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Chapter 4

Physiology of *Euphausia superba*

Bettina Meyer and Mathias Teschke

Abstract Since the 1920s, *E. superba* is one of the best studied species in the Southern Ocean in terms of their general biology. The main driver for this research focus has been the fisheries' requirements for stock forecasting and conservation measures. Nowadays this is joined by concerns over climate change effects and the requirement to take a more holistic view to understand food web structures. So far, however, we do not have a clear understanding of the physiological response of krill and hence their adaptability to cope with ongoing environmental changes, caused by the anthropogenic carbon emissions. This is due to the extreme lack of intense studies on krill physiology, especially of their larval stages in relation to their seasonal environment. A major aim of this book chapter is on the one hand to summarize how physiological functions such as lipid accumulation and utilisation, metabolic activity and growth change with ontogeny and season and to demonstrate which environmental factors are the main drivers for seasonal variability of these functions in adult and larval krill. On the other hand, we draw the attention to the importance of photoperiod (day length) as an entrainment cue for endogenous rhythms and clocks in the life cycle of krill. Furthermore, we give an overview of the current knowledge on the impact of elevated seawater temperature and ocean acidification on krill.

Keywords Krill physiology • Larval krill physiology • Krill growth • Photoperiod

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4.1 General

E. superba is one of the best studied Antarctic species in terms of general biology and ecology, with emphasis on growth, biochemical composition, reproduction and on their distribution and abundance in the Southern Ocean. The main drivers for these research foci have been the fisheries' requirements for stock forecasting and conservation measures. Nowadays, this is joined by concerns over climate change effects and the requirement to take a more holistic view to understand food web structures (Quein and Ross 1991; Teschke et al. 2008; Meyer 2012). While there is considerable scientific knowledge about krill's biology and ecology, relative little is known how physiological functions are mediated in the different ontogenetic stages in krill.

Physiology aims to understand the mechanisms how organisms are functioning at different organismic levels (genes, cells, the whole organism) and how they adapt to vastly different environmental condition.

Table 4.1 summarises physiological studies that reviewed previous and recent findings and mirrored the emphasis that physiological studies had at this time. In the 1980s, the focus was to calculate an energy budget of adult krill in summer (Clarke and Morris 1983; Miller and Hampton 1989), whereas in the 1990s the winter period was identified as important part in krill's annual cycle to understand its recruitment success as well as the relation of adult and larval krill with the winter sea ice (Quein and Ross 1991; Ross and Quein 1991; Quein et al. 1994). Two studies, focusing on long term abundance data of adult krill in relation to environmental parameters, strongly influenced the scientific view of the sensitivity of krill to climate induced environmental changes and influenced the further directions in physiological krill research. Siegel and Loeb (1995) and Loeb et al. (1997) demonstrated first that the recruitment success and, hence population size of krill, are

Table 4.1 Overview of physiological papers that summarised recent findings at the time they were published

Researcher	Topic addressed
Clarke and Morris (1983)	Adult krill in summer: oxygen consumption, excretion and filtration rates, growth, moulting and reproduction
Miller and Hampton (1989)	Adult krill in summer: metabolic activity at different temperatures, excretion, filtration and feeding, growth, moulting, reproduction, biochemistry of egg production
Quein and Ross (1991)	Adult krill: foraging and gathering ability, overwintering mechanisms
Ross and Quein (1991)	Larval krill: starvation tolerance, growth, lipid content and shrinkage in winter
Quein et al. (1994)	Adult krill: filtration and digestion, reproduction, seasonal growth, respiration, and lipid content, role of sea ice in krill energetics
Meyer (2012)	Adult and larval krill: seasonality of metabolic and feeding activity, biochemical composition, and growth, overwintering strategies, the importance of sea ice

linked to extent and duration of winter sea ice cover, with low ice years related to poor recruitment. The investigations of Atkinson et al. (2004) showed a krill decline of almost 80% since the mid 1970s in the SW Atlantic sector in concert with a decline in winter sea ice extent and duration (see also Chap. 2, Siegel and Watkins 2016). Both studies made us aware that sea ice seems to be important for the recruitment success of krill but the mechanistic relationship between a successful larval krill development to 1 year juveniles during winter and the winter sea ice coverage is still lacking. Therefore, it is essential to go beyond correlative studies towards a mechanistic understanding of the linkage of all life stages of krill with their environment.

Today, krill physiology aims to understand the performance of all ontogenetic stages of krill to environmental stressors caused by anthropogenic warming. In this respect it is important to investigate the seasonality of important physiological life cycle functions such as body lipid dynamic, metabolic activity, and growth in adults and larvae from different regions in the Southern Ocean in relation to environmental variables such as food availability, photoperiod (day length) and winter sea ice coverage (Meyer 2011). Krill live in a highly seasonal environment in terms of sea ice cover, food availability, and photoperiod (day length) and their annual life cycle has been synchronized to this seasonality over millions of years. However, to understand the adaptability of krill to the ongoing environmental changes caused by the global warming and to make reliable predictions as to how the population might change in the future, we have to understand the cues that are related (e.g. food quantity and quality, timing of phytoplankton spring bloom) and unrelated (photoperiod) to climate induced environmental changes and their impact on krill's annual cycle. Due to logistical constraints to obtain sufficient ship time and to keep krill in captivity for long periods over month or even over 1 year, seasonal investigations on physiological function of all ontogenetic stages of krill are rare. Table 4.2 gives an overview of seasonal investigations on larval and adult krill and illustrates why our knowledge is still limited to understand the principle mechanisms behind important life cycle functions of krill.

In the present chapter, we summarise the current knowledge on seasonal metabolic activity, feeding and growth of larval and adult krill with emphasis on the winter period and larval krill. The impact of global warming on the density of Antarctic krill suggests that the overwintering success especially of the larval stages (the new recruits) is regarded as the major single factor that dictates recruitment success, and hence population size of krill in the Southern Ocean (Siegel and Loeb 1995; Loeb et al. 1997; Atkinson et al. 2004). However, the potential overwintering mechanisms of krill, especially of their larval stages, are still poorly researched (Meyer 2011). In addition, we draw the attention on the impact of rising seawater temperature and ocean acidification on physiological functions and Krill's ontogeny, respectively and to the important role of endogenous rhythms and clocks in the function of important life cycle functions of krill.

As outlined above, the understanding of how krill survive the winter season in general and of their interaction with the sea ice in particular, is crucial to predict the impact of climatic warming on krill. It has been demonstrated that adult krill

Table 4.2 Summary of seasonal investigations of physiological functions and/or biochemical composition of larval and adult krill

Parameter analysed	Region	Season	References
Adult krill			
	Bransfield Strait, north of South Shetland Islands	Feb–Apr 1984, 1985, Aug–Sept 1985	Quetin and Ross (1991)
Growth, feeding activity (gut fluorescence, faecal pellet production), lipid content, metabolic activity	Northern Antarctic Peninsula, Eastern and Western Weddell Sea, Lazarev Sea	Oct, Nov 1983, Jan, Feb, 1985, July, Aug 1986, Oct, Nov 1986, Apr, May 1992	Hagen et al. (2001)
Metabolic and feeding activity, elemental and biochemical composition, growth	Lazarev Sea	Mar–May 2004, Nov–Jan 2005/2006, June–Aug 2006	Meyer et al. (2010)
Feeding activity	Scotia Sea, Bransfield Strait	Jan, Feb 2002, 2003, 2005, 2006, Mar 2004, Apr 2007, June–Aug 2004, July–Aug 2005, 2006, Nov 2006	Schmidt et al. (2012)
Feeding activity	Lazarev Sea, Bransfield Strait, Scotia Sea, South Georgia	Jan–Feb 2002, 2003, 2005, 2006, Mar 2004, Apr 2004, July 2005, June–Aug 2006, Nov 2006, Dec 2005	Schmidt et al. (2014)
Larval krill			
Morphometrics, growth	Bransfield Strait, Marguerite Bay	June, July 1987, July 1989, May, Sept 1991, Apr–Sep 1993, June, July 1994, June 1999	Quetin et al. (2003)
Morphometrics, elemental composition, feeding activity, growth	Marguerite Bay	Apr–June 2001, July, Aug 2002	Daly (2004)
Metabolic and feeding activity, elemental and biochemical composition, growth	Lazarev Sea	Mar–May 204, June–Aug 2006	Meyer et al. (2009)

Modified according to Meyer (2011)

employ a suite of overwintering mechanisms, which provide considerable flexibility in their response to winter conditions. Proposed mechanisms of adult krill fall into two major categories: (a) Non-feeding strategies and (b) Utilisation of food sources other than phytoplankton in the water column. The first category consists of the reduction in metabolic rates (Kawaguchi et al. 1986; Quetin and Ross 1991; Torres et al. 1994a), the utilisation of body lipids (Quetin and Ross 1991; Hagen et al. 2001), and shrinkage in size (Ikeda and Dixon 1982; Quetin and Ross 1991). Alternative food sources might be zooplankton (Huntley et al. 1994) and seabed detritus in shallow regions (Kawaguchi et al. 1986). The utilisation of ice algae by

krill during winter was discussed (e.g. Hammer et al. 1983; Marshall 1988; Spiridonov 1992).

Larval krill appear during summer, develop during Antarctic winter and recruit to the postlarval population during the following spring. Recruitment success depends both that potential recruits enter winter in an advanced stage (reflecting reproductive output and growth and survivorship of larvae during summer and autumn) and on larval growth and survival during their first winter (Quetin and Ross 1991; Siegel 2005). However, up to recently, most studies on larval krill have focused on their distribution and abundance (Hempel 1981; Hempel and Hempel 1978, 1982; Makarov and Soyoyeva 1985; Hubold and Hempel 1987; Daly and Macaulay 1988, 1991; Makarov and Maslennikov 1992; Menshenina 1992; Siegel et al. 1992; Melnikov and Spiridonov 1996; Frazer et al. 1997; Siegel 2005, see also Chap. 2, Siegel and Watkins 2016). Until the end of the 1990s, we had only anecdotal information on larval krill physiology and development through winter. At this time, it was not clear if larval krill have adapted similar overwintering mechanism as the adults, although it was presumed that dependence on ice becomes progressively less with ontogeny (Quetin et al. 1996). The review of Meyer (2011) on the overwintering of krill demonstrates to what extent seasonal variation in larval and adult krill physiology is mediated by those environmental factors that show a strong seasonality in the Southern Ocean, such as food supply or day length, and which physiological functions are adopted by adults and larvae to survive the winter season.

4.2 Seasonal Physiological Functions in Adults and Larvae and the Critical Winter Period

4.2.1 Metabolic Activity

Adult krill show a clear seasonal pattern in their metabolic activity (Fig. 4.1), with highest values in late spring and summer. In autumn and winter oxygen consumption rates were 50% and 30% of summer rates, respectively (Meyer et al. 2010). The activities of the enzymes citrate synthase (CS) and malate dehydrogenase (MDH), proxies for metabolic activity, mirror the pattern of the oxygen uptake rates shown in Fig. 4.1 (Meyer et al. 2010). In autumn and winter, respectively, the CS and MDH activities in krill were 47% and 39% (CS), and 77 and 66% (MDH) of those in summer (Meyer et al. 2010).

In contrast to the adult stage, larvae from different regions showed no significant differences in metabolic activity between summer and autumn, ranging from 0.7 to 1.4 $\mu\text{l O}_2 \text{ mg DW h}^{-1}$ (Ikeda 1981; Meyer et al. 2002a, b, 2003, 2009), whereas in winter the respiration rates were only half of those in summer (Daly and Macaulay 1991; Daly 2004; Frazer et al. 2002a; Meyer et al. 2009), with $0.95 \pm 0.28 \text{ mL O}_2 \text{ mg}^{-1} \text{ DW h}^{-1}$ and $0.54 \pm 0.19 \text{ mL O}_2 \text{ mg}^{-1} \text{ DW h}^{-1}$ in autumn and winter,

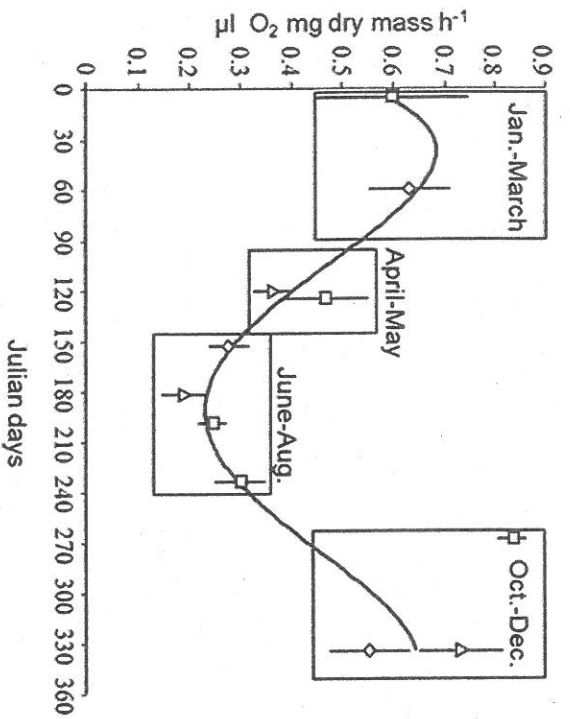


Fig. 4.1 From Meyer 2011: seasonal respiration rates of adult krill from different study sites. Δ Lazarev Sea (Meyer et al. 2010), \diamond Southern Scotia-Northern Weddell Sea (Torres et al. (1994b)), \square Lütz-Holm Bay (Kawaguchi et al. 1986)

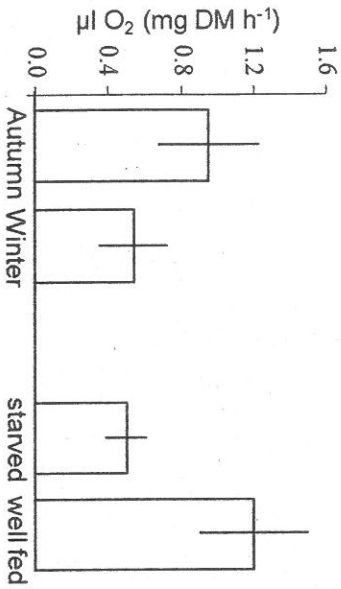


Fig. 4.2 Mean oxygen uptake rates of freshly caught furcilia larvae in autumn (1999, 2000) and winter (2006) in the Lazarev Sea and after 1 week starvation or exposure to high food concentrations

respectively. However, shipboard experiments demonstrate that the oxygen uptake rates of winter larvae are comparable with rates of starved furcilia (Meyer et al. 2002a; Frazer et al. 2002a) and winter larvae from open water areas in pack ice regions (Fig. 4.2), which is supposed to be an unfavourable feeding ground for krill larvae in winter (Quein et al. 2003).

Based on the correlation between the size and consequently age of krill and their corresponding individual oxygen uptake rates (Fig. 4.3), it appears that the clear

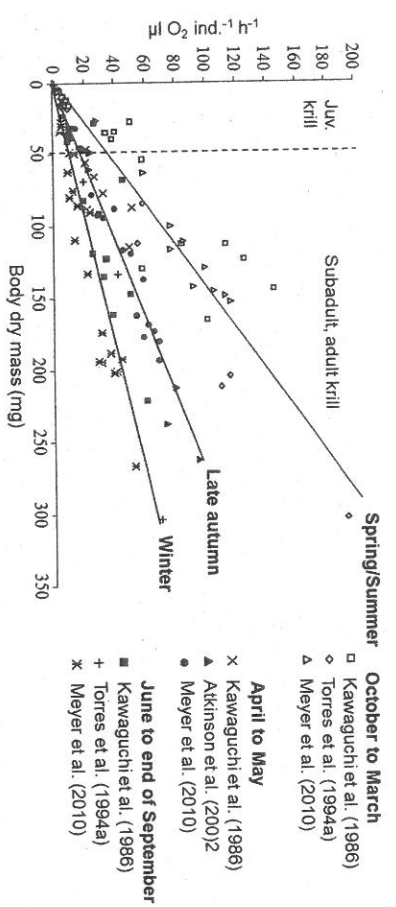


Fig. 4.3 From Meyer (2011): relationship between body dry mass and individual oxygen uptake rates in different seasons and latitudinal regions in the Southern Ocean. Juvenile, subadult and adult krill were defined according to Siegel (1987). The equations are as follows: Spring/Summer: $y = 0.69x$, $r^2 = 0.86$, $n = 36$; late autumn: $y = 0.37x$, $r^2 = 0.93$, $n = 29$; winter: $y = 0.22x$, $r^2 = 0.78$, $n = 49$. The regions were the oxygen uptake rates were measured are as follows: Lütz-Holm Bay (Kawaguchi et al. 1986), Southern Scotia-Northern Weddell Sea (Torres et al. 1994a), Lazarev Sea (Atkinson et al. 2002; Meyer et al. 2010)

seasonal pattern in metabolic activity varies during krill ontogenesis. The regression lines demonstrate that the clear seasonal pattern in metabolic activity is most pronounced in the adult stages. It is unknown to date, whether the shift of metabolic activity between seasons takes place abruptly with the final larval moult or if there is a subtle transition period during juvenile stage. Until the end of the 1990s, the prevailing view was that the differences in metabolic activity between seasons are the result of the low food supply during winter. Other studies, however, have mentioned the possibility that the seasonal changes in day light duration in the Southern Ocean might also be able to cause the seasonal variability in metabolic activity (Kawaguchi et al. 1986; Torres 1994a). We will take up this view in more detail in Sect. 4.2.3.

4.2.2 Feeding

The feeding activity of krill follows the highly seasonal pattern in food availability with high food intake during spring and summer, whereas in the winter month of low food supply, the feeding activity is reduced. The reduced feeding activity of adults in the field during winter has been indicated by a low stomach- and/or gut fullness (Morris and Priddle 1984; Kawaguchi et al. 1986; Buchholz 1989a; Lanerati et al. 1991; Daly and Macaulay 1991; Nishino and Kawamura 1994) and reduced digestive gland size compared with summer animals (Fig. 4.4). In the Western Antarctic Peninsula (WAP) region, the rates of fecal pellet production

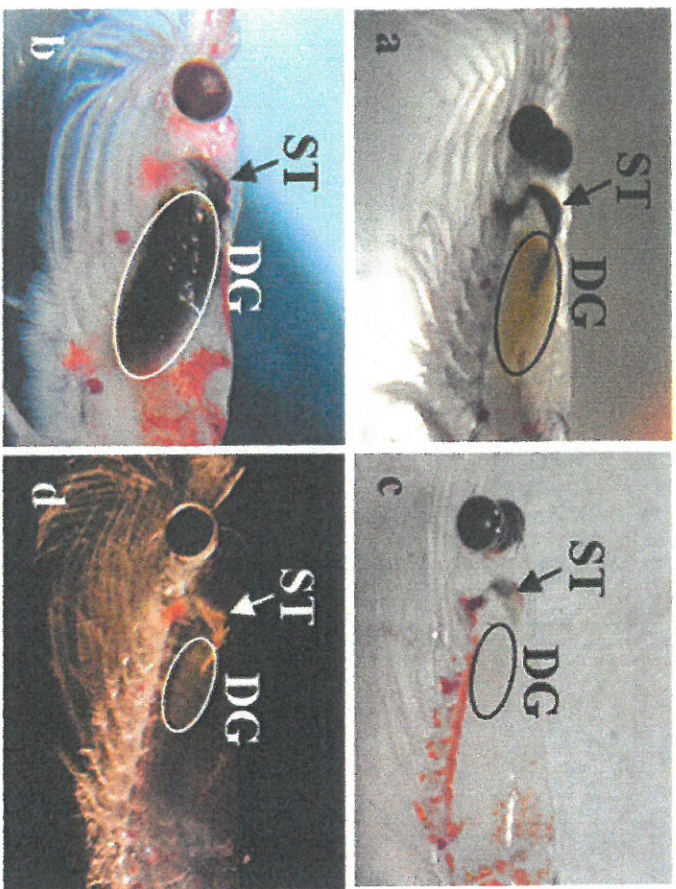


Fig. 4.4 From Meyer et al. (2010): carapace with digestive gland (DG) and stomach (ST) of freshly caught adult krill. (a) Yellow and (b) green-black DG in spring, and (c) milky white and (d) pale yellow DG in winter

and ingestion of phytoplankton of krill in winter were less than 2–3% of summer rates (Quetin and Ross 1991). Recent investigations on the seasonal feeding activity of adult krill show that, in winter, the feeding activities seem to differ with the latitudinal location of krill. The stomach fullness of krill from the Bransfield Strait and the Lazarev Sea was only 77% and 10% of the ones from South Georgia respectively (Schmidt et al. 2014). The quality of food ingested by krill in the different seasons will be discussed in detail in Chap. 5, (Schmidt and Atkinson 2016).

Shipboard experiments in different seasons demonstrated that the functional response of krill to increasing food supply was significantly different between seasons (Fig. 4.5). In early December, late spring krill displayed a clear functional response with increasing food availability. In autumn and winter, when adults were exposed to similar food concentration than in late spring, they ingested only 20% and 14% of the maximum daily ration determined in late spring. These findings, in combination with the winter feeding activity of krill from different latitudes (Schmidt et al. 2014), indicate that another factor than food supply must be responsible for the low oxygen uptake rates during winter in adults. The impact of photoperiod on physiological functions of adult krill will be discussed in detail in the following paragraph (Sect. 4.2.3).

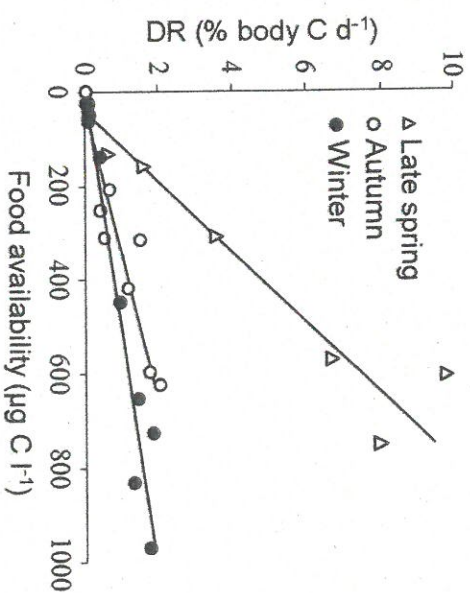


Fig. 4.5 From Meyer et al. (2010). Seasonal daily C ration (DR) as a function of food availability. Data points represent individual experiments

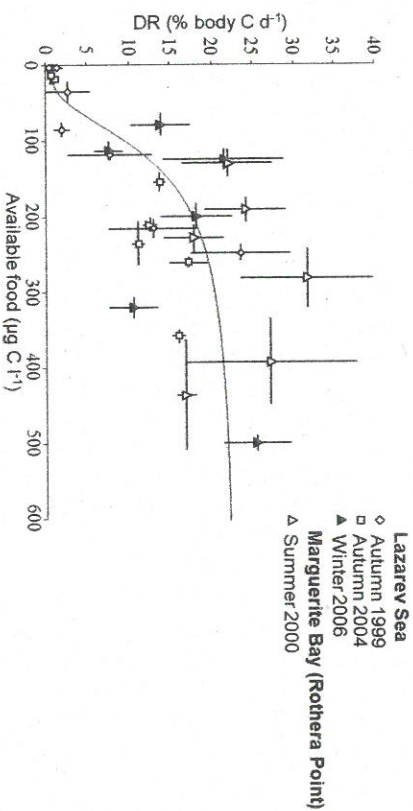


Fig. 4.6 Mean daily ration (DR) of furcilia larvae in different seasons and regions when exposed to different concentration of natural food assemblages

In contrast to adult krill, autumn and winter larvae showed a positive functional response in metabolic (Fig. 4.2) and feeding activities (Fig. 4.6) when exposed to increasing food concentrations (Meyer et al. 2002b, 2003, 2009). A maximum daily food intake was reached in larval krill at a food concentration of ca. 200 $\mu\text{g C l}^{-1}$, which corresponded to a Chl *a* concentration of 3–4 $\mu\text{g l}^{-1}$ (Ross et al. 2000; Meyer et al. 2009). These findings, in combination with the respiration rates of starved and well fed larvae shown in Fig. 4.2, suggest that the low oxygen uptake rates measured in winter larvae may be a flexible adaptive behaviour to cope with the low food supply.

4.2.3 The Role of Photoperiod in Controlling Physiological Functions in Krill

Biological timing that guarantees regulation of krill's physiology and behaviour in reaction to annual fluctuations of biologically significant factors seems of particular advantage and the ability of krill to anticipate and prepare for forthcoming environmental changes and synchronize seasonal events (e.g. reproduction) to environmental fluctuations is likely to be a major factor behind its success in the Southern Ocean. Results from previous and recent studies on seasonal feeding and metabolic activity on krill point to the impact of photoperiod (day length) in mediating physiological functions in krill.

In the field Kawaguchi et al. (1986) demonstrated a decline of feeding and metabolic activity from April to May to the end of September and a slow but steady increase thereafter, at a time when food was still scarce in the water column. In addition, freshly caught krill feed on natural food assemblages in autumn and winter are unable to respond to high food concentrations despite exposure to abundant food for almost 2 weeks (Atkinson et al. 2002; Meyer et al. 2010). The maximum feeding activity of krill was only 20% (autumn) and 14% (winter) of summer rates (Meyer et al. 2010). Both studies were the first that were indicating a food independent component in the regulation of metabolic activity in krill and therefore suggesting that other environmental factors such as photoperiod might play a functional role. Further experiments to test this hypothesis in terms of krill's behaviour, specific enzyme activities, and gene expression levels were therefore needed.

Long-term experiments with krill in the laboratory demonstrated that feeding and metabolic activity was affected by different simulated light-dark cycles (LD) irrespective of food supply suggesting that light simulations of prolonged photoperiod can force animals into a state of increasing metabolic activity and vice versa (Teschke et al. 2007). In addition, it was demonstrated that seasonal patterns of maturity are maintained, independent of direct control by factors such as food, light or temperature (Thomas and Ikeda 1987; Kawaguchi et al. 2006; Brown et al. 2013), indicating that krill passes through a fundamental inherent seasonal transition in maturity development. Other experiments showed that light conditions of prolonged photoperiod can force krill into maturity while shortened photoperiods force animals into regression of maturity faster than under a natural light-dark regime (Teschke et al. 2008; Brown et al. 2011). These experiments strongly indicate that the overt cycles of maturity and metabolic activity represent endogenous seasonal rhythms, controlled by an endogenous timing system in krill (endogenous clock) in which photoperiod act as a main *Zeitgeber* (entrainment cue), synchronizing the clock with the natural year.

Indeed, molecular analyses (Seear et al. 2009) revealed differential gene expression of target genes (i.e. involved in metabolism) in response to photoperiodic changes indicating a signaling cascade that link the photoperiod cue to the target response. The experiments demonstrated that autumn krill exposed to a winter

photoperiod showed a pattern of gene expression consistent with known features of regression and quiescence, such as the slowing of moult rate, the lowering of activity levels, and the reduction in metabolic rate while under the natural light cycle in autumn gene expression levels were significantly higher (Seear et al. 2009). The molecular response became evident after just 7 days of exposure to winter light conditions. The results indicate that krill can switch rapidly between active and quiescent states and that the photoperiodic cycle plays a key role in this process. Seear et al. (2009) also found a down-regulation of myosin when krill were exposed to the winter photoperiod, suggesting that krill are less active in winter. Together with a present study where the author makes similar findings within a freshly captured wild krill population caught during summer and winter near the Antarctic Peninsula (60° S) (Seear et al. 2012), these results indicate that wintertime metabolic depression is accompanied by lower activity levels consistent with krill entering a winter quiescent state, where foraging decreases and the level of muscular activity becomes reduced. If seasonal metabolic depression were simply a matter of specific dynamic activity in terms of feeding and digestion, it is likely that muscle use would be similar year-round, since foraging for patches of food would need to continue.

Antarctic krill with its circumpolar distribution shows a latitudinal range from approx. 51 to 74° S meaning that the seasonal photoperiodic regime as well as the accompanied seasonal food pattern experienced by krill may be very different at a given point during the season. An individual krill may be capable of travelling across many degrees of latitude within one season (Thorpe et al. 2007). Taking this into consideration a central question is whether photoperiod as a dominant *Zeitgeber* would leave krill too inflexible for the array of environmental conditions it encounters? In this sense, a comparison between two different overwintering locations for krill, namely the Antarctic Peninsula (62° S) and South Georgia (54° S) showed no differential expression levels of genes involved in respiration, motor activity or vitellogenesis, suggesting that both populations of krill are undergoing a phase of physiological quiescence at the same time of the year and thereby coordinating their general life-cycle despite the very different seasonal cycles of photoperiod prevailing at the two different latitudes (Seear et al. 2012). However, winter krill from the South Georgia region, with favorable feeding conditions even in winter, showed an up-regulation of genes involved in feeding, digestion, and immunity, indicating that krill are capable of adjusting specific functional physiological pathways to prevailing environmental conditions.

The results may also indicate that the power of photoperiod as an environmental *Zeitgeber* may lose strength towards lower latitudes (Helm et al. 2013). At lower latitudes a hierarchy of external signals or interplay of different environmental cues with day length may become more important to modulate the life-cycle of krill, and food in particular may play a prominent role as modulating factor. The importance of temporal synchronization through internal clocks in adult krill, triggered by photoperiod and food, could be recently demonstrated by use of an individual-based model (Groeneveld et al. 2015). To conclusively understand a potential interplay of photoperiod and food supply as environmental *Zeitgebers*, more

complex, two-factor experiments have to be conducted in the future. These studies will have to combine different photoperiods and different levels of food supply at the same time and in which krill can feed freely. Moreover, such experiments should be performed at different times of the year to take into account the potential seasonal effects.

The clock mechanism that seems to be involved in the modulation of krill's seasonal cycles is yet not understood. Critical molecular components of an endogenous circadian clock, such as a *cry*-gene, have been identified in Antarctic krill and evidence of its functional significance in the clock machinery has been found (Mazzotta et al. 2010). The authors observed daily changes in krill *cry2* mRNA throughout a 24 h cycle and proposed an endogenous circadian time-keeping system in krill. A similar conclusion resulted from a laboratory study on circadian behavioural patterns of krill (Gaten et al. 2008). The first report of an endogenous circadian timing system in Antarctic krill and its link to metabolic key processes was demonstrated by Teschke et al. (2011). The study found that expression levels of the canonical clock gene *cry2* were highly rhythmic both in a light-dark cycle and in constant darkness. An ongoing rhythm even in constant darkness is evidence for the presence of an endogenous clock in krill. Surprisingly, the authors found a remarkable short circadian period, which they interpreted as a special feature of the krill's circadian clock that helps to entrain the circadian system to the extreme range of photoperiods krill are exposed to throughout the year. Furthermore, important key metabolic enzymes of krill showed bimodal circadian oscillations (9–12 h periods) in transcript abundance and enzymatic activity. Oxygen consumption of krill showed (9–12 h) oscillations that correlated with the temporal activity profile of key enzymes of aerobic energy metabolism. The 12 h bimodal oscillatory pattern in aerobic energy metabolism may reflect distinctive 12 h behavioural patterns in locomotor activity of krill. Indeed, Gaten et al. (2008) identified a 12 h rhythmic component in the diel vertical migration (DVM) of Antarctic krill during laboratory experiments, which correlate with findings from the field (Godlewaska 1996), where a 12 h component in DVM of krill becomes predominant at certain times during the year when food is scarce. Often, these rhythms have been interpreted as bimodal patterns of one circadian-behavioural output.

De Pittà et al. (2013) performed the first diurnal transcriptome characterization of krill in natural conditions on a summer day in Antarctica. About 609 genes were found to be periodically expressed across the time points analysed and many of these showed a cyclic sinusoidal expression. Bimodal oscillatory patterns showed 60% of the transcripts (371 out of 609) with a periodicity of approximately 12 h, as recently reported for key enzymes involved in aerobic energy metabolism (see above, Teschke et al. 2011). The majority (56.5%) of the transcripts characterized by a 12 h periodicity showed two high expression peaks at 10:00 h and consequently 22:00, after the morning and evening light transitions represented, respectively, by the increase (10:00, 2.98 W/m²) and the decrease (06:00, 0.36 W/m²) of light irradiance at the fishing depth. About 40% (238 out of 609) of periodically regulated genes showed only one peak of expression during the 24-h cycle with a significant enrichment (47.8%) in the early day (01:00–06:00). Interestingly, genes

belonging to a number of specific functional categories showed peak expressions limited to distinct temporal intervals, confining specific biological processes to particular times of the day. Thus, the breakdown of energy-yielding nutrients (glycolysis, the Krebs cycle and the electron transport chain) and energy storage pathways (glycogen synthesis and fatty acid synthesis) are specifically activated in the early morning, while glycogen mobilization, gluconeogenesis and fatty acids catabolism are used as a stored energy source in the evening and throughout the night. Together these results indicate the presence of a functional circadian clock in krill that controls a chronological progression of biochemical and physiological events throughout the 24-h cycle. This system is most likely of essential importance for krill as it facilitates synchronization of its physiology and behaviour to daily environmental cycles. Future studies are necessary, to define the circadian transcriptome of *E. superba* analyzing the expression levels of light: dark and dark: dark (LD/DD) entrained krill samples to get a better understanding of the physiological processes that are regulated by krill's circadian clock.

Generally, our understanding of how circadian clocks of high latitude organisms such as krill might have adapted to the strong variability in annual day length that at the extreme may range from constant darkness in winter to constant light in the summer is small. The results of De Pittà et al. (2013) indicate that krill do not become arrhythmic under constant photoperiodic conditions and we have some evidence that at least *cry2* levels are still showing daily oscillations under summer conditions of constant light (Mazzotta et al. 2010). A central question in this context is the putative role of the krill's circadian clock in photoperiodic time measurement. There is some evidence that organisms might be using components of the circadian system to sense changes in day length and to mediate the photoperiodic response (Oster et al. 2002; Schultz and Kay 2003). What will be the plasticity of krill's circadian clock in the context of different seasons? Determining transcript levels of canonical clock genes in correlation with key physiological target genes around the circadian cycle under different LD conditions throughout simulated seasonal courses of photoperiod will potentially answer this question and should be the focus of future laboratory and field studies.

The phenology of environmental conditions to which the seasonality of krill is adapted is changing, due to the increasing anthropogenic CO₂ emission, whereas the Zeitgeber cue (photoperiod) will remain unchanged. For making reliable prediction how the krill population might change in the future we have to identify how important life cycle parameters in all developmental stages of krill are mediated by environmental cues such as photoperiod via endogenous timing systems (circadian/circannual). A prerequisite for future research in this respect is the functional characterization of the endogenous clock machinery in krill itself. The identification of the molecular components of the *E. superba* clock machinery is currently under way by combining the classical gene candidate approach (primer design on orthologous genes, 5' and 3' RACE) with next generation sequencing data (ESTs: (De Pittà et al. 2008; Seear et al. 2010); 454 sequencing data: (Clark et al. 2011; De Pittà et al. 2013; Meyer et al. 2015).

4.2.4 Growth and Shrinkage

In krill physiology, growth, estimated by the Instantaneous Growth Rate (IGR) method¹ is used as a parameter to quantify the condition of adult and larval krill in different seasons (Ross et al. 2000; Daly 2004; Meyer et al. 2009, 2010). One of the main assumptions of the IGR method is that the growth increment at moult (GI), measured in the first few days, reflects the in situ conditions experienced by krill in the previous intermoult period (Tarlant et al. 2006). The IGR method was first described by Quetin and Ross (1991) and modified by Nicol et al. (1992). Large scale investigations, that related growth to environmental variability, are rare (see also Chap. 3, Reiss 2016). They investigated natural growth rates of juvenile krill in spring and summer at the WAP region (Ross et al. 2000), growth rates on adults in summer across the Southwest Atlantic sector of the Southern Ocean (Arnold et al. 2004; Atkinson et al. 2006) and in East Antarctica (Nicol et al. 2000). Krill maintain high growth in summer to take advantage of short-term fluctuations in food (Arnold et al. 2004). The variability in growth rates at this time of the year fit best with food concentration in terms of Chla (Atkinson et al. 2006; Ross et al. 2000). During the highly productive summer month in the Scotia Sea growth rates in adult krill were between 0.013 and 0.32 mm d⁻¹, with mean values of 0.1 mm d⁻¹ (Atkinson et al. 2006). An average growth rate of 0.1 mm d⁻¹ in adult krill during summer can be found in different regions such as around South Georgia (Arnold et al. 2004), in the Lazarev Sea (Meyer et al. 2010) and off East Antarctica (Nicol et al. 2000). In juvenile krill, during a 4 years study, growth rates ranged on average between 0.072 mm d⁻¹ and 0.082 mm d⁻¹ and reaching maximum growth rates above a critical concentration of about 3.5 µg Chla l⁻¹ (Ross et al. 2000).

In austral winter, the low feeding activity in adults is accompanied by zero to low individual growth rates (Meyer et al. 2010) up to shrinkage (Quetin and Ross 1991). Previous studies, which estimated growth at the population level, reported similar results compared with the IGR method, namely zero to low growth during winter (Mackintosh 1972; Stepanik 1982; Morris and Priddle 1984; Kawaguchi et al. 1986; Buchholz et al. 1989b).

Growth rates of larval krill measured by the IGR method are calculated as the % change in uropod or telson length, based on the GI at moult, these values are highly variable from the onset of winter in April until its end in September. They range on average from 15% growth in autumn (Pakhomov et al. 2004) to extreme low (Daly 2004; Meyer et al. 2009) or negative values (body shrinkage) in mid-winter (Quetin et al. 2003; Ross et al. 2004). A comparison of growth rate data from autumn and winter larvae from different regions have demonstrated that larval krill follow a specific growth pattern from late autumn to winter, reflecting the high variability in food supply from late autumn, during winter, until the end of winter (Fig. 4.7). The larvae had a clear positive growth in April, a steady decrease in growth until a minimum in mid-winter (from June to August) and a recurring increase of their growth rates in later winter (end September). A summary of daily larval growth rates from laboratory experiments and field data are shown in Table 4.3.

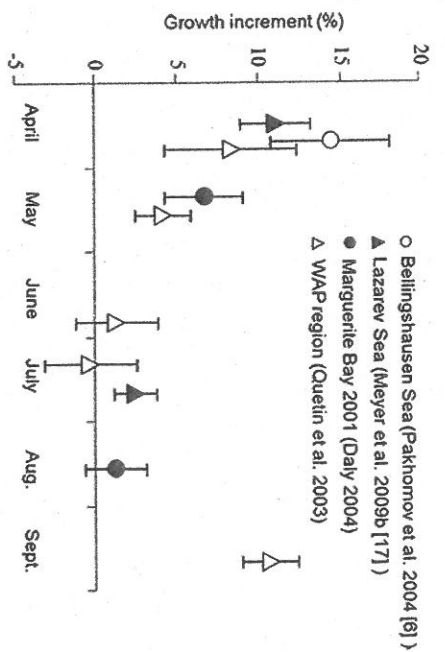


Fig. 4.7 From Meyer (2011): average growth rates of larval krill, measured with the instantaneous growth rate (IGR) method, from different regions and years given as growth increment (GI) in % change in uropod or telson length at moulting (Meyer et al. 2009). WAP means different study regions west of the Antarctic Peninsula. The data from Fig. 4.5 in Quetin et al. (2003) were extracted with the Image processing program Image. The number of growth data were as follows: Pakhomov et al. (2004), April: n = 9; Meyer et al. (2009), April: n = 6, July: n = 5; Daly (2004), May: n = 7, August: n = 6; Quetin et al. (2003), April n = 3, May: n = 8, June: n = 13, July: n = 3, September: n = 16

Table 4.3 Average daily growth data of larval krill from laboratory experiments and different field seasons. WAP means Western Antarctic Peninsula

Laboratory/field/season	Region	Daily growth rates (mm)	References
Laboratory/summer food condition		0.06–0.11	Ikeda (1984, 1985)
Laboratory/winter food condition		0.02	Ross and Quetin (1991)
Field/summer		0.06	Wirek et al. (1980) and Brinton (1991)
Field/autumn	WAP	0.013–0.036	Daly (2004)
	Lazarev Sea	0.006–0.015	Meyer et al. (2009)
Field/mid-winter (June–August)	WAP	0.017	Ross and Quetin (1991)
	WAP	0.00–0.013	Daly (2004)
	Lazarev Sea	0.001–0.002	Meyer et al. (2009)
	WAP	0.0005–0.002	Quetin et al. (2003)
Field/late winter (Sept./Oct.)	WAP	0.05 Pack ice region	Quetin et al. (2003)
	Northern Weddell Sea	0.07 Pack ice region	Daly (1990)

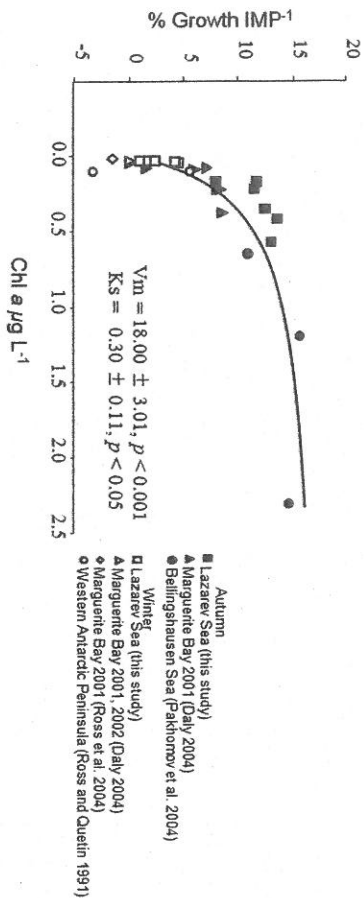


Fig. 4.8 From Meyer et al. (2009): relationship between mean chlorophyll *a* (Chl *a*) concentration and % growth per intermoult period (IMP⁻¹) of larval krill from autumn and winter in different regions in the Southern Ocean. Data are expressed as a Michaelis-Menten uptake function as follows: % growth IMP⁻¹ = $18.00 \times [\text{Chl } a] / (0.30 + \text{Chl } a)$, $r^2 = 0.68$, $n = 25$. V_m and K_s are constants representing, respectively, maximum growth and the Chl *a* concentration at which growth is half the maximum. K_s reflect the ability to grow at low food concentrations

When plotting larval growth rate data from different regions and seasons versus food supply in terms of ambient Chl *a* concentration in the surface layer, the Chl *a* is a surprisingly good overall predictor of larval growth (Fig. 4.8). This basic relationship, however, only holds because winter Chl *a* concentrations and larval growth rates are much lower than those during autumn. Therefore, the use of water column Chl *a* concentration as a food proxy to predict growth is most precise in autumn, but less reliable in winter when growth varies greatly, e.g. from 1% to 4% in urupod length at moulting (Daly 2004; Meyer et al. 2009), despite very low Chl *a* concentrations (<0.03 µg Chl *a* l⁻¹). Thus, some other energy sources than algal diet must be used by the larvae to explain the high variability in their growth rates during winter. Stomach analyses demonstrated that larval krill made use of heterotrophic diet during winter (Meyer et al. 2009; Töbe et al. 2010). In autumn, maximum growth was reached by the larvae at a Chl *a* concentration >1 µg l⁻¹.

During winter, larvae not only showed a high variability in their growth rates, but also a large flexibility in their growth pattern following direct and indirect developmental pathways and prolonged intermoult period (IMP). During direct development, larvae moult to the following ontogenetic stage, whereas during indirect development, they moult to the same stage (delayed development) or to an intermediate form. During both developmental pathways, winter IMP was mainly that of summer and autumn (Quetin et al. 2003; Meyer et al. 2009). Consequently, the amplitude in seasonal variation in daily growth rates (in mm per day, defined as the GI divided by the IMP) would be roughly twice that depicted in Fig. 4.7.

Indirect development was mainly observed in older furcilia stages. In mid-winter, the majority of FVI larvae moulted to the same stage, whereas FIV and FV larvae moulted to an intermediate from where an indirect developmental

pathway was observed (Daly 2004; Meyer et al. 2009). This might be a strategy to survive the severe winter condition in pack ice regions with low food supply because moulting to the next advance stage means higher energy demands, which have to be covered to survive.

The debate over whether adult krill regularly shrink in the field is still ongoing, ever since the long term krill starvation study of Ikeda and Dixon was published in 1982. This study demonstrated that krill are able to shrink when food is scarce or absent. Based on this study, it was hypothesised that krill do not grow in winter (Ikeda 1985; Ikeda and Thomas 1987). However, the results available so far are controversial. In the Lazarev Sea, the low feeding activity in winter was accompanied by low individual growth rates but not shrinkage (Meyer et al. 2010), whereas shrinkage was determined in the Bellinghousen Sea (Quetin and Ross 1991). Other studies, which measured growth by traditional length-frequency analysis, reported zero or low growth (Mackintosh 1972; Stepnik 1982; Morris and Priddle 1984; Kawaguchi et al. 1986; Siegel 1987; Buchholz et al. 1989b) as well as shrinkage (Ettershank 1983). Determining shrinkage of krill by length-frequency analysis at the population level is problematic though. Different size structures of krill within a population might occur due to selective size mortality (predation) and/or due to selective size immigration/emigration and exchange of water masses (see also Chap. 3, Reiss 2016).

Shrinkage has been recorded in the laboratory and in nature in various decapod species such as crabs (Guyseleman 1953; Skinner 1985; Hopkins 1985; Asakura 1992), shrimps (Lloyd and Yonge 1947), lobsters (Marshall 1945; Lindberg 1955; Sweat 1968; Little 1972) and spiny lobsters (Cockcroft and Goosen 1995), euphausiid crustaceans in general (Laaker 1966; Hosie and Ritz 1989; Nicol et al. 1992) and *E. superba* in particular (Ikeda and Dixon 1982). Such negative growth has been associated with adverse experimental conditions such as starvation (Ikeda and Dixon 1982; Nicol et al. 1992) or unfavourable environmental conditions (Cockcroft and Goosen 1995; Atkinson et al. 2006) and/or severe physiological conditions in terms of body lipid levels (Nicol et al. 2004; Meyer et al. 2010). Atkinson et al. (2006) have demonstrated that unfavourable environmental conditions in terms of Chl *a* concentration do not result in negative growth per se as models predict (e.g. Hofmann and Lascara 2000; Fach et al. 2008). The available data suggest that adult krill might be able to shrink in the field during winter but the data also suggest that such behaviour may not be the rule but rather the exception, due to unfavourable conditions. During future seasonal growth studies, condition parameters of krill such as body carbon and lipid content, or length-mass relationships should be analysed in addition to environmental conditions such as food supply in terms of Chl *a*. This would certainly help to explain when and why shrinkage in krill occurs in the field. In growth experiments with larval krill in different regions during winter 13 to up to 40% of larvae were shrinking (Ross and Quetin 1991; Quetin et al. 2003; Ross et al. 2004; Daly 2004; Meyer et al. 2009). In some studies shrinkage was related to

very low body lipid levels ($\leq 5\%$ DM⁻¹) of larvae (Meyer et al. 2009), suggesting that shrinkage, similar to adult krill, is an indicator of unfavourable food conditions and hence severe physiological condition in terms of body lipid reserves.

4.2.5 Energy Provision

Energy must be provided in order for the organism to function. In this respect, the winter season is most critical due to the absence of autotrophic food in the water column for several months. There seem to be two adaptations to accomplish survival: (1) accumulation of large lipid reserves during summer for winter consumption and (2) an omnivorous feeding at low rates during winter. In the following we will outline in more detail the utilisation of energy reserves by krill, whereas their feeding behaviour during winter will be discussed in Chap. 5, (Schmidt and Atkinson 2016).

The body lipid contents of adult krill from different regions show a strong seasonality, with highest levels in late autumn (35–48% DM⁻¹) and minimum values in mid spring (5–20% DM⁻¹, Hagen et al. 2001), demonstrating the accumulation of large lipid reserves until the onset of winter and a depletion of these reserves during winter each year. The accumulation of energy reserves during the feeding season depends on the quantity and quality of phytoplankton during the preceding summer and autumn (Hagen et al. 2001). The lipid depletion in krill from the WAP region (Quetin and Ross 1991), the southern Scotia-northern Weddell Sea region (Torres et al. 1994b), the eastern and western Weddell Sea (Hagen et al. 2001) and from the Lazarev Sea (Meyer et al. 2010) correspond to a utilisation of body lipids in krill at a rate of 10% DM⁻¹ month⁻¹ from their initial values in April/May to October/November. The molar ratio of oxygen uptake to ammonia excreted (O:N ratio) provide information at which relative proportion lipids, proteins, and carbohydrates are being utilized as metabolic substrates (Ikeda 1974). When zooplankton utilizes proteins as the only metabolic substrate, the O:N ratio is generally about 8, but the ratio increased greatly the more lipids are metabolised. An O:N ratio of 24 is observed when equal amounts of protein and lipid are metabolised (Ikeda 1974; Omori and Ikeda 1984). The O:N ratio of adult summer krill is between 12 and 17 (Ikeda and Mitchell 1982; Ishii et al. 1987). The low O:N ratio of late autumn krill (average 15) indicates that they had not resorted to burning their reserves at the onset of winter (Atkinson et al. 2002), while the high O:N ratios of adult winter krill (average 66) suggests that they were relying on body lipids only until the forthcoming spring (Meyer et al. 2010). In addition, the metabolic enzyme 3-hydroxyacyl-CoA dehydrogenase (HOAD), an indicator for lipid catabolism (Turnover, Auerswald et al. 2009), showed significantly higher activities in winter krill than in those from summer and autumn. This highlights the importance of lipid utilization of krill during winter (Meyer et al. 2010).

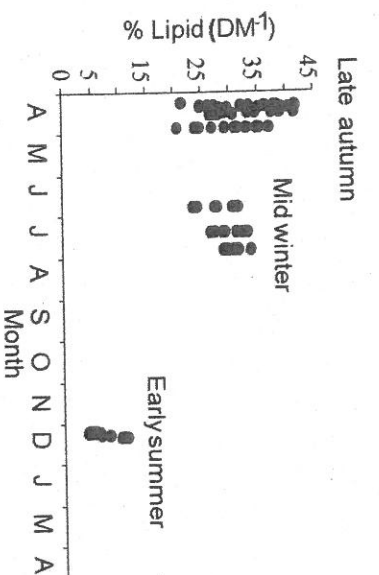


Fig. 4.9 Seasonal lipid levels of adult krill in the Lazarev Sea (Modified after Meyer et al. 2010)

The remaining lipid content of 5% DM⁻¹ in December 2005 of adults from the Lazarev Sea (Fig. 4.9) is very low and on the border of what is deemed essential for the functioning of bio-membranes and hence survival (Saether et al. 1985). Such low reserves in krill were documented previously in late October/mid November (Hagen et al. 2001). However, survival of winter and reproductive success in the subsequent summer depend on the accumulated energy reserves at the onset of winter. Completely depleted body lipids at the start of the reproductive season would affect the onset and maintenance of reproduction in krill negatively and hence their reproductive success (Clarke and Morris 1983; Cuzin-Roudy and Labat 1992; Quetin et al. 1994). This is particularly true when the spring phytoplankton bloom is delayed (Auerswald et al. 2009). The importance of a sufficient accumulation of lipids until the commencement of winter is also supported by results of Teschke et al. (2008), indicating that development of external maturation is fuelled preferentially by lipid reserves, whereas the following internal maturation is fuelled by grazing on large diatom blooms (Schmidt et al. 2012). Compared with lipids, proteins play a minor role as an energy provision for overwintering. Krill depleted protein levels from March to August by 16% (Torres et al. 1994a, b). Such utilization is minor (ca. 3% month⁻¹) compared to the lipid depletion during winter as outlined above.

In contrast to adults, larvae have no seasonal pattern in their lipid dynamics and the same larval stages show a high variability in their lipid level within one season and year (Fig. 4.10) and between years (Table 4.4, Deibel and Daly 2007). The average body lipid content in larvae increased with ontogenetic stage (CIII: 7%, FI: 10%, FII: 15% DM⁻¹), and hence their tolerance to short starvation periods from days to a few weeks (Meyer and Oetli 2005; Daly 2004; Meyer et al. 2009). In late autumn, the body lipid content of larval krill do not exceed 20% DM⁻¹ compared with 40% DM⁻¹ in adult krill. This implies that, unlike adults, no larval stage could survive several months or even the entire winter without food.

Fig. 4.10 Variability of body lipid content of larval stages in late autumn (April) and mid-winter (June, July) in the Lazarev Sea (Modified after Meyer 2011)

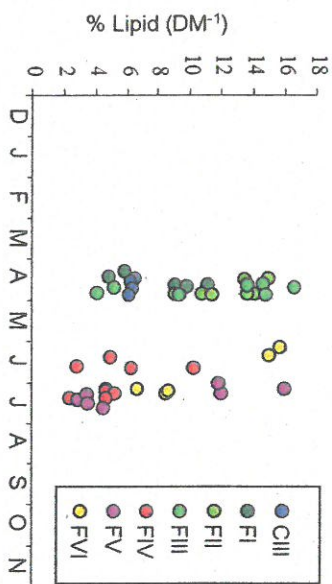


Table 4.4 Body lipid content per dry mass (DM) in different ontogenetic stages of krill and different regions

Season	Larval stages	Lipid (% DM ⁻¹)	Region	Month and year	References
Mid-summer	CI, II	12.3 ± 1.4 (8)	Weddell Sea	Jan–Feb 1986	Hagen et al. (2001)
	CIII	15 (1)	Weddell Sea	Apr–May 1992	
	CIII	6.6 ± 0.1 (5)	Lazarev Sea	Apr–May 2004	Meyer et al. (2009b)
Late autumn	FI–FIII	12.4 ± 2.2 (14)		Apr–May 1999	Meyer et al. (2002a)
	FIII	15.5 ± 4.3 (18)		Apr–May 1992	Hagen et al. (2001)
	FI–FIV	18.4 ± 5.4 (12)	Weddell Sea	Apr–May 1992	Hagen et al. (2001)
Winter	FIV–FVI	7.4 ± 3.8 (19)	Lazarev Sea	July 2006	Meyer et al. (2009b)
Mid spring	FV	7.3 ± 1.6 (2)	Lazarev Sea	Oct–Nov 1986	Hagen et al. (2001)
	FV, FVI	9.7 ± 1.2 (5)	Antarctic Peninsula	Oct–Nov 1983	

Number of replicates in brackets
C calyptopis, *F* furcilia

4.2.6 Energy Demand of Krill in Winter

While there is considerable knowledge of krill's high energy demands in summer (see Table 4.1) in the following section we will focus on krill's energy demands in winter.

According to the seasonal physiological functions of adults outlined above the energy demand was calculated for adult krill (Fig. 4.11) for the winter period, i.e. from the start of April to the end of September (183 days). According to recent results on the seasonal metabolic activity of krill from the Lazarev Sea

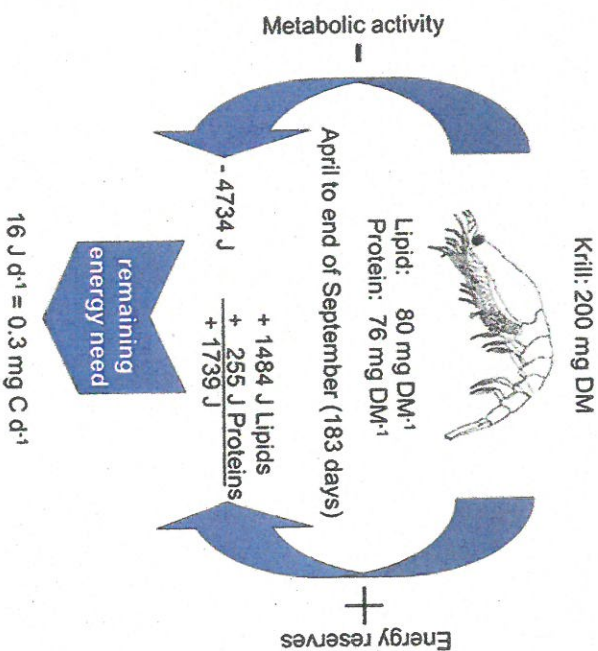


Fig. 4.11 From Meyer (2011): energy demand of adult krill of 200 mg dry mass (DM) from the onset of winter to beginning of spring (begin of April until the end of September) south of 66°S from the Lazarev Sea

(Meyer et al. 2010), metabolic depression was already initiated in April, whereas at the end of September, i.e. in early spring, adult krill reverted to an active mode again in late autumn and winter. For calculation of the daily energy requirements from the start of April to the end of September, the equations of the regressions in Fig. 4.3 were used (April and May, 61 days: $\mu\text{l O}_2 \text{ ind. h}^{-1} = 0.37 \times \text{DM in mg}$; June until end of September, 122 days: $\mu\text{l O}_2 \text{ ind. h}^{-1} = 0.22 \times \text{DM in mg}$). The resulting calculated respiration rates were converted to energy consumption rates, assuming an equivalent of 19.4 J ml O₂⁻¹ (Brett and Groves 1979). Hence, a 200 mg model krill consumes about 1.8 ml O₂ daily in April and May and 1.1 ml from June to the end of September. This translates into a total demand of 4,734 J to cover metabolic activity for the 6 month of winter "hibernation".

Previous and recent investigations as well as our own data have shown that krill use high amounts of body lipid and moderate amounts of body protein reserves at rates of 10% and 3% month⁻¹, respectively (Lit. summarised in Meyer 2011). During the 6-month of metabolic winter depression, krill consume 37 mg of body lipids and 13 mg of body proteins, which correspond to an energy yield of 1,484 J from lipids and 255 J from proteins, assuming conversion factors of 39.6 J mg⁻¹ for lipid and 20.1 J mg⁻¹ for proteins (Brett and Groves 1979). Consequently, the total energy krill obtain from both stores amounts to 1,739 J. At the end of "hibernation"

(end of September), krill still contained 42 mg lipids and 63 mg proteins, which correspond to ca. 20% and 30% DM⁻¹, respectively. This is a reasonable amount to start the spring season in favourable physiological conditions.

Our calculation above revealed a difference of 2,995 J between the energy consumed and that provided from body reserves of lipids and proteins, corresponding with a lack of energy of 16 J d⁻¹ for the period from April to the end of September. This daily energy requirement equates to 0.3 mg C, assuming an energy yield of 45.7 J mg⁻¹ C (Salonen et al. 1976). According to microscopic analyses of the stomach and gut contents of winter krill (see Chap. 6), 0.3 mg C d⁻¹ is an amount of energy that krill can gain by occasional feeding, even at low rates. This budget of the energy demand in winter demonstrates that the low feeding activity during winter is an important part for a successful overwintering of krill. It enables krill to start the spring season with a reasonable lipid level to survive when, after the metabolic winter depression, a high energy demand is needed by krill and the spring diatom blooms might be delayed or less extent.

In larval krill, lipid levels are highly variable, reflecting the high variability in food availability, outlined above. Therefore food quality and quantity is the major factor needed to cover the energy demands for their metabolic activity and growth. According to seasonal investigations on larval krill by Meyer et al. (2009) it can be summarised:

1. In autumn, the larvae from within the ice were in better physiological condition than those from open water.
2. Within the ice, autumn larvae were in better physiological state than winter larvae.
3. Different food sources were used in autumn and winter. While in autumn larvae were mainly feeding on autotrophic food sources, during winter heterotrophic organisms (small copepods, protozoans, or both) were important food items for larvae.
4. High amounts of larvae are observed in rafted sea ice regions with high structured under ice topography. This might dictate whether larval krill can exploit the food associated with sea ice or are drifted away from suitable feeding habits.

In addition, this habitat might not only favourable food regions but also protected areas due to predation. The measured growth and respiration rates of furcilia in autumn ($0.95 \pm 0.28 \mu\text{l O}_2 \text{ mg}^{-1} \text{ DW h}^{-1}$, 0.011 mm d^{-1}) and winter ($0.54 \pm 0.19 \mu\text{l O}_2 \text{ mg}^{-1} \text{ DW h}^{-1}$, 0.001 mm d^{-1}) in the Lazarev Sea, correspond to a C allocation of 2.5% of body C d⁻¹ into growth in autumn and 1.2% in winter and 3.3% body C d⁻¹ to fuel respiration in autumn and 1.6% in winter (Meyer et al. 2009), with a respiratory quotient of 0.97 (Ikeda et al. 2000). In winter, this corresponds for a slow growing furcilia VI (0.001 mm d^{-1}) of 1 mg DW and 37% body C to an energy demand of 0.01 mg C. The average POC concentration in the water directly under sea ice was $0.07 \pm 0.04 \text{ mg C L}^{-1}$ and corresponds to the low growth rates and even shrinkage of larval krill in winter.

4.3 The Impact of Elevated Seawater Temperature and Ocean Acidification on Krill

The life cycle of krill is characterized by a strong interaction between endogenous physiological functions and seasonal environmental factors (Teschke et al. 2011). Therefore, it is crucial to understand how important physiological life cycle functions are affected by stressors such as seawater temperature rise, increasing ocean acidification and decreasing salinity due to glacier melt caused by anthropogenic CO₂ emission. Several studies have linked climate-induced environmental changes (temperature, pH, ice cover) to krill habitat (Hill et al. 2013) and krill distribution, recruitment and survival (Atkinson et al. 2004; Kawaguchi et al. 2013; Quein et al. 2007). However, studies on the performance of krill to these stressors are rare and focused mainly on temperature. Previous field and laboratory studies have demonstrated an increasing moulting frequency with rising temperatures (Brown et al. 2010; Buchholz 1991) and accelerated maturation (McWhinnie and Marciniak 1964), increasing respiration rates with temperature up to 5 °C (McWhinnie and Marciniak 1964; Rakus-Suszczewski and Opaliński 1978; Opaliński et al. 1993; Opaliński 1991), altered lipid metabolism at different temperatures between seasons (Mayzaud et al. 2000) and declining growth rates at temperatures between 3 and 4 °C (Atkinson et al. 2006). Some of these findings suggest that krill seem to be relatively sensitive to rising temperatures. However, previous studies also show that krill are able to tolerate temperatures up to 10 °C for short periods of time (Opaliński 1991; Hirche 1984).

Only few studies exist so far on the impact of ocean acidification on krill. Laboratory experiments show that early larval stages seem to be most affected by increasing pCO₂ and especially in combination with rising temperatures (Kawaguchi et al. 2011, 2013).

A powerful approach to examine organismal responses to environmental change is by combining physiology performance indicators with transcriptomic changes, as demonstrated by recent characterization of the optimal thermal window for Antarctic fish (Windisch et al. 2011, 2014), showing a hepatic metabolic reorganization, indicating an alteration from a lipid-based metabolic network to pathways associated with carbohydrate metabolism. This picture of cellular adjustments to the warmth illustrate that we have to take a holistic view by identifying molecular networks rather than single genes to understand marine ectotherms capacities to cope with environmental change caused by the anthropogenic CO₂ emission (e.g. elevated seawater temperature, ocean acidification or reduced salinity due to glacier melt etc.). In adult Antarctic krill, a shift in metabolic pathways as shown for the Antarctic eelpout would have profound implications for krill's overwintering and spawning activity in the forthcoming spring. Krill build up considerable amount of body lipid reserves during the austral summer for their utilization during winter (Hagen et al. 2001). Increasing energy demands due to a warming environment (Pörtner and Farrell 2008) may impede the buildup of sufficient reserves

during summer to allow survival of the winter season (Hagen et al. 2001) and to fulfill the external maturation process (Teschke et al. 2008).

Long-term experiments focusing on the impact of krill to rising seawater temperature, ocean acidification and reduced salinity, using physiological performance indicators with transcriptomic changes are needed to understand the flexibility of krill to the ongoing environmental changes and to make reliable predictions how the krill population might alter in the future. The only means by which an organism may respond to temperature change are physiological flexibility in the short-term, adaptation in the long-term or migration to a more favourable environment as an evasion strategy (Peck et al. 2010). In terms of krill we have only a rudimentary knowledge in this respect.

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Chapter 5 Feeding and Food Processing in Antarctic Krill (*Euphausia superba* Dana)

Katrin Schmidt and Angus Atkinson

Abstract *Euphausia superba* is exceptional among euphausiids for the large filtering surface of the feeding basket and its fine mesh size (2–3 µm), which remain into adulthood. This enables them to feed efficiently on nano- and microplankton, and to reach substantial growth rates with food concentrations as low as 0.5 µg Chlorophyll *a* L⁻¹. Even though phytoplankton – in particular diatoms – are their staple food, protozoans and small copepods are ingested simultaneously and represent an important supplementary food source year-round. However, krill feeding behaviour is more complex than just filter-feeding in the water column; it includes raptorial capture of larger zooplankton, handling of ‘giant’ diatoms, scraping algae from beneath sea ice and lifting detritus from the seabed. High mobility and physiological robustness enable krill to explore three feeding grounds – the water column, the sea ice and the benthos. Variability in access and productivity of these feeding grounds leads to fundamental differences in krill overwintering across their habitats. Gut passage time, absorption efficiency and fecal pellet density vary with food concentration and nutritional needs. Therefore krill fecal pellets have a dual role; some promote the export of carbon and nutrients while others facilitate the recycling of material in the upper water column. Krill grazing can suppress phytoplankton blooms, but this tends to be a localised phenomenon where krill abundances are exceptionally high. Conversely, krill appear to have major conditioning effects due to nutrient supply (e.g. ammonium, iron), although their role in Southern Ocean biogeochemical cycles is only starting to be discovered.

Keywords Diet • Ingestion rates • Stable isotopes • Polyunsaturated fatty acids • Fecal pellets

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