA (1998) The trophic role of the tunicate *Salpa thompsoni* in the Antarctic marine ecosystem. J Mar Syst 17:361–374. https://doi.org/10.1016/S0924-7963(98)00049-9

Perry FA, Atkinson A, Sailley SF et al (2019) Habitat partitioning in Antarctic krill: spawning hotspots and nursery areas. PLoS ONE 14:e0219325. https://doi.org/10.1371/journal.pone.0219325

Plum C, Hillebrand H, Moorthi S (2020) Krill vs. salps: dominance shift from krill to salps is associated with higher dissolved N:P ratios. Sci Rep 10:5911. https://doi.org/10.1038/s41598-020-62829-8

Quetin LB, Ross RM (1991) Behavioral and physiological characteristics of the Antarctic krill, *Euphausia superba*. Am Zool 31:49–63. https://doi.org/10.1093/icb/31.1.49

Quetin LB, Ross RM (2001) Environmental variability and its impact on the reproductive cycle of Antarctic krill. Am Zool 41:74–89. https://doi.org/10.1093/icb/41.1.74

Quetin LB, Ross RM (2003) Episodic recruitment in Antarctic krill *Euphausia superba* in the Palmer LTER study region. Mar Ecol Prog Ser 259:185–200. https://doi.org/10.3354/meps259185

Quetin LB, Ross RM, Fritsen CH, Vernet M (2007) Ecological responses of Antarctic krill to environmental variability: can we predict the future? Antarct Sci 19:253–266. https://doi.org/10.1017/S0954102007000363

Railsback SF, Grimm V (2012) Agent-based and individual-based modeling - a practical introduction. Princeton University Press

R Core Team (2020) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Reiss CS, Cossio AM, Loeb V, Demer DA (2008) Variations in the biomass of Antarctic krill (*Euphausia superba*) around the South Shetland Islands, 1996–2006. ICES J Mar Sci 65:497–508. https://doi.org/10.1093/icesjms/fsn033

Ross RM, Quetin LB (1991) Ecological physiology of larval euphausids, *Euphausia superba* (Euphausiacea). Mem Qld Mus 31:321–333

Ross RM, Quetin LB, Baker KS et al (2000) Growth limitation in young *Euphausia superba* under field conditions. Limnol Oceanogr 45:31–43. https://doi.org/10.4319/lo.2000.45.1.0031

Royston P (1995) Remark AS R94: a remark on algorithm AS 181: the W-test for normality. Appl Stat 44:547–551. https://doi.org/10.2307/2986146

Ryabov AB, de Roos AM, Meyer B et al (2017) Competition-induced starvation drives large-scale population cycles in Antarctic krill. Nat Ecol Evol 1:0177. https://doi.org/10.1038/s41559-017-0177

Siegel V (2000) Krill (Euphausiacea) demography and variability in abundance and distribution. Can J Fish Aquat Sci 57:151–167. https://doi.org/10.1139/f00-184

Siegel V (2005) Distribution and population dynamics of *Euphausia superba*: summary of recent findings. Polar Biol 29:1–22. https://doi.org/10.1007/s00300-005-0058-5

Siegel V (2016) Biology and Ecology of Antarctic Krill. Springer, Cham

Siegel V (2017) Krill und Salpen prägen das antarktische Ökosystem. In: Hempel G, Bischof K, Hagen W (eds) Faszination Meeresforschung. Springer, Berlin, pp 121–134

Siegel V (1988) A concept of seasonal variation of krill (Euphausia superba) distribution and abundance west of the Antarctic Peninsula. In: Sahrhage D (ed) Antarctic ocean and resources variability. Springer, Berlin, pp 219–230

Siegel V, Loeb V (1995) Recruitment of Antarctic krill *Euphausia superba* and possible causes for its variability. Mar Ecol Prog Ser 123:45–56. https://doi.org/10.3354/meps123045

Siegel V, Skibowski A, Harm U (1992) Community structure of the epipelagic zooplankton community under the sea-ice of the Northern Weddell Sea. Polar Biol 12:15–24. https://doi.org/10.1007/BF00239961

Siegel V, Bergström B, Mühlenhardt-Siegel U, Thomasson M (2002) Demography of krill in the Elephant Island area during summer 2001 and its significance for stock recruitment. Antarct Sci 14:162–170. https://doi.org/10.1017/S095410200200072X

Sousa T, Domingos T, Poggiale J-C, Kooijman SALM (2010) Dynamic energy budget theory restores coherence in biology. Philos Trans R Soc B Biol Sci 365:3413–3428. https://doi.org/10.1098/rstb.2010.0166

Southeast Fisheries Science Center (2020) US AMLR Program zooplankton dataset from 1996–2011. In: NOAA Natl. Cent. Environ. Inf. https://www.fisheries.noaa.gov/inport/item/11426

Torres JJ, Lancraft TM, Weigle BL et al (1984) Distribution and abundance of fishes and salps in relation to the marginal ice zone of the Scotia Sea, November and December 1983. Antarct J US 19:117–119

Trathan PN, Brierley AS, Brandon MA et al (2003) Oceanographic variability and changes in Antarctic krill (*Euphausia superba*) abundance at South Georgia. Fish Oceanogr 12:569–583. https://doi.org/10.1046/j.1365-2419.2003.00268.x

Vaughan DG, Doake CSM (1996) Recent atmospheric warming and retreat of ice shelves on the Antarctic Peninsula. Nature 379:328–331. https://doi.org/10.1038/379328a0

Wickham H (2016) ggplot2: elegant graphics for data analysis. Springer, Cham

Wickham H (2021) tidyr: Tidy Messy Data. R package version 1.1.4.

Wilensky U, Rand W (2015) An introduction to agent-based modeling. Modeling natural, social, and engineered complex systems with NetLogo. The MIT Press, Cambridge

Publisher's Note