

Antarctic Krill, *Euphausia superba*, a Model Organism to Understand the Impact of Global Warming on the Marine Antarctic Ecosystem*

by Bettina Meyer

Abstract: A tractable approach to understand the effects of climate change on Ecosystems is the focus on “keystone” species whose biology is so pervasive as to dictate ecosystem functioning. A critical aspect in the understanding of the effect of climate change on pelagic systems is the need to progress beyond correlative studies towards a mechanistic understanding. How exactly do changes—oscillations—trends in the environment affect sensitive life cycle stages and thus dictate population size of key species, which in turn have a large impact on the environment? The Polar Regions represent one of the most rapidly warming areas on the globe. Therefore, a model polar organism to study and to understand the effect of climate change on the Southern Ocean ecosystem is Antarctic krill (*Euphausia superba*). This organism plays a key role in the food web of the Southern Ocean both as grazer of a variety of pelagic invertebrates and algae and as prey for a wide range of Antarctic fish, birds and mammals. The progressing climate change might alter krill’s habitat in different ways (e.g. reduced sea ice coverage, changes in food quality and quantity, and a rise in sea water temperature). Long-term studies have already demonstrated that the krill population in the SW Atlantic decreased by about 80 % over the last 30 years and that this decrease is associated with a decline in winter sea ice coverage. It is suggested that the recruitment success of krill is related to seasonal sea ice dynamic but the knowledge of the mechanisms, which link krill population size to environmental variability is lacking. Up to now, the adaptability of krill to their extreme changing environment in short terms due to seasonality (daylight duration, food availability, sea-ice cover) and in long terms due to climate change (increasing sea-water temperature, decline in sea-ice cover, food quantity and quality) is unknown in many cases. However, this knowledge is essential to understand the impact of the progressing global warming trend on the population size of krill and consequently on the Antarctic marine ecosystem.

Zusammenfassung: Ein Ansatz Auswirkungen der Klimaveränderung auf Ökosysteme zu verstehen ist der Fokus auf Schlüsselorganismen, welche die Funktion von Ökosystemen maßgeblich beeinflussen. In diesem Zusammenhang ist es notwendig, sich neben der reinen Beschreibung von Korrelationen zwischen Populationsdichten und spezifischen Umweltparametern, sich mit deren funktionellem Zusammenhang zu beschäftigen. Umweltveränderungen können sensible Stadien im Lebenszyklus eines Schlüsselorganismus beeinflussen, was wiederum Auswirkungen auf deren Populationsgröße und letztendlich auf das Ökosystem hat. Die polaren Gebiete zählen heute zu den sich am schnellsten erwärmenden Regionen der Erde. Dementsprechend stellt der antarktische Krill (*Euphausia superba*) einen Modellorganismus dar, um die Auswirkungen der Klimaveränderung auf das Ökosystem des Südozeans zu untersuchen und zu verstehen. Dieser Organismus nimmt im Nahrungsnetz des Südlichen Ozeans eine Schlüsselstellung ein, da er die Hauptnahrung zahlreicher Fische, Vögel und Säuger darstellt. Die globale Erwärmung verändert den Lebensraum von Krill in vielfältiger Weise (z.B. Reduktion der Meereisbedeckung, Veränderung der Nahrungsquantität und -qualität, Anstieg der Meerwassertemperatur). Langzeituntersuchungen haben bereits gezeigt, dass der Krillbestand im SW-Atlantik um ca. 80 % in den letzten 30 Jahren zurückgegangen ist. Es wird angenommen, dass der Rekrutierungserfolg von Krill im Zusammenhang steht mit der saisonalen Meereisbedeckung. Insgesamt sind die Adaptationsmechanismen von Krill an seine durch extreme saisonale Veränderungen charakterisierte Umwelt (z.B. Futterangebot, Eisbedeckung und Tageslichtdauer) sowie an die, durch die globale Erwärmung verursachten, langzeitlichen Veränderungen kaum verstanden (z.B. Rückgang

der Meereisbedeckung, Veränderung der Nahrungsquantität und -qualität, Anstieg der Meerwassertemperatur). Dieses Wissen ist aber essentiell um den Einfluss der fortlaufenden globalen Erwärmung auf die Populationsdichte von Krill und folglich auf das marine antarktische Ökosystem zu verstehen.

INTRODUCTION

Polar and sub-polar latitudes include the fastest warming regions on the planet, and future models of climate change predict a continued amplification of warming at the poles. Studies of how ecosystems cope with present day changes provide a glimpse of potential future changes that may be even more rapid and widespread. In this perspective polar regions can be considered as a natural laboratory. A tractable approach to this problem is the focus on “keystone” species whose biology is so pervasive as to dictate ecosystem functioning. A critical aspect in the understanding of the effect of climate change on pelagic systems is the need to progress beyond correlative studies towards a mechanistic understanding. How exactly do changes—oscillations—trends in the environment affect sensitive life cycle stages and thus dictate population size of key species? A model polar organism for this type of study is Antarctic krill (*Euphausia superba*, Fig. 1, hereafter krill).

Within its distribution range in the Southern Ocean, Antarctic krill constitutes the largest stock of crustacean biomass in the world’s ocean. The abundance of krill is estimated to be between 100 and 500 million tonnes (SIEGEL 2005). To put this amount into perspective, annually, less than 100 million tonnes of all species of fish and shellfish are currently harvested from the world’s oceans. Consequently, this species plays a central role in the Southern Ocean food web, both as grazer of a huge variety of pelagic invertebrates and algae and as prey for a wide range of Antarctic fish, birds and mammals (Fig. 1). The main spawning and nursery areas of krill are located in the southwest (SW) Atlantic, which contains over 50 % of Southern Ocean’s krill stocks (ATKINSON et al. 2004, Fig. 2). In this region the western Antarctic Peninsula domain is one of the fastest warming marine areas on the planet.

Long-term studies have demonstrated that the krill population in the SW Atlantic decreased by about 80% over the last 30 years (ATKINSON et al. 2004, Fig. 3a) with profound implications for the marine food web. In the western Antarctic Peninsula region, predators of krill such as Adelie penguins have shown corresponding declines in breeding success or population size (DUCKLOW et al. 2007). These long-term data have also shown that the population size of krill can vary greatly

* Extended contribution presented at the conference “The Changing Earth” in Berlin, 02 November 2009.

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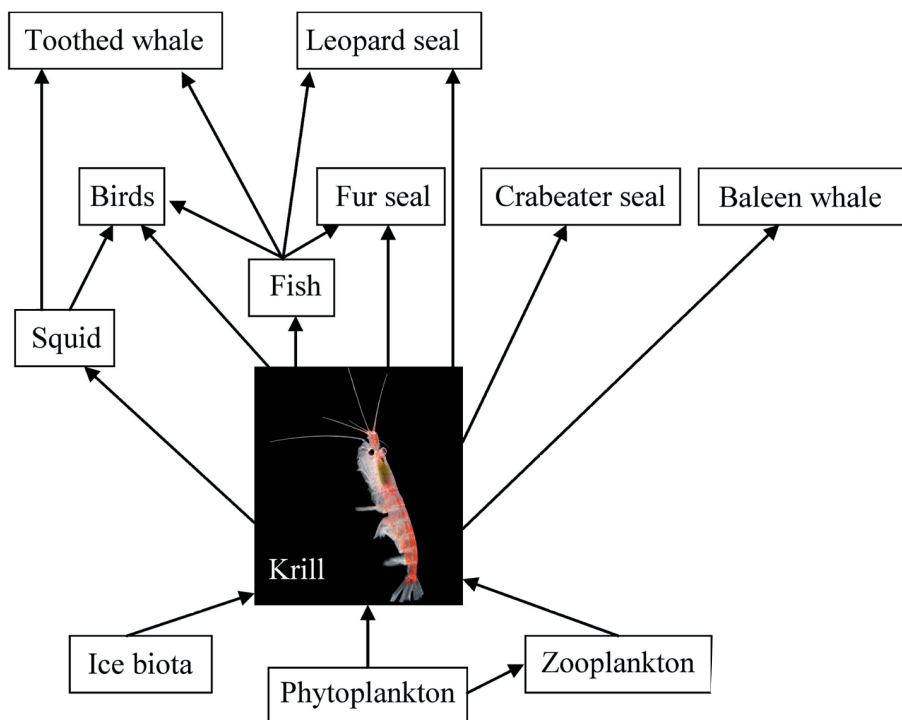


Fig. 1: Adult Antarctic krill, *Euphausia superba* and its central position in the marine food web in the Southern Ocean (after EVERSON 2000, photo: C. Pape).

Abb. 1: Adler Krill, *Euphausia superba* und seine zentrale Position im marinen Nahrungsnetz im Südlichen Ozean (nach EVERSON 2000, Foto: C. Pape).

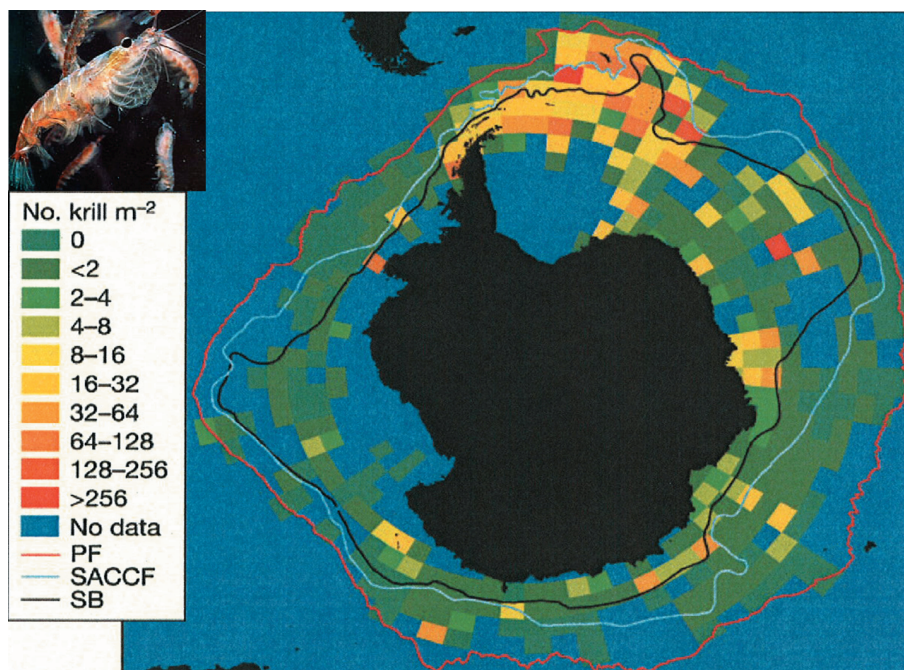


Fig. 2: Mean density and distribution of *Euphausia superba* in the Southern Ocean (6,675 stations; 1926-2003; number of krill = Log 10 m²; mean position of Polarfront = PF; front of Southern Antarctic Circumpolar Current = SACCF, Southern Boundary of Antarctic Circumpolar Current = SB; mean northern 15 % sea-ice concentrations in February and September 1979 to 2004 (from ATKINSON et al. (2004).

Abb. 2: Mittlere Individuendichte und -verteilung von *Euphausia superba* im Südlichen Ozean (6675 Stationen, 1926-2003, Anzahl Krill = Log 10 m², mittlere Positionen: Polarfront = PF, südliche Grenze des antarktischen Zirkumpolarstroms = SACCF, mittlere nördliche 15-prozentige Meereisbedeckung in Februar und September von 1979-2004 (aus ATKINSON et al. 2004).

from year to year (Fig. 3a) and that these oscillations are driven by recruitment, rather than by predation pressure on adult krill. In addition, it is suggested that recruitment success is related to seasonal sea-ice dynamics (SIEGEL & LOEB 1995, ATKINSON et al. 2004, Fig. 3b). Knowledge of the mechanisms, however, which link krill population size to environmental variability is lacking. Despite 80 years of krill research, the mechanistic understanding how krill respond to environmental changes is unclear in many cases. This weakness can be explained by looking into the history of krill research.

THE HISTORY OF KRILL RESEARCH

In the beginning of the 1970s a significant commercial krill fishery started, and ever since this has been the largest in the Southern Ocean in terms of tonnage caught. Until the early 1990s krill research was mainly driven by commercial interest. Therefore, the main research focus was to study krill distribution, abundance and stock assessment and not krill's interactions with their environment. The late 1980s marked a step-change in our understanding of krill because it was demonstrated for the first time that the seasonal pack ice plays an integral part in the life of krill (MARSHALL 1988, DALY & MACAULEY 1991). However, the mechanisms by which krill

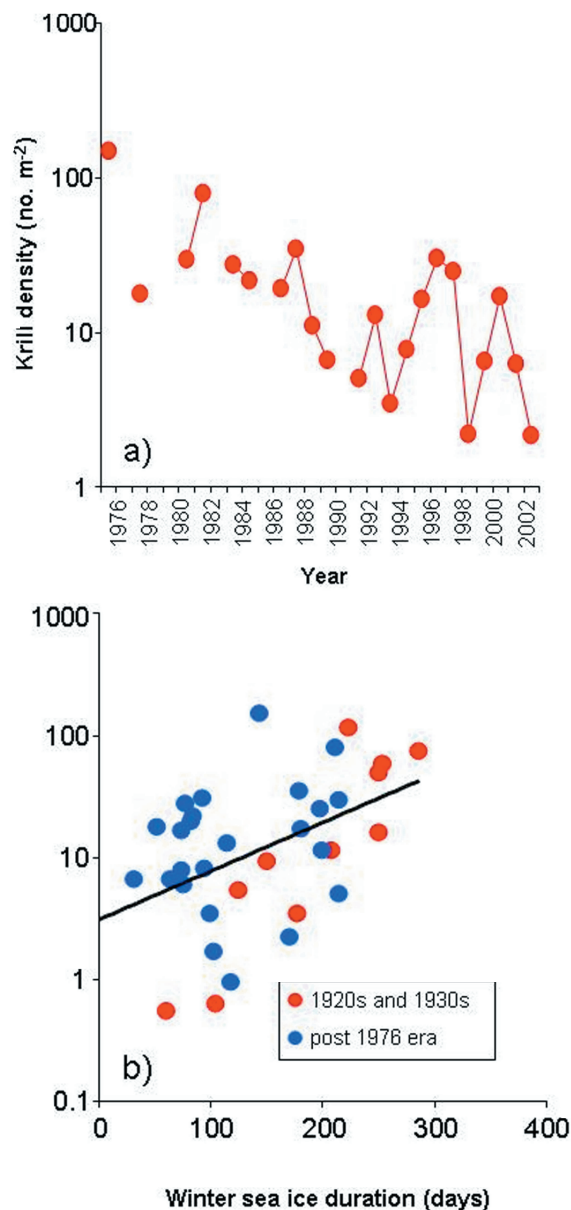


Fig. 3: Temporal change of *Euphausia superba* density in the southwest Atlantic (a); annual mean density of krill across the SW Atlantic versus sea-ice duration (b). $\log_{10} = \text{number of krill m}^{-2} = 0.49 + 0.0040 (\text{sea-ice duration, days})$ $r^2 = 21$, $p = 0.006$, $n = 35$ (from ATKINSON et al. 2004).

Abb. 3: Zeitliche Veränderung der Individuendichte von *Euphausia superba* im südwestlichen Atlantik (a). Die im Mittel jährliche Individuendichte von Krill im südwestlichen Atlantik in Abhängigkeit von der Dauer der Meereisbedeckung in Tagen (b).

rely on ice in general and their larval stages in particular have remained unanswered. An overview of major krill programmes from 1980-1990 is given in Table 1. After the international BIOMAS program, the research on krill distribution, abundance and stock assessment continued on a national level with the German and US AMLR programme (Antarctic Marine Living Resources), the US Palmer LTER programme (Long-term ecological research at Palmer station) in the Atlantic sector and the Australian BROKE studies (Biological/ oceanographic survey off the coast of east Antarctica) in the Indian sector as well as the monitoring studies within the scope of the CCAMLR convention (Commission for the Conservation of Antarctic Marine Living Resources). The main driving factor

Programmes and time span	Topics addressed
BIOMASS Biological Investigation of Marine Antarctic Systems and Stocks 1980s – early 1990s	<i>Large scale studies</i> Distribution, abundance, stock assessment and developmental ascent theory
AMERIEZ Antarctic Marine Ecosystem Research at the Ice-Edge Zone, 1983 – 1988	<i>Process-oriented studies:</i> The integral part of seasonal pack ice in the life history of krill
EPOS European Polarstern Study 1988 – 1989	Distribution of krill and its developmental stages in relation to sea-ice

Tab. 1: Summary of major krill programmes from 1980-1990.

Tab. 1: Zusammenstellung der größeren Krill-Forschungsprogramme von 1980-1990.

is an expected increase in the demand of krill products, particularly for aquaculture feeds but also for other uses including omega-3 fatty acid diet supplements (NICOL & FOSTER 2003). The use of krill for aquaculture feed, especially salmon farming, seems to be the most important market development that is triggering investments in krill harvesting. The scientific interest on krill was not mainly driven by commercial interest but rather due to the observations that global warming seems to have an impact on krill recruitment, which was first raised by SIEGEL & LOEB (1995). In 1999, the Southern Ocean Global Ecosystem Dynamic program was initiated (SO-GLOBEC, 1999-2009). This programme investigated the physical and biological factors that promote krill growth, reproduction, recruitment, and survival throughout the year through field studies in only a few regions of the Southern Ocean (western Antarctic Peninsula, Bellingshausen Sea, Scotia Sea, Lazarev Sea, and East Antarctic).

Recent knowledge of krill from the SO-GLOBEC programme

The results on the impact of global warming on the density of Antarctic krill, mentioned above, suggest that the overwintering success especially of the larval stages (the new recruits), is a critical factor in determining recruitment success in the following years, and hence population size of krill in the Southern Ocean (SIEGEL 2005). Even after the recent SO-GLOBEC initiative, this is a poorly understood part of krill's life cycle. Recent findings have demonstrated that the various maturity stages of krill (larvae, juveniles, one year old and adults) have different dependencies on ice biota, with seemingly decreased reliance with increasing age (DALY 2004, MEYER 2009, MEYER et al. 2009, MEYER et al. 2010). Results on adult krill have shown that specific physiological adaptations during autumn and winter, such as reduced metabolic rates and feeding activity, are not caused simply by the scarcity of food, as was previously assumed. They represent an inherent adaptational strategy that appears to be influenced by the local light regime (TESCHKE et al. 2007, 2008. MEYER et al.

2010). The seasonal lipid dynamics in adult krill consist of a clear annual pattern of accumulation of lipids during summer until the onset of winter and their utilisation during winter. It is most likely that this pattern is also an inherent strategy of krill that has evolved in anticipation of the succession of seasons (MEYER et al. 2010). Due to these inherent physiological adaptations, the sea-ice biota seems to play as feeding ground only a minor role for adults during winter. However, with the onset of spring, when metabolic rates increase again due to a photo-periodic cue (a specific day-light duration) and lipid levels are low due to winter depletion, the sea-ice biota appears to become an important feeding ground for adult krill to accumulate lipids and to develop gametes to undergo a successful spawning (SIEGEL 2005, MEYER et al. 2010).

On the other hand, the physiological functions of larval krill adopted during winter (reduced metabolism, delayed development, lipid utilization) are, in contrast to adults, the result of a behaviour under stronger direct control from the available food supply (MEYER et al. 2009). Autotrophic food plays an important role during summer and autumn, whereas heterotrophic food becomes increasingly important during winter (MEYER et al. 2009). Larvae have to feed to meet their energetic needs since their lipid levels are too low to sustain long starvation periods (QUETIN & ROSS, 1991, DALY 2004, MEYER et al. 2002, 2009, MEYER & OETTLE 2005). Therefore, sea ice with the associated sea-ice biota plays an essential role for larval krill during winter.

In krill's life cycle, recruitment success has been suggested to depend on a series of critical stages (QUETIN et al. 2003). In the first year of krill's life, the larvae have to successfully pass four potentially critical stages to ensure a good reproductive output in the forthcoming spring ("Critical stage concept", Fig. 4). The first feeding stage of krill (*Calyptopsis* I), which reaches the surface after the developmental ascent, has to find food within the first ten days to enable further development (ROSS & QUETIN 1989). The next critical situation is the food

availability during summer. Favourable feeding conditions enable the larvae to develop to an advanced stage with sufficient lipid reserves until the onset of winter. It is therefore most likely that young larvae stages from late spawning krill, will not survive the winter season, due to the lack of lipid reserves (PAKHOMOV et al. 2004, MEYER et al. 2009). The last important step for a large recruitment output in the following spring is a successful development of the larvae to juveniles. Over-wintering studies of larval krill in different regions of the Southern Ocean have demonstrated that, in late autumn, ice-related larvae are in much better condition than those from open water areas (ROSS & QUETIN 2004, DALY 2004, MEYER et al. 2009). It is not clear, however, which under-ice habitat is in favour of successful larval development and consequently recruitment success during winter. The timing (SIEGEL 2005) and latitudinal range of ice formation (QUETIN et al. 2007) as well as the under ice topography (MEYER et al. 2009) seem to be determining factors for successful development and survival.

RESPONSES OF KRILL TO CLIMATE CHANGE

The general question in the debate on the ecological effects of climate change is whether species will be able to adapt fast enough to keep up with their changing environment. According to VISSER (2008) three types of responses to climate change have been described:

- 1) Dispersal to suitable habitats elsewhere.
- 2) Changes in the phenotype (i.e. morphology, development, biochemical or physiological properties, or behaviour).
- 3) Genetic change, i.e. microevolution.

The ongoing ecosystem changes in response to climate change are largely driven by environmental temperature (PÖRTNER & FARRELL 2008). Up to now, laboratory work of physiologists has mostly focused on thermal adaptation and limitation at genetic, molecular and stress levels but has largely neglected

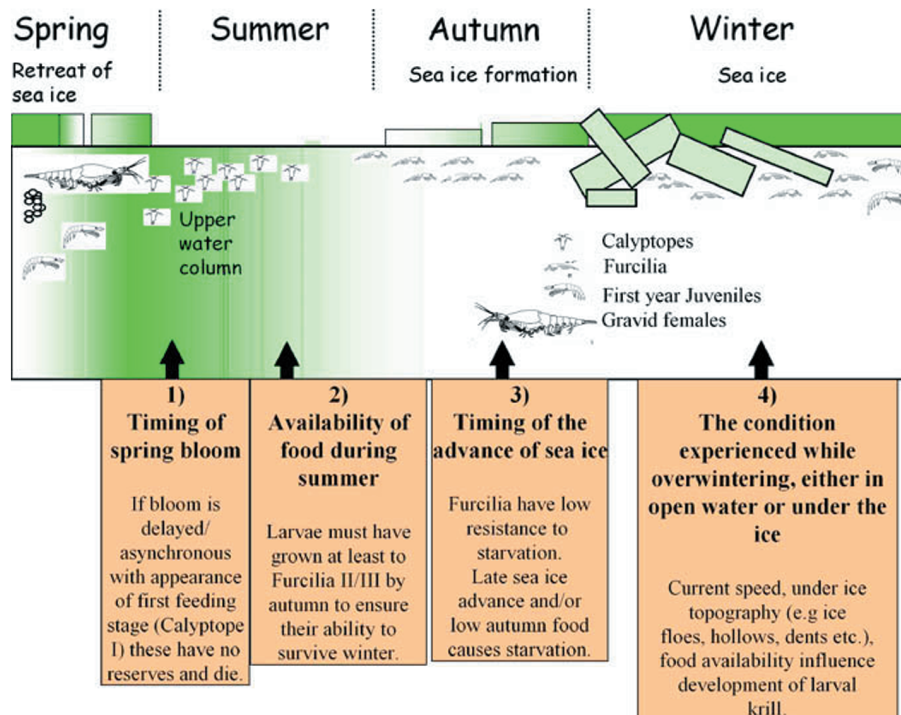


Fig. 4: Scheme of potentially critical stages in the early life cycle of *Euphausia superba*. Green shading represents food concentration in sea-ice and upper water column.

Abb. 4: Schema der potentiell kritischen Larvenstadien im frühen Lebenszyklus von *Euphausia superba*. Die grüne Schattierung beschreibt die relative Futterkonzentration im Meereis und der obersten Wassersäule.

organism performance (DRINKWATER et al. 2010). Furthermore, most studies focus mainly on adult specimens but to understand the sensitivity of a species to climate change, it is important to take the entire life cycle into account when predicting future shifts such as in phenology – the timing of seasonal activities like spawning, migration etc. – (VISSER & BOTH 2005). A problem for organisms posed by climate change is that some species of the food chain and even ontogenetic stages of a species use temperature unrelated cues such as photoperiod (the duration of day length) to time their annual cycle.

How sensitive krill might be to climate change scenarios is so far unknown in many cases. On the one hand krill seems to be sensitive to change because the larval stages have only low starvation tolerance (ROSS & QUETIN 1991, MEYER & OETTL 2005) and adult krill have a narrow temperature range for optimal growth because they showed a rapid decline at seawater temperature of only 3–4 °C (ATKINSON et al. 2006). On the other hand, however, krill are very flexible in their behaviour and adaptation to environment variability. For example, the larval stages cannot sustain a long starvation period but they are surprisingly adaptable when food is scarce. During winter, when phytoplankton in the water column is rare, they have the ability to either shrink and/or to have an indirect development or they switch to feeding on copepods (MEYER et al. 2009). This flexibility was once thought to be characteristic only of the adults. In adult krill, *E. superba* schools have been observed swimming horizontally for over 100 miles at a ground speed of 20 cm s⁻¹, even against the prevailing current (KANDA et al. 1982). Furthermore, they make offshore spawning migrations (SIEGEL 1988) and migrate vertically to exploit alternative food sources, either in spring sea-ice (O'BRIEN 1987) or even at the abyssal sea floor (CLARKE & TYLER 2008).

The progressing climate change might alter krill's habitat in different ways (e.g. reduced sea-ice coverage, changes in food quality and quantity, and a rise in sea-water temperature). Studying the adaptation of organisms such as krill to a changing environment needs to consider the functional integration of single molecules into higher organisational levels up to the whole organism and its evolutionary genetic history. Therefore, from an ecophysiological point of view, the following questions are of interest:

a) On an organismic level.

- How might changes in food quality and quantity affect the nutrition of mature females (egg production, hatching success) and secondary production in general (nutritional status of larvae, larval development, and survival)?
- What sea ice conditions, in terms of biotic and abiotic factors, favour larval development and survival during winter? The “critical stage concept” (outlined above), while intuitively appealing, has never been tested, and a detailed larval life-cycle model has not yet been constructed. Such a stage structured life-cycle model of the first year of krill's life will help to explain how recruitment success (and thus population size) of krill is controlled and how it will be influenced under different scenarios of climate change. A reduced ice cover could have a particularly large affect on krill's food-sensitive larval stages and, in turn, affecting recruitment and population size. Understanding the recruitment process will be important for a

sustainable management of an expanding krill fishery and its influence on krill's predators.

b) On a molecular level.

- How sensitive is krill to global warming, due to its (a) evolutionary genetic history and (b) molecular response mechanisms to environmental variability?

Population genetic markers estimate historical changes in the population demography of krill, which in turn shows how krill has responded to climate variability in the past.

Transcriptomic studies enable to identify molecular response mechanisms to environmental changes within the ontogeny of krill. The genome-wide screening of substitutions and regulatory sequences will uncover structural patterns of molecular thermal adaptations. Together with high throughput expression analyses genes and clusters contributing to thermal plasticity and adaptation, respectively, can be identified. The results from both, the studies on the evolutionary history of krill and their actual molecular response mechanisms to global warming will give us information how this species came to the way they are and how they might change in the future.

In general, to understanding krill's sensitivity to different climate change scenarios we have to consider the resulting response mechanism of krill to the questions outlined above in combination with their seasonal behaviour (vertical distribution), body condition (energy content, metabolism, feeding, growth) and the biotic and abiotic environment to identify critical life cycle phases, which are vulnerable to climate change.

References

- Atkinson, A., Meyer, B., Stübing, D., Hagen, W. & Bathmann, U.V. (2002): Feeding and energy budgets of Antarctic krill *Euphausia superba* at the onset of winter – II. Juveniles and adults.- *Limnol. Oceanogr.* 47: 953–966.
- Atkinson, A., Siegel, V., Pakhomov, E.A. & Rothery, P. (2004): Long-term decline in krill stock and increase in salps within the Southern Ocean.- *Nature* 432: 100–103.
- Atkinson, A., Shreeve, R.S., Hirst, A.G., Rothery, P., Tarling, G.A., Pond, D.W., Korb, R.E., Murphy, E.J. & Watkins, J.L. (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.
- Clarke, A. & Tyler, P.A. (2008): Adult Antarctic krill feeding at abyssal depth.- *Curr. Biol.* 18: 282–285.
- Daly, K.L. (2004): Overwintering growth and development of larval *Euphausia superba* an interannual comparison under varying environmental conditions west of the Antarctic Peninsula.- *Deep Sea Res. II.* 51: 2139–2168.
- Daly, K.L. & Macaulay, M.C. (1991): Influence of physical and biological mesoscale dynamics on the seasonal distribution and behaviour of *Euphausia superba* in the Antarctic marginal ice zone.- *Mar. Ecol. Prog. Ser.* 79: 37–66.
- Drinkwater, K.F., Beaugrand, G., Kaeriyama, M., Kim, S., Ottersen, G., Perry, R.I., Pörtner, H.-O., Polovina, J.J. & Takasuka, A. (2010): On the processes linking climate to ecosystem changes. *J. Mar. Sys.* 79: 374–388.
- Ducklow, H.W., Baker, K., Martinson, D.G., Langdon, B.Q., Ross, R.M. Smith, R.S., Stammerjohn, S.E., Vernet, M. & Fraser, W. (2007): Marine pelagic ecosystems: the West Antarctic Peninsula.- *Phil. Trans. Royal Soc. B* 362: 67–94.
- Everson, I. (2000): Introducing Krill.- In: I. Everson (ed), *Krill Biology, Ecology and Fisheries*, Blackwell Cambridge, 150–181.
- Kanda, K., Takagi, K. & Seki, Y. (1982): Movement of the larger swarms of Antarctic krill *Euphausia superba* off Enderby Land during 1976–1977.- *J. Tokyo. Univ. Fish.* 68: 25–42.
- Marschall, H.P. (1988): The overwintering strategy of Antarctic krill under pack-ice of the Weddell Sea.- *Polar Biol.* 9: 245–250.

- Meyer, B. (2009): Ecophysiological studies of overwintering krill.- In: G. HEMPEL & I. HEMPEL (eds), Biological studies in Polar Oceans, Wirtschftsverlag NW, 111-114.
- Meyer, B., Atkinson, A., Stübing, D., Oettl, B., Hagen, W. & Bathmann, U.V. (2002): Feeding and energy budgets of Antarctic krill *Euphausia superba* at the onset of winter - I. Furcilia III larvae.- Limnol. Oceanogr. 47: 943-952.
- Meyer, B. & Oettl, B. (2005): Effects of short-term starvation on composition and metabolism of larval Antarctic krill, *Euphausia superba*.- Mar. Ecol. Prog. Ser. 292: 263-270.
- Meyer, B., Fuentes, V., Guerra, C., Schmidt, K., Atkinson, A., Spahic, S., Cisevski, B., Freier, U., Olariaga, A. & Bathmann, U.V. (2009): Physiology, growth and development of larval krill *Euphausia superba* in autumn and winter in the Lazarev Sea, Antarctica.- Limnol. Oceanogr. 54: 1595-1614.
- Meyer, B., Auerswald, L., Siegel, V., Spahic, S., Pape, C., Fach, B.A., Teschke, M., Lopata, A. & Fuentes, V. (2010): Seasonal variation in body composition, metabolic activity, feeding, and growth of adult krill *Euphausia superba* in the Lazarev Sea.- Mar. Ecol. Prog. Ser. 398: 1-18.
- Nicol, S. & Foster, J. (2003): Recent trends in the fishery of Antarctic krill.- Aquat. Living Res. 16: 42-45.
- O'Brien (1987): Direct observations of the behaviour of *Euphausia superba* and *Euphausia crystallorophias* (Crustacea: Euphausiacea) under pack ice during the Antarctic spring of 1985.- J. Crust. Biol. 7: 437-448.
- Pörtner, H.-O. & Farrell, A.P. (2008): Physiology and climate change.- Science 322: 690-692.
- Quetin, L.B. & Ross, R.M. (1991): Behavioural and physiological characteristics of the Antarctic krill, *Euphausia superba*.- Amer. Zool. 31: 49-63.
- Quetin, L.B., Ross, R.M., Frazer, T.K., Amsler, M.O., Wyatt-Evens, C. & Oakes, S.A. (2003): Growth of larval krill, *Euphausia superba*, in fall and winter west of the Antarctic Peninsula.- Mar. Biol. 143: 833-843.
- Quetin, L.B., Ross, R.M., Fritsen, C.H. & Vernet, M. (2007): Ecological responses of Antarctic krill to environmental variability: can we predict the future?.- Ant. Science 19: 253-266.
- Ross, R.M. & Quetin, L.B. (1991): Ecological physiology of larval euphausiids, *Euphausia superba* (Euphausiacea).- Mem. Queensl. Mus. 31: 321-333.
- Siegel, V. (1988): A concept of seasonal variation of krill (*Euphausia superba*) distribution and abundance west of the Antarctic Peninsula.- In: D. SAHRHAGE (ed), Antarctic Ocean and Resources variability, Springer-Verlag, Berlin, Heidelberg, 219-229.
- Siegel, V. (2005): Distribution and population dynamics of *Euphausia superba*: summary of recent findings.- Polar. Biol. 29: 1-22.
- Siegel, V. & Loeb, V. (1995): Recruitment of Antarctic krill *Euphausia superba* and possible causes for its variability.- Mar. Ecol. Prog. Ser. 123: 45-56.
- Teschke, M., Kawaguchi, S. & Meyer, B. (2007): Simulated light regimes affect feeding and metabolism of Antarctic krill, *Euphausia superba*.- Limnol. Oceanogr. 52: 1046-1054.
- Teschke, M., Kawaguchi, S. & Meyer, B. (2008) Effects of simulated light regimes on maturity and body composition of Antarctic krill, *Euphausia superba*.- Mar. Biol. 154: 315-324.
- Visser, M.E. (2008): Keeping up with a warming world; assessing the rate of adaptation to climate change.- Proc. Royal Soc. B. 275: 649-659.
- Visser, M.E. & Both, C. (2005): Shifts in phenology due to global climate change: the need for a yardstick.- Proc. Royal Soc. B. 272: 2561-2569.