EUPHAUSIA SUPERBA OR *SALPA THOMPSONI* – WHO IS GOING TO WIN?

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ABSTRACT

Antarctic krill *Euphausia superba* and the salp *Salpa thompsoni* are major grazers in the Antarctic ecosystem, in which krill plays a major role in the link between primary producers and higher trophic levels. Both species are widely distributed in the Southern Ocean, but they exhibit a spatial segregation. Krill is predominantly found in colder waters of the high latitudes, whereas salps occupy warmer water masses in the lower latitudes. Over the last decades a shift in salp distribution into regions further south has been observed. Simultaneously krill abundance in those areas has decreased. This might indicate that a large-scale environmental shift in Antarctic regions may have occurred, or is in progress which will have major impacts on the cycling of biogenic carbon the Southern Ocean as well as on krill-dependent species.

INTRODUCTION

Antarctic krill, *Euphausia superba*, (hereafter "krill") and the tunicate, *Salpa thompsoni*, (hereafter "salps") are regarded as two of the most important filter-feeding organisms and grazers in the Southern Ocean (see [1]). Both species are also recognized as two of the most efficient re-packagers of small particles thereby playing a major role in the biogenic carbon cycle of the Southern Ocean [1, 2]. Whereas krill is the key link in transferring energy from the primary production level to higher trophic levels, such as fish, birds, seals and whales, salps are removing vast amounts of fixed carbon from the surface waters and burying them into the deep ocean via fast sinking faecal pellets [1, 3].

Even though krill and salps both have a circumpolar distribution, they typically inhabit different ranges of the Southern Ocean [4, 5]. Whereas krill received much research attention due to its role as a key species, salps have traditionally been regarded as minor components of the Southern Ocean. However, recent investigations have shown that salps are more abundant than previously thought. Additionally they have increasingly been recorded in higher latitudes (krill habitat) usually associated with warm water intrusions and less sea-ice formation [5]. This southward shift might indicate that a large-scale environmental shift in Antarctic regions may have occurred, or is in progress [6-8]. As a consequence, the ecological role of these two key species in the Antarctic food web has received much attention in recent times (e.g. [3, 5, 7, 9]).

This review will present some general background about krill and salps in terms of life history, distribution and interannual fluctuation. Subsequently krill/salp interactions and recently observed changes in the distribution of both species will be addressed. Finally hypotheses, which have been proposed to explain distributional segregation and possible implications for the future of the Antarctic marine ecosystem, will be discussed.

General krill background

Euphausia superba is probably one of the most-studied zooplankton species in the Southern Ocean [10]. Krill are shrimp-like pelagic crustaceans (Fig 1, Tab 1) and form huge swarms during the summer months. Such swarms can extend over kilometres and can consist of many billions of individuals [10, 11]. Krill are filter feeders preying efficiently on phytoplantkon particles from 10–50 μm [12]. They grow to a size of around 6cm and reach a life span of 5-7 years, an unusually high age for a plankton species [4, 11].

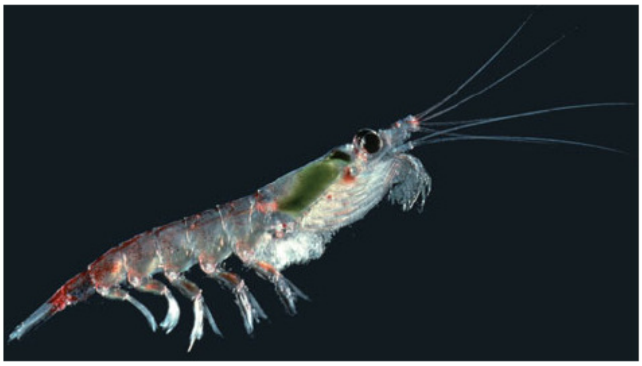


Figure 1. Antarctic krill, *Euphausia superba* [4]

Table 1. Taxonomic hierarchy of *Euphausia superba*, www.itis.gov

Phylum	Arthropoda
Subphylum	Crustacea
Class	Malacostraca
Order	Euphausiacea
Family	Euphausiidae
Genus	Euphausia
Species	*Euphausia superba*

The life cycle of krill is closely related to sea ice. In summer krill feed on phytoplankton in the open waters, whereas they retreat to the ice to feed on ice algae during the winter months [13]. Krill has a high nutritional value and it a key player in the Antarctic ecosystem. It provides a direct link between primary producers and higher trophic levels and is the major food source for a range of predators such as various fish species, seals, penguins, and whales [3] (Fig 2).

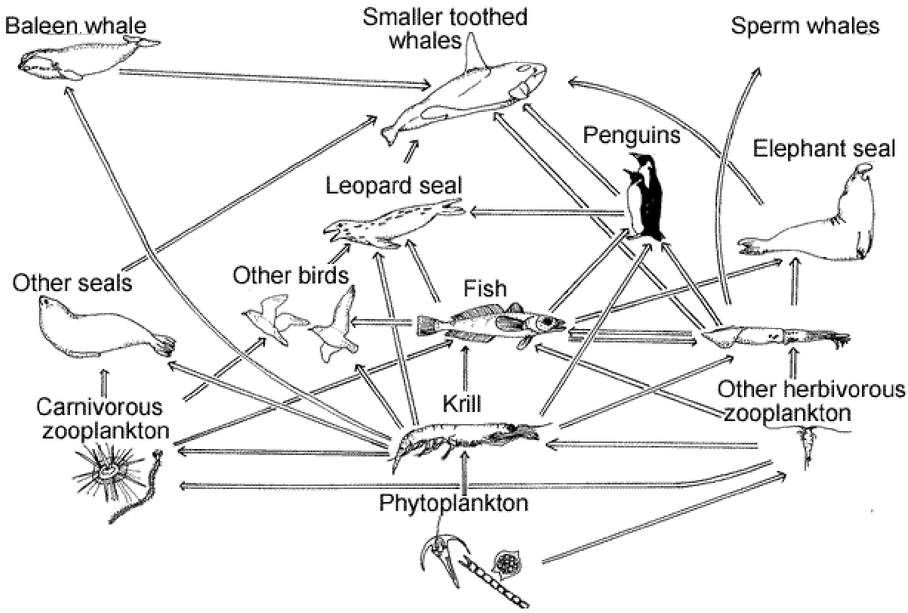


Figure 2. Simplified Antarctic food web with krill as the key player, www.coolantarctica.com

*D*ISTRIBUTION OF KRILL

In the Southern Ocean, krill has a circumpolar distribution and potential krill habitat lies between the Polar Front to the north and the ice-covered Antarctic shelves to the south [7] (Fig 3). Within this area krill shows, however, a strong asymmetry: 50-70% of the krill stock occur in the productive south-western Atlantic sector of the Southern Ocean (between 0-90°W) [4, 7]. Factors regulating krill distribution are still not fully understood. Whereas Atkinson *et al.* (2008) found that 87% of the overall krill stock lives in oceanic waters, suggestions also propose a close correlation to sea ice, shelf edges, high food concentrations, and predator avoidance mechanisms as factors determining krill distribution (see [4] for a comprehensive review on krill distribution and habitat preference).

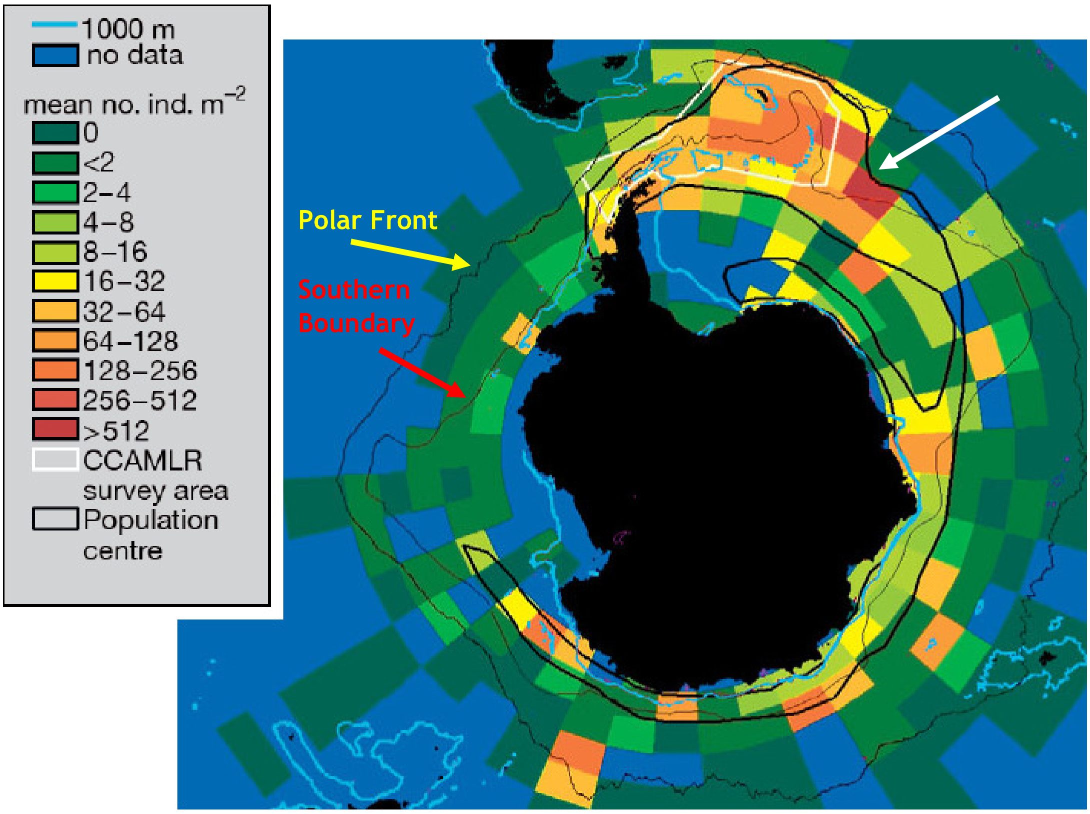


Figure 3. Circumpolar distribution *Euphausia superba* based on standardised data (8789 stations from 1926-2004). Fronts shown in black lines (north to south) are the Polar Front (indicated in yellow) and the Southern Boundary of the Antarctic Circumpolar Current (indicated in red). Population centres of krill were drawn by eye (indicated by white arrow), relative to the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) Survey [4].

While interpreting krill distribution maps and for the discussion of research results in this review, it has to be kept in mind that data sets are still incomplete, especially in terms of quantity and demography [10]. Research focuses on easily accessible areas and during summer months. Well studied areas that also provide time series for krill data include the Antarctic Peninsula, the western Scotia Sea, and the Indian Ocean. Remote and hard accessible areas such as the Bellingshausen- and Amundsen-Sea in the Pacific sector are still insufficiently sampled, and often provide data from only a single year [11] (Fig 4).

Figure 4. Indication of easily accessible, well studies (blue circle) and remote research areas (red circle), www.nationsonline.org

FLUCTUATIONS IN KRILL ABUNDANCE

Krill abundance can vary from year to year and fluctuations in density of more than one order of magnitude have been observed between years [11]. Variations of krill year-class success are the major cause of such interannual fluctuations in krill abundance: high krill populations result from good recruitment from the previous spawning season [14]. Good recruitment is positively correlated with an early seasonal spawning (in December–February), and both are positively correlated with sea-ice extent and duration the preceding winter. Accordingly low densities follow several years of poor or intermediate recruitment, which is correlated to late spawning (in March) and reduced regional sea-ice formation and duration [3]. Due to its lifespan of 5-7 years the krill stock size is not heavily influenced by recruitment success or failure in a single year. After a sequence of 3 or more years of poor recruitment, krill stocks are dramatically declining and two or three subsequent years of good recruitment are necessary to rebuild the stock size [14].

General salp background

Salpa thompsoni is the most numerous salp species of the Southern Ocean (Fig 5+6). Still, little is known about its general ecology and most of our knowledge comes from the classical work by Foxton (1966) based on data collected during the Discovery expeditions (1925-1951), citation in [15].

Figure 5. Solitary form of *Salpa thompsoni*, www.whoi.edu

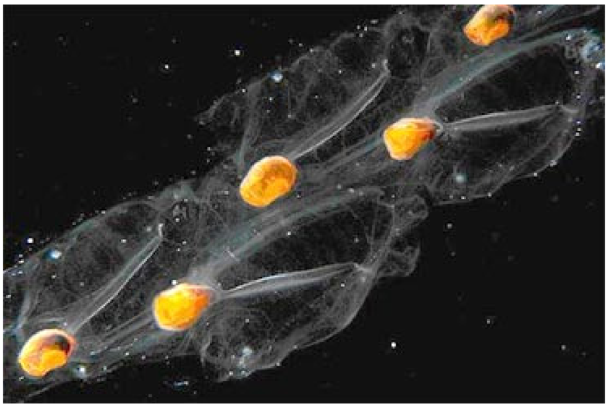


Figure 6. Chain of an aggregate stage of *Salpa thompsoni*. Every salp is a separate individual, but they are elegantly connected into a coordinated chain of animals, www.imr.no

Salps belong to the tunicates and live less than one year [3] (Tab 2). They are indiscriminate filter feeders and collect food particles of varying sizes ranging from 1-1000 µm using mucous nets. They prey most efficiently on particles >4 µm [16]. As a result of their high filtration rate, salps are widely considered as serious competitors for the other herbivorous zooplankton species, such as Antarctic krill (e.g. [3, 5, 14]). Salps exhibit a complex life cycle with an alternating sexual and asexual phase. The sexual phase consists of chain forming colonies, whereas the asexual form is solitary. This reproductive cycle allows salps to generate dense swarms (thousands of individuals) in very short periods of time, once conditions are favourable [16]. The solitary form can grow up to 10cm and the aggregate form forms long, connected chains, which can consist of 100-150 members. Salps they consist to 95% of water and have thus a low nutritional value [16, 17]. They are generally regarded to play an insignificant role in the diets of Antarctic organisms, but several authors suggest that they may be consumed by a number of bird and fish species, (see [17]).

Salps, however, play a major role in the biogenic carbon cycle. They are very efficient phytoplankton grazers and among the most efficient pelagic re-packagers of small particles (phytoplankton), which they release in form of large fast-sinking faecal pellets. Most of the primary production is thus not transferred to higher trophic levels, as in the case of krill, but lost from the surface and buried in long-living ''pools'' in the deep sea [1].

Table 2. Taxonomic Hierarchy of *Salpa thompsoni*, www.itis.gov

Kingdom	Animalia
Phylum	Chordata
Subphylum	Tunicata
Class	Thaliacea
Order	Salpida
Family	Salpidae
Genus	Salpa
Species	*Salpa thompsoni*

DISTRIBUTION OF SALPS

Distribution data for salps is even less available than compared to krill. From what is known, salps, also have a circumpolar distribution, are usually associated with the less productive warmer oceanic water masses and thus predominantly found in low Antarctic waters (45–55°S) [3, 15] (Fig 7). The reason for their absence from areas of high productivity is correlated with their feeding strategy. As they can't regulate their filtration rate, their mucous nets become clogged when chlorophyll-a concentrations are high [9, 12].

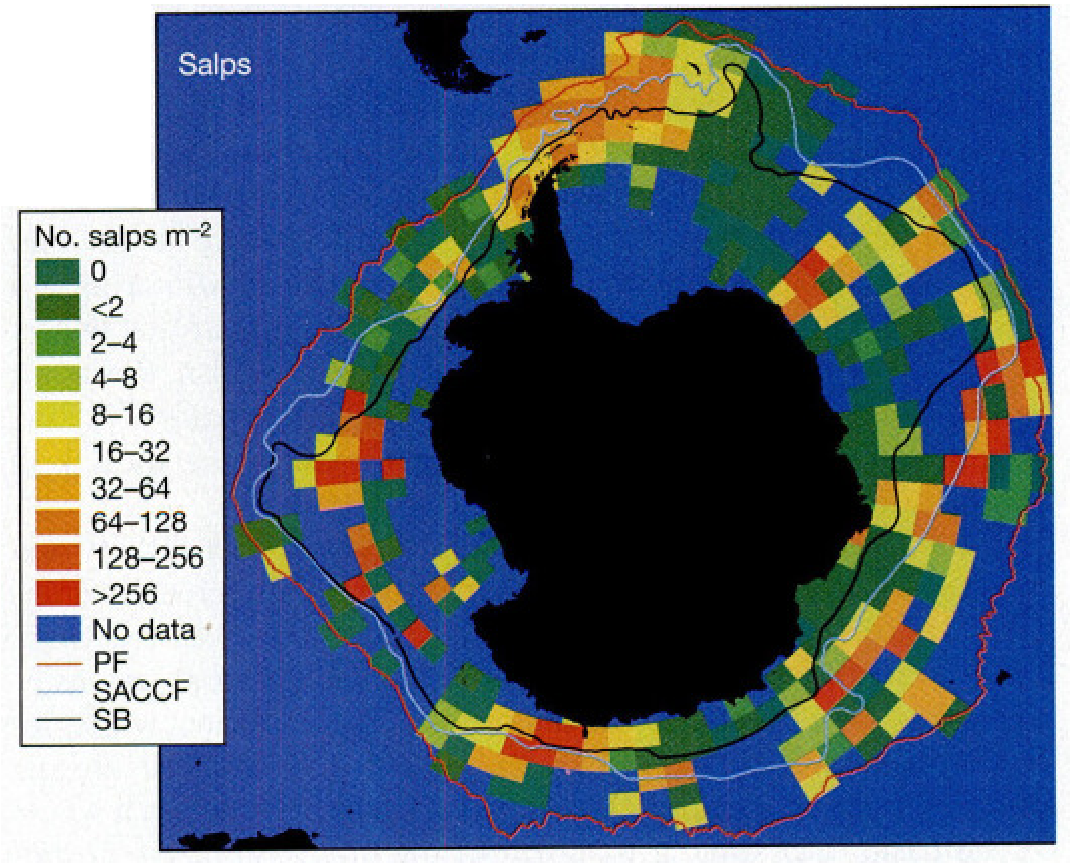


Figure 7. Mean salp densities from scientific net sampling data (5,030 stations, 1926-2003) [7]

Fluctuations in salp abundance

With shorter life cycles than krill and explosive population growth rates, salps can respond to environmental variations over shorter timescales [1, 6]. This also results in higher interannual fluctuations (over more than three orders of magnitude) than krill [11].

Loeb *et al.* (1997) could correlate that exceedingly high salp densities followed winters with relatively low sea-ice development. The negative correlation with sea-ice may result from salps being obligate filter feeders that benefit from open-water conditions and are unable to use ice algae as food resource [3].

Table 3. Major features of krill and salps

Major features	Krill	Salp
Size	~ 6cm	~10 cm (solitary stage)
Life cycle	5-7 years	< 1 year
Distribution	Circumpolar, high latitudes	Circumpolar, low latitudes
Importance	Key link between primary producers and higher trophic levels	Important for exporting fixed carbon into long-lived pools at the seafloor
Correlation with sea-ice	positive	negative
Future trend	Decrease in abundance	Increase in abundance and distribution further south

KRILL/SALP INTERACTIONS

Antarctic krill and salps generally show a pronounced spatial segregation in the Southern Ocean, which seems to be the result of a clear biotopical separation of these two species. As mentioned above, salps are usually restricted to the low-latitude warmer water masses, whereas krill inhabits to the colder high latitude regions [3]. However, in the Atlantic sector of the Southern Ocean, particularly in the waters off the Antarctic Peninsula and around the South Shetland Islands, krill and salps show some degree of overlap [6]. In such regions krill and salps may be in direct competition with each other, which might have important implications for the Antarctic ecosystem in terms of energy transfer and carbon cycling [3].

Since 1970 a decrease in krill density has been measured in the south-western Atlantic sector of the Southern Ocean [3, 4] (Fig 8). *S. thompsoni* in contrast has been observed to regularly appear at high latitudes and 'salp years', during which local swarms of salps dominate the planktonic biomass, often to the exclusion of other zooplankton, have been reported with increased frequency in high Antarctic waters [5, 6] (Fig 9).

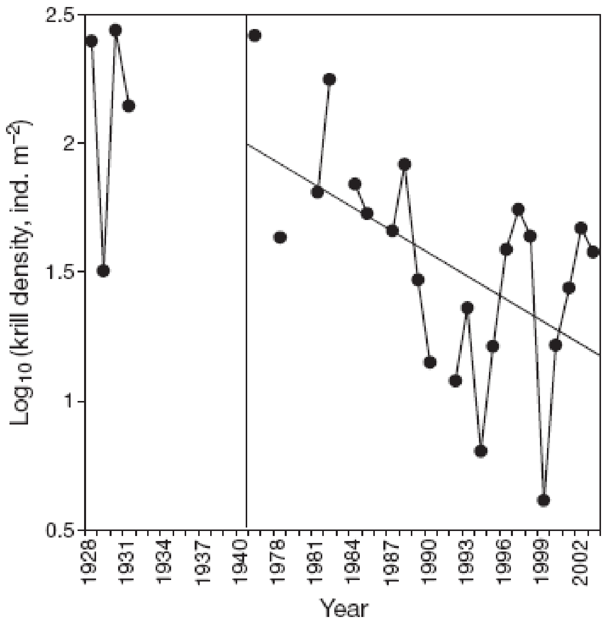
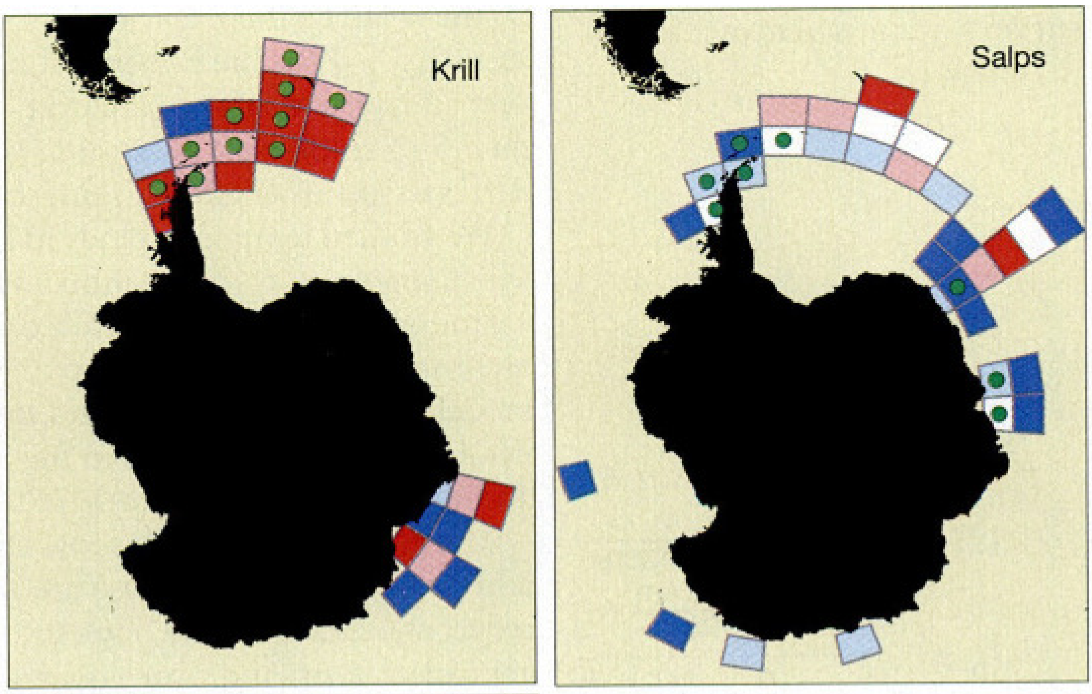


Figure 8. Change in mean density (ind. m^{-2}) of *Euphausia superba* within the SW Atlantic sector (30 to 70° W). based on standardised densities. Only years with >50 stations are plotted. The vertical line separates the 1926 to 1939 and post-1976 eras [4].



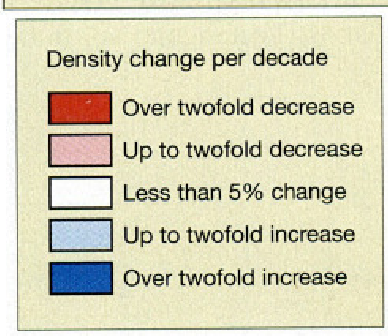


Figure 9. Temporal change of krill and salps. Krill data from scientific trawls post-1976; salp data from 1926-2003 [7].

DIFFERENT THEORIES FOR KRILL/SALP DOSTRIBUTIONAL CHANGES

Environmental conditions that favour krill/salp development and distribution are still not fully understood [18]. Due to the apparent southward shift of salps and the possible overlap/interaction with krill, research on those areas has increased over the past few decades. This has led to the formulation of several hypotheses to explain their spatial distribution [19].

CORRELATION WITH SEA ICE

As discussed above, krill and salps are both correlated to sea ice extent and duration. Krill shows a positive correlation, salps a negative [3].

The major relationships between krill recruitment and sea ice parameters, timing of krill spawning, and salp abundance are established on different levels of interaction. Some parameters are directly linked with krill recruitment, others are indirectly related [14] (Fig 10).

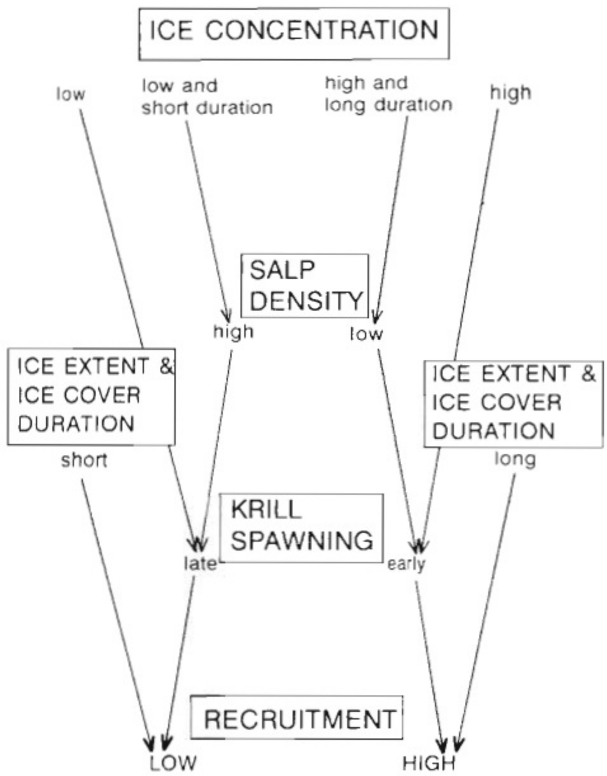


Figure 10. Concept of the relationships between krill recruitment and sea ice parameters, timing of krill spawning, and salp abundance [14].

Extensive and long sea-ice duration promote early krill spawning which is positively correlated with good krill recruitment. Early spawning permits larval growth and development over a much longer portion of the summer season than late spawning. The resulting larvae would be in more advanced stages and presumably in better condition to survive food-limited winter conditions [20]. Dense and long ice cover may therefore establish the basis for a minimum, but necessary, food resource for larvae to survive the winter, reduce the risk of starvation and increased mortality, and serve as an important nursery/feeding ground larvae and larger krill stages. Prolonged ice cover may also protect the stock from strong predation [14].

In contrast to krill, salps are directly affected by sea-ice conditions the following spring and summer season [14]. If ice concentration is high and of long duration, then density can be expected to be relatively low. Development of high spring/summer salp densities is probably dependent on sufficient food resources during early spring, allowing rapid early reproduction and a prolonged period of population growth. Dense and prolonged ice cover cause a delayed seasonal peak of phytoplankton production, thus providing suboptimal conditions for salp population growth as salps are not able to use the ice algae as a food resource [3, 14].

Loeb *et al* (1997) analysed the relationship between annual sea-ice cover and air temperature measurements. Over the last 50 years, a decreased frequency of winters with extensive sea-ice development has been observed (Fig 11). Additionally, advection of warmer water masses has been observed in regions further south, which might explain the repeatedly occurrence of salp in higher latitudes during recent years [6, 7].

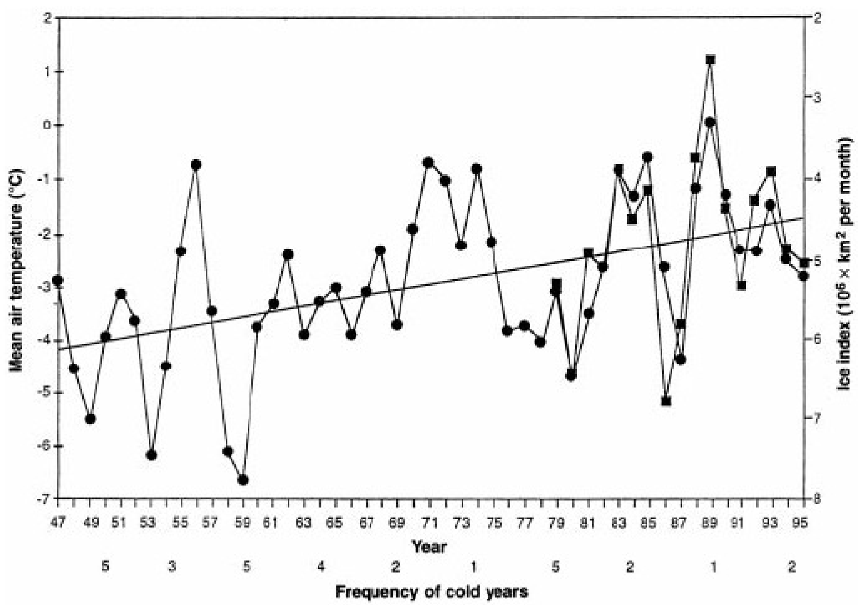


Figure 11. Long-term trends in mean annual surface air temperature in the Antarctic Peninsula region 1947–1995 (circles) and the regional sea-ice index 1979–1995 (squares). Frequency of cold years reflects the number of years per respective five-year period that mean air temperature was ≤ -2.5°C [3].

Predation

Salps might, while filter feeding, accidentally prey on eggs and early larval stages of krill, thus, affecting krill recruitment in following years. Krill debris and larvae were found in guts of *S. thompsoni*, (see [19]). Those findings were, however, low indicating that this effects seems to be negligible. Suggestions in the literature indicate, that salps might consume krill eggs more extensively than larval stages but further studies are lacking [5].

Deterrence

Salps may produce distasteful metabolic products, which may drive other organisms, including krill, away. However, recent observations rather suggest the opposite in the areas of krill/salp spatial overlap. Kawaguchi and Takahashi (1996) showed that krill were attracted to salp extracts and did even successfully prey on salps (up to 0.5 salp per krill per day) (citation in [6]).

Overlap but still separation

Despite the spatial overlap of krill and salps in certain areas, fine-scale surveys demonstrated a pronounced spatial, horizontal or vertical separation between krill and salps. Even in overlapping areas, krill and salps are confined to different water masses, (see [19, 21]). Depth stratified surveys revealed that *S. thompsoni* avoids cold-water layers, concentrating in either deep warm waters and/or in surface layers warmed during summer [6]. This hypothesis seems to explain limited spatial overlap in krill/salp distribution outside the Antarctic Peninsula region.

Exclusion

As salps have the ability to undergo an explosive development they may act as strong competitors for food [14]. They might thus exclude krill from areas of high salp density as they feed more efficiently on a wide range of particles (see above) [16]. Perissinotto and Pakhomov (1998b) showed that salp swarms can graze more then 100% of the daily primary production, which supports that completive removal of food might be a major reason for low krill abundance in salp-dominated. This hypothesis, however, might only be valid in areas of phytoplankton concentrations below the threshold feeding levels of salps. High phytoplankton concentrations can cause clogging in the filtering apparatus to the advantage of krill, which are adapted to feed in the presence of high particle densities [2, 5 19]. Additionally the mentioned segregated distribution patterns of salps and krill indicate a low probability for competition of the same food source.

CHANGES IN FOOD SOURCE

Along the Antarctic Peninsula, elevated temperatures have led to increased glacial melt-water runoff, which reduced surface water salinities. This in turn affects the development and composition of the phytoplankton community. A change from diatoms to smaller sized cryptophytes has been observed in consecutive years in the 1990s and has been positively correlated to elevated temperature and lower salinity waters (Fig 12+13) [18]. An increase in the frequency and abundance of large salp swarms within the region has been observed and explained by the difference in efficiently filtered food particles by krill and salps. Cryptophytes, which have been measured at sizes of 8 ± 2 µm, allow efficient grazing by salps but exclude krill [16, 18].

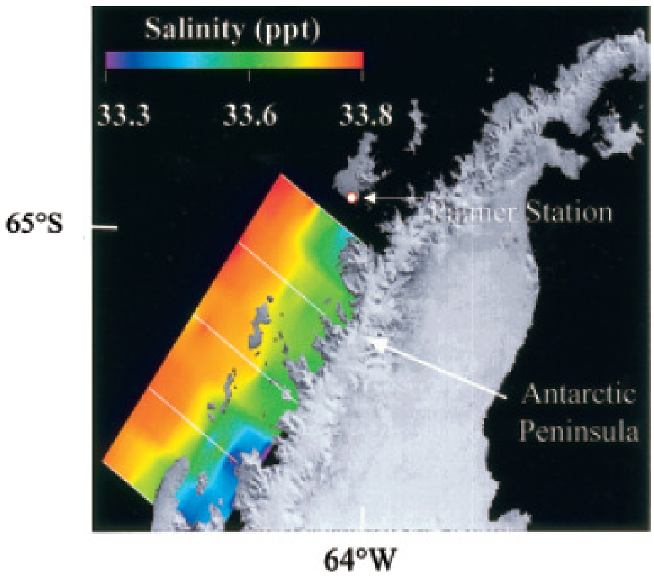


Figure 12. Surface water salinity along the total Antarctic Peninsula (Dec 1991- Jan 1992). Stations were occupied every 20km (white lines) [18].

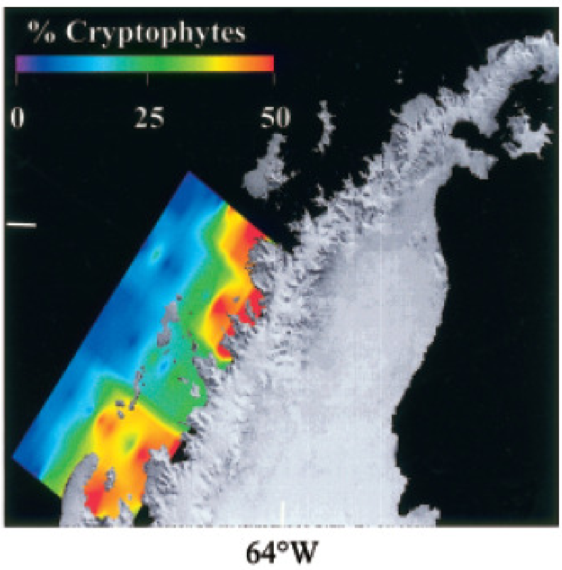


Figure 13. Contribution of cryptophytes to phytoplankton biomass [18].

FUTURE PERSPECTIVES

Predictions of climate change on the ecosystem of the Southern Ocean are difficult to obtain and controversial [22]. Clear trends of climate change include to the western Antarctic Peninsula, which has been identified as one of the world's fastest warming areas [23, 24]. A general warming of the Southern Ocean south of 45°S has also been documented [25] (Fig 14).

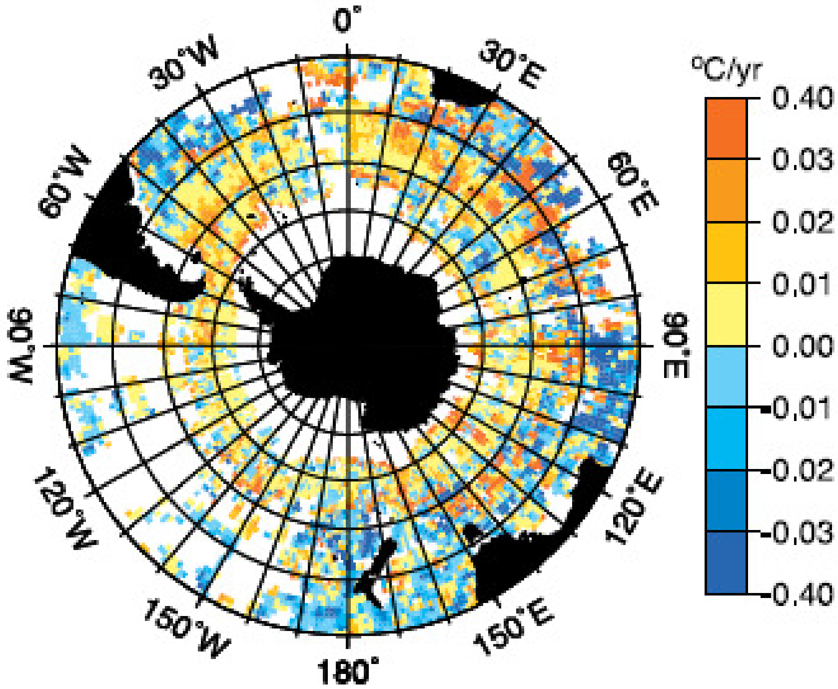


Figure 14. Temperature change in the Southern Ocean in the last 50 years [25].

The effects of warmer water masses on the Antarctic ecosystem in terms of krill and salp abundance/distribution are widely agreed on in the literature. Warmer temperatures will alter sea ice and ice shelf dynamics, which will lead to significant decreases in krill abundance [26, 27]. Salps are assumed to propagate further south where they might dominate the zooplankton and outcompete krill in its typical habitat range. This in turn is supposed to have significant impacts on ecosystem structure and carbon cycling within the food web (e.g. [3, 5, 17]). As discussed above, energy would no longer be successfully transferred from the primary production level to higher trophic level, but sink and be buried into the deep ocean. A decline in krill abundance is also expected to significantly decrease numbers of krill predators, such as several seal, penguin and whale species [3]. As an example, studies on Adélie penguins showed, that in correlation to years with low krill abundance, foraging trips of parents and chick mortality increased [28]. On the contrary, it has recently been suggested that the nutritional value of salps is higher than previously thought and that they might play a more important role in the food chain, but it remains unclear whether salps will be able to meet energetic demands of higher trophic level predators [5, 9, 17].

Probably one of the major questions for future research will be on which level the major ecosystem change is going to occur. Is a change in the phytoplankton community, as observed in the case of diatoms/cryptophytes around the Antarctic Peninsula, the major force defining the future development of the ecosystem, or will the shift be more pronounced on the zooplankton or higher trophic levels, as a result of success/failure in adaptation to a changed system?

Krill has survived for millennia in much warmer and colder conditions than today. Their flexibility in feeding in open waters during summer and use of sea ice algae in winter is often stated as a key to their success (see [4]). In order to predict how resilient their populations are to climate change, long-term data are essential, which are often only available for a few regions of the Southern Ocean [4, 26]. If phytoplankton concentrations remain elevated in high Antarctic waters salps may stay restriction in their southern distribution. It might thus be possible that a spatial segregation between krill and salps might persist allowing a further co-occur of the two species in the Southern Ocean. Specific effects, however, will depend on how fast those changes occur and if and how quickly different species can adapt [29].

GLOSSARY

Biogenic carbon:	atmospheric carbon that is fixed by primary producers
Biotopical separation:	separation of different biotopes
Cryptophytes:	a phytoplankton species
Herbivorous:	feeding on plant material (=phytoplankton)
Indiscriminate:	unable to select particle sizes for feeding
Mucous nets:	feeding device that filters particles out of the water

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