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Metabolic properties of Northern krill, *Meganyctiphanes norvegica*, from different climatic zones. I. Respiration and excretion

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Abstract Adaptive processes linked to overall metabolism were studied in terms of oxygen consumption and ammonia excretion in each of three self-contained krill populations along a climatic gradient. In the Danish Kattegat, krill were exposed to temperatures which ranged from 4°C to 16°C between seasons and a vertical temperature gradient of up to 10°C during summer. In the Scottish Clyde Sea, water temperatures varied less between seasons and the vertical temperature gradient in summer was only 3°C. Temperatures in the Ligurian Sea, off Nice, were relatively constant around 12–13°C throughout the year, with a thin surface layer (20–30 m) of warm water developing during summer. The trophic conditions were rich in the Kattegat and, particularly, in the Clyde, but comparatively poor in the Ligurian Sea. Oxygen consumption increased exponentially with increasing experimental temperature, which ranged from 4°C to 16°C. Overall respiration rates were between 19.9 and 89.9 μmol O_2 g^{-1} dry wt h^{-1}. Krill from the Kattegat, the Clyde Sea, and the Ligurian Sea all exhibited approximately the same level of oxygen consumption (30–35 μmol O_2 g^{-1} dry wt h^{-1}) when incubated at the ambient temperatures found in their respective environments (9°C, 5°C, and 12°C). This indicates that krill adjust their overall metabolic rates to the prevailing thermal conditions. The exception to this were the respiration rates of Ligurian krill from winter/spring, which were about twice as high as the rates from summer krill despite the fact that the thermal conditions were the same. This effect appears to result from enhanced somatic activity during a short period of increased food availability and reproduction. Accordingly, krill appears to be capable of adapting to both changing thermal and trophic conditions, especially when nutrition is a limiting factor in physiological processes.

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Introduction

Northern krill, *Meganyctiphanes norvegica* (Euphausiacea), is a typical component of zooplankton communities in the northern and northeastern parts of the Atlantic Ocean and the adjacent seas. It is one of the most wide-spread euphausiid species in the northern hemisphere and constitutes an important link in marine trophic chains (Pearcy et al. 1979). The distributional range includes the east coast of Canada from the Gulf of St. Lawrence, over the shelf south of Greenland and Iceland, to the British Isles and the Norwegian coast. The Greenland Sea and the Barents Sea are the northern limits of its distribution. To the south, krill are found in the Mediterranean and around the Canary Islands (Mauchline 1960; Mauchline and Fisher 1969).

Within this wide geographical range, Northern krill are exposed to a large variety of different bathymetric, hydrographic, seasonal, and trophic conditions. However, besides food availability, temperature is the major abiotic factor that directly and indirectly dominates the physiological ecology of this poikilothermic euphausiid. Krill occur in waters from 2°C to 15°C (Einarsson 1945; Lindley 1982). Low temperatures, on the one hand, have rate-limiting effects on metabolic processes. High temperatures, on the other hand, accelerate metabolic performance, but also directly increase energy demands. In contrast to its Antarctic relative, *Euphausia superba*, which is restricted to a narrow thermal range between –1.8°C and 2.5°C, Northern krill experience both low and high temperatures. Accordingly, Northern krill seems to

be a suitable organism to study how physiological and biochemical processes are adapted to different climatic extremes.

Concepts of metabolic adaptation and acclimation that are based on physiological responses of marine animals have been critically reviewed by Clarke (1987). Our study takes a comparative approach by focussing on populations of krill in three oceanic basins with different temperature regimes. Two of the study sites, the Clyde Sea and the Mediterranean, exhibited relatively constant temperatures over the annual cycle. The subsurface and deep waters of the Ligurian Sea are constantly at 12–13°C during summer and winter, while only a thin surface layer (ca. 30 m) increases in temperature during summer (up to 24°C). During vertical migration krill enter the surface layers only for short periods, but generally remain below the thermocline (Tarling et al. 1999a). The Scottish Clyde Sea exhibits temperatures between 6°C and 8°C in most of the water column throughout the year, with a relatively weak thermocline developing in summer. In sharp contrast to these conditions, the Danish Kattegat shows highly variable thermal conditions, with a seasonal shift of up to 12°C in upper water column temperatures and a vertical temperature gradient of 10°C in summer (Matthews et al. 1999).

Our sampling strategy involved ship-based campaigns at all three locations during two different seasons. Overall metabolic rates were determined through measuring respiration and excretion rates in on-board experiments carried out during each of the cruises. The results are discussed in view of possible adaptive processes in Northern krill that may be related to the climatic gradient, within which it occurs.

Materials and methods

Sampling locations and dates of expeditions

The areas investigated (Fig. 1) were the Ligurian Sea, off Nice (Ligex); the Arran Deep in the Clyde Sea, Scotland (Scotex); and the Læsø Deep in the Danish Kattegat (Kattex). Sampling was carried out during two different seasons. The respective positions and sampling periods are presented in Table 1. All cruises were carried out on board the R.V. "Heincke".

Northern krill, *Meganyctiphanes norvegica*, were caught either with a ringtrawl (1.4 m diameter, 500 μm mesh size) or a MOCNESS (multiple opening–closing net and environmental sensing system; Wiebe et al. 1976) equipped with 2,000 and 300 μm mesh nets. In order to prevent damage of the animals, hauls were kept short (10–20 min) and were carried out predominately during the night, when the krill migrated from the deep into the upper water layers. After capture, krill were separated immediately into aquaria with cooled and aerated seawater. Animals used for respiration measurements were allowed to recover for several hours before they were used in experiments.

Hydrography

Temperature and salinity of the water column were measured with an OTS-probe (Meerestechnik Elektronik, Kiel, Germany) at least every other day. Continuous monitoring of salinity and temperature was also carried out during the MOCNESS hauls.

Biometry

In the home laboratory, samples were thawed, and the total length (L_t) was measured from the front of the eyes to the tip of the telson. Carapace length (L_c) was determined as the distance between the front of the eyes and the transition between carapace and first abdominal segment on the dorsal side. The relation between carapace length and total length was linear.

The wet weight (W_w) was determined on frozen krill (–80°C) after the specimens were left to thaw at room temperature and relieved of adhering water by gently blotting them on absorbent paper tissue. For the measurement of dry weight (W_d), animals were lyophilized for 36 h in a freezer-dryer (Leybold-Heraeus, GT 2). The relation between length and weight was best characterized by an exponential equation (see Table 2).

Respiration and excretion

Respiration rates were measured at 4, 8, 12, and 16°C. Six chambers (1.64 l) with a self-generating current system (Saborowski and Buchholz 1998) were used in combination with a Strathkelvin model 928 oxygen interface, model 1302 oxygen electrodes with polypropylene membranes, and an electromagnetic stirrer system (Variomag). Five chambers were supplied with krill in filtered seawater (0.2 μm), while one chamber received only water and served as a control. The number of krill used in the experiments varied between 2 individuals at 16°C, where metabolic rates were high, to 5 individuals at 4°C where metabolic rates were low. This experimental design allowed monitoring of distinct and well-detectable changes in oxygen concentration at low and high temperatures. Although the chambers used were designed to maintain the best conditions for krill, they were a compromise between the most natural conditions for the animals under study and the practicability for experimentation. Accordingly, a mutual influence between the animals cannot be excluded. Moreover, a potential influence cannot be quantified. In order to keep conditions as reproducible as possible, we always used at least 2 individuals in each experiment. To circumvent variability in respiration due to different maturity stages, we used males exclusively, as they do not develop large gonads as females do. The chambers were placed inside an incubator. During the first 3–4 h of the experiment, krill were allowed to adapt to experimental conditions. This was also a period when temperature and electrodes stabilized. The subsequent period (max. 8 h) of continuous oxygen decrease (not below 70% saturation) was recorded and used to calculate respiration rates. The variation in temperature did not exceed ± 0.5°C during the measurement. Bacterial respiration was determined routinely in all chambers immediately after the measurement on krill was terminated. These rates were treated as a blank and subtracted from the calculated rates.

In a second experimental series, krill were incubated in stoppered glass bottles (1 l) to obtain simultaneous measurements of oxygen consumption (determined with the Winkler method) and excretion determined with the indophenol method according to Koroleff (1983). Numbers of krill, incubation temperatures, and experimental duration were the same as described above for the self-generating current system. The determinations were carried out immediately after the experiments were terminated. The results from the simultaneous measurements were used to calculate the atomic O/N ratios.

Statistics

Respiration rates were normalized to a 30 mm standard-sized krill (200 mg wet wt and 50 mg dry wt) by applying a modified equation according to Dr. J. Voss (personal communication). This relation takes into account that the metabolic turnover follows an

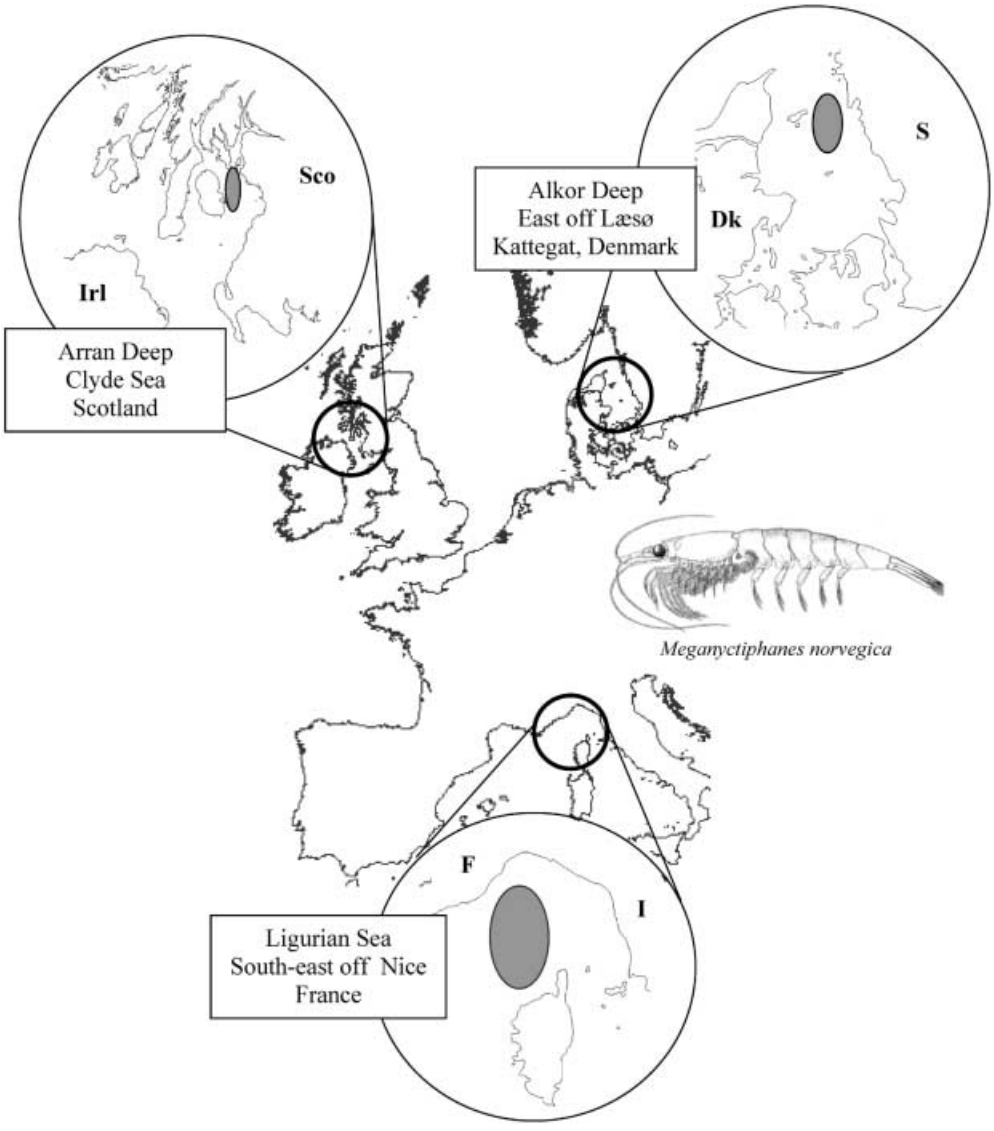

Fig. 1 Sampling locations of Northern krill, *Meganyctiphanes norvegica* (*shaded areas*) within the climatic gradient: the Arran Deep in the Firth of Clyde, the Alkor Deep in the Kattegat Channel, and the Ligurian Sea in the Mediterranean

allometric relation, in that larger animals have lower metabolic rates per unit weight than smaller animals have. When the respiration rate of a standard krill was set to be 100%, the resulting generalized relation is: $R_{rel} = 153.8 W_d^{-0.11}$ (R_{rel} is the relative respiration rate, W_d is the dry weight in mg). For example, the relative respiration rate for a 50 mg krill would correspondingly result in 100%; a 60 mg krill would have a rate of 98%; and a 30 mg krill, a rate of 106% compared to the standard krill. Since it is in practice more convenient to use a factor by which any krill can be converted into a standard krill we modified the equation as follows: $F = 0.65 W_d^{0.11}$ (F is the converting factor and W_d again the dry weight in mg). For a 50 mg krill this factor would be 1.00; for a 60 mg krill the factor would amount to 1.02; and for a 30 mg krill, the factor would be 0.95. Multiplying the respiration rate of any sized krill with the corresponding conversion factor will result in a standardized respiration rate, i.e. that which a 50 mg krill would exhibit.

Q_{10}-values of respiration rates were calculated by applying van't Hoff's generalization. In the following equation R_1 and R_2 represent the respiration rates at the temperatures T_1 and T_2:

$$Q_{10} = \left(\frac{R_2}{R_1}\right)^{10/(T_2 - T_1)}$$

Results

Hydrography

In April, during Ligex I, the temperature profile showed a thin layer (about 10 m) of comparatively warm surface water (14–16°C), while the subsurface and deep layers (up to 500 m) were uniformly at 12–13°C (Fig. 2a). In summer, the temperature of the surface water exceeded 22°C. Below the thermocline at about 20 m the subsurface and the deep water remained at 12–13°C.

In the Arran Deep winter temperatures were constantly at 6–7°C throughout the water column (Fig. 2b). During summer a slight stratification appeared which showed warmer surface waters of up to 12°C.

The summer surface temperatures of the Kattegat reached 16–18°C. With depth, temperature decreased

Table 1 Sampling locations and periods (*W* winter; *S* summer)

Location	Cruise	Season	Position	Max. depth (m)	Sampling period
Ligurian Sea	Ligex I	W	43°00′N; 07°00′E	2000	1–29 Apr 1996
	Ligex II	S			5–25 Sep 1997
Clyde Sea	Scotex I	S	55°41′N; 05°04′W	150	2–11 Jul 1996
	Scotex II	W			15–28 Feb 1997
Kattegat	Kattex I	S	57°16′N; 11°25′E	125	14–29 Jul 1996
	Kattex II	W			4–19 Mar 1997

Table 2 Morphometric parameters of *Meganyctiphanes norvegica* from all sampling locations (terms *a* and *b* refer to the equation $W_f = a \times L_t^b$)

	Abbrev.	Unit	Cruise					
			Ligex I	Ligex II	Scotex I	Scotex II	Kattex I	Kattex II
Males								
Number	n		148	341	170	295	314	207
Total length	L_t	(mm)	25.6–33.5	23.6–36.7	30.0–43.1	28.3–41.8	23.7–40.6	20.3–40.9
Carapace length	L_c	(% of L_t)	31.9 ± 1.2	30.4 ± 0.9	31.0 ± 1.2	30.5 ± 0.9	30.1 ± 2.1	30.2 ± 1.1
Fresh weight	W_f	(mg)	127–286	87–341	181–560	135–523	80–430	75–435
a			0.02417	0.00939	0.01571	0.00551	0.00577	0.0049
b			2.647	2.907	2.781	3.055	3.028	3.073
r			0.909	0.968	0.955	0.949	0.974	0.954
Number	n		151	317	169	296	314	209
Dry weight	W_d	(% of W_f)	25.7 ± 1.9	25.2 ± 1.9	27.4 ± 1.9	24.2 ± 1.9	24.7 ± 1.7	25.2 ± 2.0
Number	n		115	315	149	289	166	200
AFDW		(% of W_f)	22.7 ± 1.6	21.6 ± 1.9	24.5 ± 2.1	21.1 ± 2.0	21.9 ± 1.9	22.2 ± 2.0
Females								
Number	n		21	95	37	27	125	81
Total length	L_t	(mm)	27.4–31.6	32.1–36.6	30.4–40.5	33.5–40.9	25.4–39.5	29.0–37.8
Carapace length	L_c	(% of L_t)	32.7 ± 1.3	31.3 ± 0.6	32.4 ± 1.3	30.9 ± 0.9	31.6 ± 1.6	31.1 ± 0.9
Fresh weight	W_f	(mg)	139–230	222–357	230–497	236–449	114–376	160–386
a			0.07067	0.00382	0.01527	0.00567	0.01101	0.00312
b			2.333	3.172	2.806	3.040	2.852	3.213
r			0.823	0.933	0.944	0.957	0.958	0.941
Number	n		21	80	37	27	125	81
Dry weight	W_d	(% of W_f)	25.1 ± 2.6	25.2 ± 1.6	26.2 ± 1.3	24.3 ± 1.9	23.8 ± 1.3	24.2 ± 3.1
Number	n		5	79	15	26	88	81
AFDW		(% of W_f)	24.5 ± 1.1	21.8 ± 1.6	23.1 ± 1.6	21.1 ± 1.8	20.6 ± 1.3	21.5 ± 3.1

continuously towards 6–8°C. During winter, surface temperatures dropped below 2°C, but increased gradually with depth to about 5°C (Fig. 2c). A detailed analysis is given by Matthews et al. (1999).

Biometry

The biometric parameters represent an average picture of the size distribution of the populations (Table 2). The smallest animals were caught during both of the Ligex cruises, while the largest animals were found in the Clyde Sea. The relation between length and weight was well expressed by the exponential equation, as indicated by high correlation coefficients. The carapace length, as expressed as a relative share of the total length, was very similar at all locations. The relative dry weight was highest in both sexes of Scotex I krill. The same tendency was obvious in the ash-free dry weight; here, however, Scotex I and Ligex I values did not differ distinctly.

Respiration

The respiration data obtained from the different experimental series measured with either Clark-type electrodes or the Winkler method followed the same pattern. However, the Winkler incubation gave lower rates than the incubation in the current chamber as a result of lower swimming activity. At each location and in both seasons, rates increased exponentially with temperature (Fig. 3). Overall averaged oxygen consumption rates ranged between 19.9 and 89.9 μmol O_2 g^{-1} dry wt h^{-1}.

In Ligurian krill significant seasonal differences in respiration rates were evident. Krill caught during late summer had consistently lower rates, ranging between

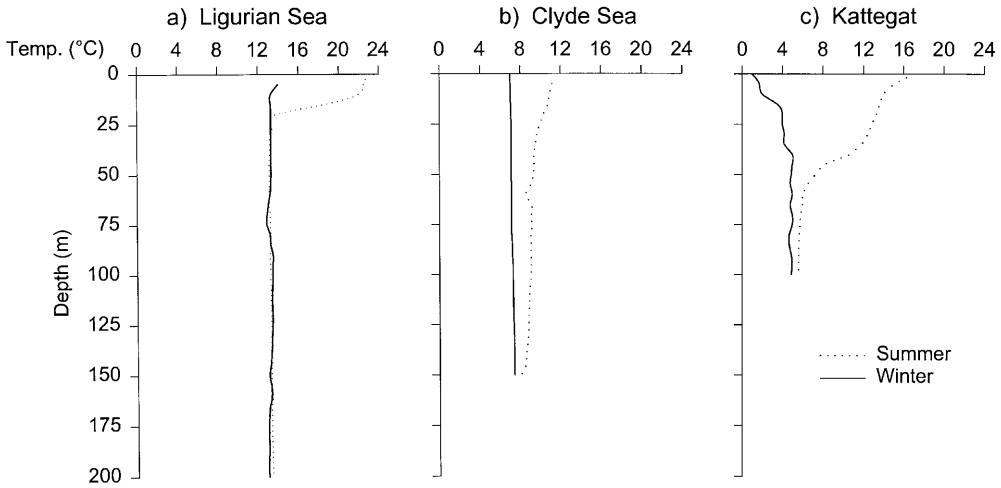

Fig. 2a–c Temperature profiles of the sampling locations at summer and winter: **a** the Ligurian Sea, **b** the Clyde Sea, and **c** the Kattegat. In the Ligurian Sea CTD-profiles were carried out to a depth of 500 m. The maximum depth exceeded 2,000 m. The profiles of the Arran Deep and the Alkor Deep correspond to the maximum depth

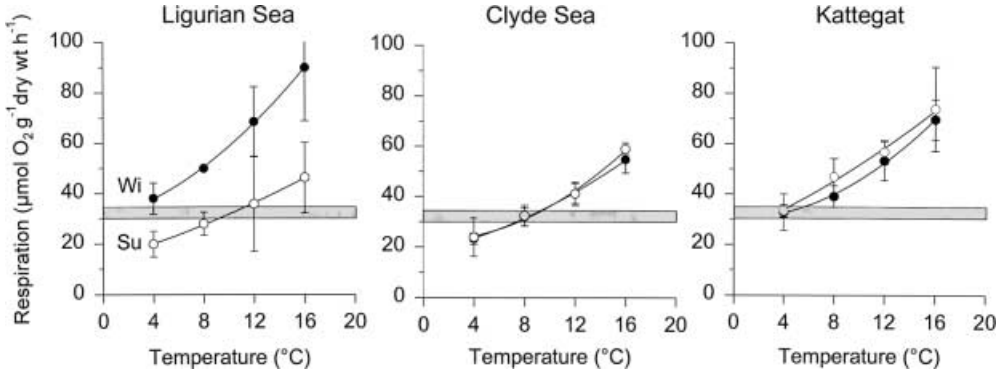

Fig. 3 *Meganyctiphanes norvegica*. Respiration rates in relation to the incubation temperature: the Ligurian Sea, the Clyde Sea, and the Kattegat (means ± SD, $n = 6$–10). The *shaded line* corresponds to the respiration rates at the respective ambient temperatures

19.9 µmol O_2 g^{-1} dry wt h^{-1} at 4°C and 46.4 µmol O_2 g^{-1} dry wt h^{-1} at 16°C, than krill from late winter. The rates of the latter ranged between 38.0 µmol O_2 g^{-1} dry wt h^{-1} at 4°C and 89.9 µmol O_2 g^{-1} dry wt h^{-1} at 16°C.

In contrast to the Ligurian krill, no significant differences between seasons appeared in krill from the Clyde Sea and the Kattegat. In the Clyde Sea, respiration rates in both seasons ranged from 23.2 µmol O_2 g^{-1} dry wt h^{-1} at 4°C to 58.9 µmol O_2 g^{-1} dry wt h^{-1} at 16°C.

In the Kattegat, respiration rates were higher than in the Clyde Sea and ranged between 33.3 µmol O_2 g^{-1} dry wt h^{-1} at 4°C and 73.8 µmol O_2 g^{-1} dry wt h^{-1} at 16°C.

At each of the ambient temperatures, i.e. 12°C in the Ligurian, 9°C in the Clyde, and 5°C in the Kattegat (assuming the deep water temperatures as ambient), krill exhibited similar respiration rates of 30–35 µmol O_2 g^{-1} dry wt h^{-1}. An exception were the Ligurian krill from the winter/spring which had rates twice as high.

The Q_{10}-values of respiration increase for the temperature increments studied ranged between 1.55 (4–8°C) in Kattegat summer krill and 2.46 (12–16°C) in summer krill from the Clyde Sea (Table 3). Q_{10}-values calculated over the entire temperature range from 4°C to 16°C ranged between 1.87 and 2.12.

Excretion

The excretion of ammonia-N rose with temperature (Fig. 4). The lowest rates of from 0.58 µmol NH_4-N g^{-1} dry wt h^{-1} at 4°C to 2.13 µmol NH_4-N g^{-1} dry wt h^{-1} at 16°C were found in Ligurian summer krill. In Ligurian krill from the winter the rates were about three times higher amounting to 3.02 µmol NH_4-N g^{-1} dry wt h^{-1} at 8°C and 4.21 µmol NH_4-N g^{-1} dry wt h^{-1} at 12°C; at 16°C rates decreased slightly. Due to technical problems, no data are available from Ligurian winter krill at 4°C.

In Clyde Sea krill excretion rates from the winter increased exponentially from 0.97 µmol NH_4-N g^{-1} dry wt h^{-1} at 4°C to 8.45 µmol NH_4-N g^{-1} dry wt h^{-1} at 16°C. Unfortunately, no summer data are available for technical reasons.

In Kattegat krill, excretion rates were similar between seasons ranging from 1.06 µmol NH_4-N g^{-1} dry wt h^{-1} at 4°C to 6.65 µmol NH_4-N g^{-1} dry wt h^{-1} at 16°C.

O/N ratios

The atomic O/N ratios of Ligurian winter krill ranged between 14 and 19 within the experimental temperature

Table 3 *Meganyctiphanes norvegica*. Q_{10}-values of respiration rates (*W* winter; *S* summer)

Cruise	Season	Temperature range		
		4–8°C	8–12°C	12–16°C
Ligex I	W	1.97	2.21	1.98
Ligex II	S	2.33	1.86	1.90
Scotex II	W	2.19	1.90	2.02
Scotex I	S	2.17	1.81	2.46
Kattex II	W	2.32	1.62	1.93
Kattex I	S	1.55	2.16	1.97

range of 8–16°C (Fig. 5). O/N ratios of summer krill were consistently higher at each temperature and varied between 20 and 30. A slight tendency towards increasing O/N ratios with temperature was evident in both seasons.

In contrast to the krill from the Ligurian, Clyde Sea krill showed a strong and consistent decrease of O/N ratios from 45 at 4°C towards 12 at 16°C. Kattegat krill from the winter showed a similar decrease with temperature. The values ranged between 41 at 4°C and about 16 at 16°C. In contrast, O/N values of Kattegat summer krill remained at an almost constant level between 15 and 20 at each temperature.

Discussion

The experiments were carried out at 4–16°C, which covers the natural thermal range of *Meganyctiphanes norvegica*. An extension of this temperature range was not possible. It was impossible to technically guarantee that a constant temperature would be maintained at a very low level, i.e. 0°C, in the system. At temperatures above 16°C the mortality of animals drastically increased and made meaningful measurements impossible. The results correspond well with previously measured respiration rates of Northern krill from different locations (Table 4).

Apparently, Northern krill adjusted overall metabolic processes, as measured by respiration rates, to obtain a constant level of 30–35 μmol O_2 mg^{-1} dry wt h^{-1} at the respective prevailing ambient temperature. This is true for Clyde Sea krill and for Kattegat krill when considering 8–9°C as ambient in the Clyde Sea and 4–6°C in the Kattegat. Compared to the Clyde Sea, thermal conditions within the water column of the Kattegat were much more variable between seasons. Although krill perform frequent vertical migration into upper water strata (Tarling et al. 1998), which are distinctly warmer during the summer, no seasonal variation in metabolic rates was evident in the Kattegat animals. It may be suggested that krill spend the bulk of their time in deep layers, below 50 m, and thus predominantly experience cold conditions, irrespective of season, to which they have physiologically adapted (Saborowski et al. 2000). This, however, does not exclude the possibility that krill utilize the temperature gradient to enhance other physiological processes such as moulting and spawning (Tarling et al. 1999b). Concerning short-term effects, no evidence was given by the experiments that krill from any location or season could rapidly compensate overall metabolic rates as a response to variable thermal conditions. Over the experimental range of temperatures, respiration rates increased exponentially, closely following van't Hoff's generalization. The calculated Q_{10}-values were not exceptionally low, as would be suggested as a result of rate compensation (Small et al. 1966), but were similar to those of Clyde Sea krill.

The most obvious difference between krill from the three locations appeared in the seasonal variation of respiration rates. While no changes between summer and winter were evident in the Kattegat and the Clyde Sea, krill from the Ligurian Sea, although exposed to the most constant thermal conditions, exhibited significant differences. Respiration rates of summer krill were constant (30–35 μmol O_2 mg^{-1} dry wt h^{-1}) at the ambient temperature of 12°C and, therefore, corresponded to the pattern found in krill from the Clyde Sea and the Kattegat. In contrast to summer krill, the respiration rates of krill from winter/spring were consistently higher at each experimental temperature, which resulted in a parallel upward shift of the respiration curve. The high rates of the winter/spring krill were confirmed during a land-based study in March/April 1998 (results not shown).

The notable characteristics of Ligurian krill cannot be explained by thermal effects, since temperature re-

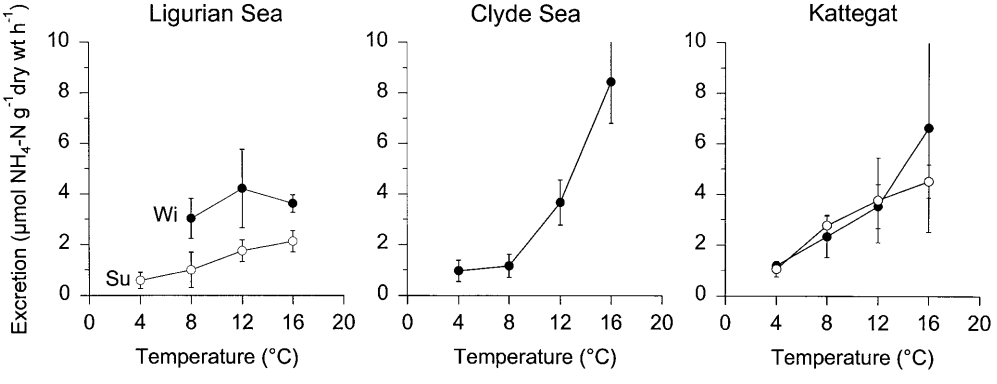

Fig. 4 *Meganyctiphanes norvegica*. Excretion in relation to incubation temperature: the Ligurian Sea, the Clyde Sea, and the Kattegat (means ± SD, $n = 6–8$)

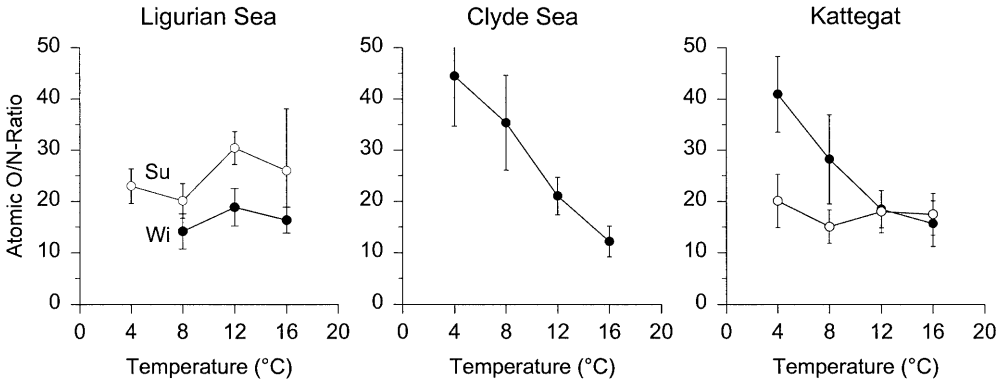

Fig. 5 *Meganyctiphanes norvegica*. O/N ratios in relation to incubation temperature: the Ligurian Sea, the Clyde Sea, and the Kattegat (means ± SD, $n = 6–8$)

Table 4 *Meganyctiphanes norvegica*. Some literature data of respiration rates

Source	Region	Season	Temperature (°C)	Respiration rate (μmol O_2 g^{-1} dry wt h^{-1})
Mayzaud (1973a)	Ligurian Sea	Nov	5–20	23.7–43.9
Mayzaud (1973b)	Ligurian Sea	Winter	13	56.7
		Spring	13	58.0
Sameoto (1976)	Gulf of St. Lawrence	Feb–Aug	2–10	60.3–92.9[a]
Båmstedt (1979)	Kosterfjorden (Sweden)	Dec–Sep	5–6	21.9–40.6
Voss (pers. comm.)	Kattegat (Alkor Deep)	Jun–Sep	5–10	50.1–73.4
Hirche (1984)	Gullmarsfjorden (Sweden)	Sep	6.5	46.9
Van den Thillart et al. (1999)	Gullmarsfjorden	Summer	10	38.7
Strömberg and Spicer (2000)	Gullmarsfjorden	Sep	7–15	16.0–30.3[b]

[a]Rates calculated for 10-mg animals
[b]Rates were recalculated from wet weight to dry weight assuming dry weight equals 25% of wet weight

mained most constant when compared with the other locations. The factor which, besides temperature, varies most distinctly between locations and significantly influences the life histories of the respective krill populations is the trophic environment.

In order to study the catabolic properties of krill, we performed a second experiment in parallel. Krill were incubated in conventional containers of 1 l volume, and oxygen consumption and nitrogen excretion were determined at the beginning and at the end of the incubation periods. This procedure allowed direct comparison of respiration and excretion over an integrated period of the same animals, maintained in the same container. Compared to the internal current system, krill respiration in the bottles was generally lower, but followed the same thermal profile. The lower rates must be attributed to the decreased encouragement to swim, due to the lack of water movement. In the same way, excretion must be expected to be lower than in the current chambers. However, the general seasonal and thermal patterns and, particularly, the ratio between respiration and excretion should remain unchanged.

A different response of NH_3-N excretion rates to the experimental temperatures was evident between the Ligurian krill, on the one hand, and, at least, the Kattegat krill, on the other hand. In the Kattegat, excretion rates increased with temperature and were similar between seasons. A strong increase was also observed in the Clyde Sea during winter. Unfortunately, no seasonal comparison can be made here because no excretion data are available from the Clyde Sea summer experiment (Scotex I). Ligurian krill, again, exhibited significant differences between seasons, with elevated excretion rates in winter/spring and lower rates during late summer.

The atomic O/N ratio is an indicator of the predominantly metabolized energy source, which can be derive from recently ingested food or the degradation of storage products. Low O/N ratios indicate elevated protein catabolism, while increasing ratios point toward the utilization of lipids and carbohydrates (Mayzaud and Conover 1988). The main energy sources in krill are protein and lipids. The latter also constitute the main storage products. Carbohydrates, in contrast, are rather low in krill (Raymont et al. 1969, 1971; Båmstedt 1976; Buchholz and Prado-Fiedler 1987).

In the winter samples from the Clyde Sea and the Kattegat, O/N ratios decreased continuously with increasing experimental temperatures. Accordingly, these winter krill utilize stored lipids to a high extent at their ambient temperatures of 7–8°C and 4°C, respectively. The O/N ratios are also similar at the respective ambient temperatures, amounting to 35–40. This indicates equally favorable trophic conditions at either location as well as to reflect similar feeding and life strategies of both populations. Furthermore, these results show that the lipid stores were not entirely exhausted at the end of

the winter, when sampling was carried out. This suggestion is also supported by lipid data. According to Virtue et al. (2000), winter krill from the Kattegat still had higher lipid concentrations than summer krill. In the Clyde Sea, concentrations were almost at the same level during either sampling period, but they were higher than in the Kattegat krill. The shift towards lower O/N ratios at higher incubation temperatures indicates that, besides lipids, an increasing amount of proteins must be mobilized to supply the accelerated metabolic demand. Ligurian krill, again, showed a different pattern with almost equal O/N ratios over the temperature range studied, during both seasons. The higher O/N ratios during summer/fall indicate a slightly higher degree of lipid utilization than during the winter/early spring.

In the Kattegat and in the Clyde Sea krill can make use of a variety of food items, including phyto- and zooplankton and even material of terrestrial origin such as detritus (Lass et al. 2001). Typically, the annual cycle in the Kattegat consists of a spring bloom, a summer low, and a pronounced autumn bloom, followed by low levels of biomass in the winter. Zooplankton production follows the chlorophyll maximum with a delay of about 1 month (Boysen and Buchholz 1984). Food availability closely correlates with growth, which proceeds from early spring to December. Kattegat krill show an extraordinarily long spawning season, which lasts from April to October (Boysen and Buchholz 1984). The period of rich food supply is also reflected by the accumulation of storage products. The highest concentration of lipids appears in November/December and then decreases continuously toward spring (Buchholz and Prado-Fiedler 1987), which indicates catabolism of food reserves as a consequence of food scarcity during the winter (Båmstedt 1976).

In the Clyde Sea the conditions for Northern krill were designated as "extremely favorable" by Mauchline (1960). Here, the spawning season lasts from March to July. The rich food availability was reflected in the present study by the superior size of the Clyde Sea animals. Krill from the Clyde Sea were more herbivorous than Kattegat krill; this, however, is correlated with the higher ratio of phytoplankton to copepod biomass in the Clyde Sea (Lass et al. 2001). Krill from the Clyde Sea had the highest contents of total lipids during either season, compared to specimens from the Kattegat and the Ligurian Sea (Virtue et al. 2000). The seasonal pattern of lipid accumulation for krill in Scottish waters is similar to that in the Kattegat, with highest concentrations in October and in November, respectively (Raymont et al. 1971). Again lipid concentration decreases towards spring, but, as mentioned above, lipid reserves were not exhausted at the end of the winter.

Compared to the two northern locations, Ligurian waters are oligotrophic, with low levels of primary production and zooplankton biomass throughout most of the year. The food-limiting conditions in the Ligurian Sea may be demonstrated best by the growth pattern of the krill population. Somatic growth slows down when gonad growth starts and does not recover after the reproductive period. The average maximum size of the 1+ cohort is smaller than that of any other in the NE Atlantic (Labat and Cuzin-Roudy 1996). Again, the length and weight data presented here correspond to this report, showing the smallest krill in the Ligurian Sea. The occurrence of krill in the >2,000 m deep Ligurian Sea is closely related to the Ligurian current system (Boucher et al. 1987; Labat and Cuzin-Roudy 1996), which parallels the Cote d'Azur in a southwestern direction. In the sampling zone, south-east of Cap Ferrat, the period of increased primary and secondary productivity appears during late spring, simultaneously with the development of the thermocline (Fabiano 1984; Goffart et al. 1995), and provides the basis for growth and reproduction. Corresponding to the seasonality of plankton production, the lipid stores of Ligurian krill are highest during late spring and are at a minimum during winter, which is almost the reverse of the seasonal lipid pattern of krill from the north (Mayzaud et al. 1999). During spring, males start to permanently develop spermatophores, while vitellogenic females produce eggs (Cuzin-Roudy 1993). However, compared to the Clyde Sea and the Kattegat, Ligurian krill have the shortest reproductive period, from about February to May (Cuzin-Roudy and Buchholz 1999).

Corner et al. (1965) observed in marine copepods an increase of nitrogen excretion when the concentration of food was raised as might occur during a spring outburst of phytoplankton. In the absence of food, nitrogen excretion rapidly decreased. This relation seems also to be valid for Northern krill, particularly from the oligotrophic Ligurian Sea: nitrogen excretion was highest and the O/N ratios were lowest during the season of high food supply, which is the late winter and the early spring for Ligurian krill.

Apparently, physiological and/or behavioral changes are associated with this period, which becomes evident in an increase of overall metabolic rates. Support for this suggestion is also given by a seasonal study on excretion rates in Ligurian krill: Roger (1978) found a sharp peak of NH_3 excretion during March and April, showing levels more than twice as high as during the other seasons. This profile corresponds to the present results on excretion. It can also support the finding of elevated respiration rates in winter/spring, assuming that excretion and respiration rise proportionally.

We conclude that krill from different climatic regions adjust overall metabolic rates, as measured by respiration, to maintain a constant metabolic level related to the prevailing ambient temperature. However, trophic conditions are capable of masking this thermal effect, particularly, when food is a limiting factor. In this respect, krill from the Clyde Sea and the Kattegat, which receive sufficient food throughout the season, seem to be predominantly affected by the thermal regime. In contrast, Ligurian krill, which inhabit oligotrophic waters, increase metabolic activity during a favorable period, e.g. elevated plankton production. Ligurian krill follow

a life strategy of utilizing as much energy as possible within the short period of increased primary productivity for growth, reproduction, and accumulation of energy stores, which guarantee survival during subsequent periods under limiting nutritive conditions. None of the krill studied, however, immediately responded to short-term thermal variation by compensating metabolic rates. Accordingly, the observed compensatory effects in the Kattegat and the Clyde Sea must be interpreted as long-term adaptations to features in the respective environments.

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