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Studies on the seasonal biochemistry of the Northern krill *Meganyctiphanes norvegica* in the Kattegat

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ABSTRACT: A well defined pelagic population of the Northern krill, *Meganyctiphanes norvegica* was sampled annually at a specific location in the Skandinavian Kattegat, and the major biochemical components were measured. Protein and lipid were the main constituents and underwent the most pronounced seasonal changes, clearly correlated to the prevailing supply of food organisms. The amount of lipid increased to a maximum of 48 % of the dry weight towards winter, out of phase with gonad maturation, and therefore interpretable as deposition of overwintering reserves. Utilisation of stored reserves proceeds over winter, with loss of lipid, and decrease in weight but not in length. Comparison with literature data showed similarities with other krill populations from different geographical locations. The biochemical components of *Euphausia superba*, the key organism of the marine Antarctic ecosystem, resembled those of *M. norvegica*. Special polar adaptations are not obviously expressed in the proximate biochemical composition.

INTRODUCTION

Meganyctiphanes norvegica is an important member of the pelagic ecosystem in the North Atlantic region, particularly as a food source for fish and whales, and also as a potential source for commercial fishery (Mauchline & Fisher, 1969; Einarsson, 1945; Falk-Petersen, 1981). It has, therefore, been studied quite intensively (cf. Boysen & Buchholz, 1984), although year round studies have been hampered by the obvious difficulties in following distinct pelagic populations for long periods (Falk-Petersen, 1981). In contrast, a unique situation was encountered in the Kattegat where the annual development of a largely undisturbed population could be investigated. This population was confined by hydrographical and topographical conditions to a specific location, the so-called Läsö-Deep (Ulrich, 1983). Concomitant with a detailed analysis of the population structure (Boysen & Buchholz, 1984), samples were taken for determination of biochemical parameters. The results of this study are presented here. Good documentation of the abiotic parameters in the investigation area was possible, and plankton-stocks were also monitored. Accordingly, the influence of the seasonally changing availability of food sources on sexual maturation and energy storage of *M. norvegica* could be well differentiated and effects on biochemical composition studied.

M. norvegica is a relatively large euphausiid, which is able to hold its position against currents as observed at the Kattegat location. In this respect, it is quite similar to the most

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abundant euphausiid species, *Euphausia superba* (see also Kils, 1982). Other ecologically important species like *Euphausia pacifica* are considerably smaller (Mauchline & Fisher, 1969). Generally, the two former species share several physiological properties (Buchholz, 1985; Adelung et al., 1987; Spindler & Buchholz, 1987) and seem to be comparable, in spite of their different habitats, boreal versus polar. Accordingly, studies on the Northern krill *M. norvegica* can also shed light on the biology of *E. superba*, one of the key organisms of the marine Antarctic ecosystem.

MATERIAL AND METHODS

Meganyctiphanes norvegica individuals were collected during the period March 1981 to February 1982 from the Läsö-Deep, located east of the Danish island Läsö at 57°16.6'N, 11°25'E (see Ulrich, 1983, for a description of the topography of the area). The sampling methods have been described in detail by Boysen & Buchholz (1984). The samples for biochemical investigations were quickly frozen and stored at −20 °C until analysed. The frozen samples were quickly thawed in sea water and separated into year-classes according to Boysen & Buchholz (1984). The specimens belonging to year-classes I and II were separated into males and females. The individuals were then quickly rinsed in distilled water, blotted dry on filter paper, and freeze-dried for approximately 36 h. Each dried specimen was weighed in tared assay tubes just before analysis, on a Mettler HK 60 semimicrobalance (accuracy ± 0.01 mg).

Biochemical analyses were carried out on individual specimens. The estimation of total protein was made using the modified Biuret method described by Båmstedt (1974). Total lipids were extracted using the method of Folch et al. (1957), by extracting with chloroform-methanol 2 to 1 using an Ultra-Turrax homogenizer followed by purification with 0.9 % aqueous sodium chloride. The lipid extract was analysed by the colorimetric sulphophosphovanillin method against a standard solution of cholesterol according to the method of Barnes & Blackstock (1973). Carbohydrate determination was made according to Raymont et al. (1964) as indicated by Båmstedt (1974), and calibrated against standard-glucose. Chitin was determined according to Båmstedt (1974). Individuals used for ash weight were incinerated in a muffle furnace at 540 °C for 24 h. Differences in the main biochemical components were tested by means of a F-Test, which was preceded by a test for normal distribution and a Bartlett-Test for variance homogeneity followed by the Multiple Range Test after Duncan. In the case of non-normal distribution or inhomogeneity of variance, the non-parametric Nemenyi-Test was used. For statistical analysis, Sachs (1984) served as a reference.

RESULTS AND DISCUSSION

Annual studies on populations of *Meganyctiphanes norvegica* including information on their biochemical composition are summarized by Båmstedt (1976). Recent data is given by Falk-Petersen (1981) and Saether & Mohr (1987). All studies on *M. norvegica* so far have been conducted in more land-influenced environments, either in Scottish firths or in Norwegian fjords. Boysen & Buchholz (1984) were the first to report in detail on a pelagic population found in the Kattegat, with reference to biotic and abiotic conditions.

Those studies are supplemented by the present investigation which provides information on its seasonal biochemistry.

Based on the uniformity of length/frequency distributions, Mauchline (1985) described an Atlantic cohort of *M. norvegica* as belonging to a coherent pelagic population. The same argument, which was extended by the even development seen in sexual maturation, was used to attribute the term true population to the Northern krill in the Kattegat. Accordingly, it was assumed that external influences on the population studied, such as immigration of animals from the Skagerak with different environmental, in particular nutritional, background were negligible. This special situation was regarded as a good prerequisite for the investigation of the annual changes of biochemical parameters.

Boysen & Buchholz (1984) describe the annual changes in the standing crops of phyto- and zooplankton of the study area. Here the typical cycle of a spring bloom, a summer low and a pronounced autumn bloom followed by very low winter levels can be seen. The peaks of zooplankton biomass follow the chlorophyll maximum with a delay of approximately one month. In spring and autumn, diatoms predominate, whilst in summer dinoflagellates are more abundant. Copepods constitute ca 95 % of the zooplankton standing stock throughout the year. *M. norvegica* is mainly carnivorous but has been shown to use phytoplankton as staple food as studied in detail in the Läsö-Deep (Klages 1983). Boysen & Buchholz (1984) found a clear relationship between the availability of food and growth in weight, Båmstedt (1976) and Falk-Petersen (1981) concur with this, although the growth curves for *M. norvegica* show some discontinuities in the latter study.

The seasonal changes in dry weight of *M. norvegica* and of the standing stocks of zoo- and phytoplankton in the Läsö area are depicted in Figure 1 (see also Boysen &

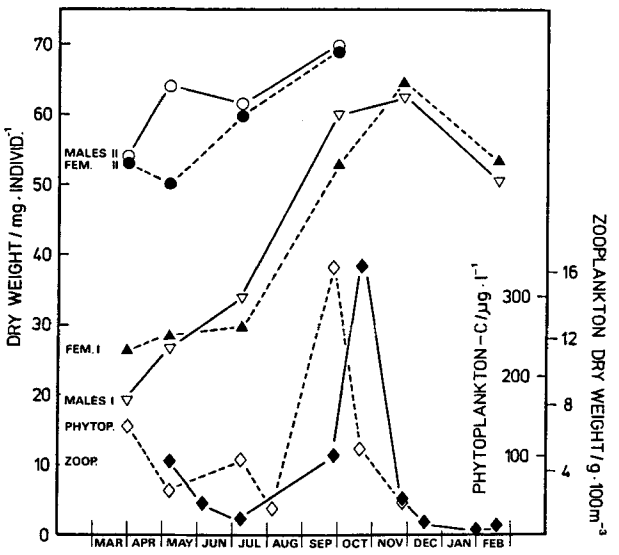


Fig. 1. *Meganyctiphanes norvegica*. Seasonal variation in dry weight (mg · individuum^{-1}) in year-class I and II. Males: continuous lines; females: dashed lines. Zooplankton (DWT = dry weight, g · 100^{-3}m) and phytoplankton (carbon, µg · l^{-1}) levels in the study area. Zooplankton: filled rhombs Phytoplankton: open rhombs

Buchholz, 1984). The phytoplankton carbon is calculated from chlorophyll a values. The zooplankton weight excludes the euphausiids.

The current material shows that the annual plankton-availability closely correlates with the growth in weight in *M. norvegica* in the year classes I and II in Figure 1. The decreasing standing stock from the downslope of the spring plankton bloom towards summer is reflected in relatively slow krill growth rates. The steeply increasing values at the time of the autumn bloom are followed by a considerable gain in weight in the animals. During winter, plankton growth stagnates and the krill loses weight accordingly. This weight regression during winter is not concomitant with a length decrease (Buchholz, 1985). According to a hypothesis by Ikeda & Dixon (1982), such winter-shrinkage does occur in *E. superba*. Consequently, body shrinkage as an overwintering strategy is not a general feature in euphausiids.

The annual biochemical changes are shown in Table 1: To aid interpretation of the

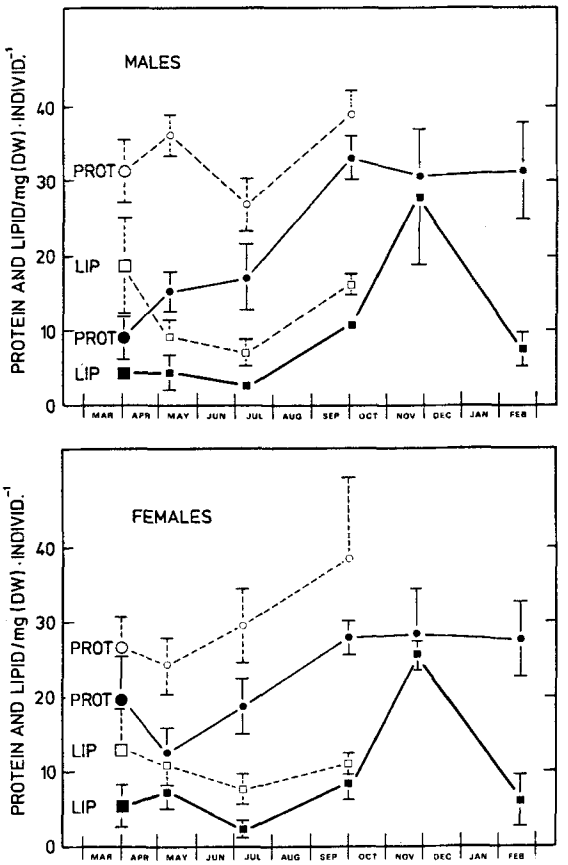
Table 1. Seasonal biochemical composition of *Meganyctiphanes norvegica*. The values are expressed as percentage of the dry weight. Mean values are given; standard deviations are summarized as average coefficient of variation (CV/%). n: number of specimens analysed; I, II, 0: year classes

Groups	Date	DWT [mg]	% DWT					
			Protein	Lipid	CH_2O	Chitin	Ash	Total
Males I	31/3	19.3	53.9	20.8	1.6	5.1	18.0	99.4
	7/5	26.6	69.4	18.3	1.4	4.2	14.0	107.3
	7/7	33.9	50.6	7.8	1.7	4.6	21.9	86.5
	30/9	59.9	56.8	18.6	1.5	4.2	15.4	96.6
	26/11	62.4	47.6	47.8	2.1	3.0	14.0	114.6
	16/2	50.4	61.7	15.5	1.6	3.1	18.1	100.0
II	31/3	53.7	55.9	28.1	1.6	4.2	16.5	106.3
	7/5	63.8	57.2	16.6	1.0	3.9	13.5	92.3
	7/7	61.4	48.1	10.8	1.0	4.2	20.8	85.0
	30/9	69.5	54.7	21.2	1.3	4.0	16.2	97.3
Females I	31/3	26.4	55.4	10.0	1.6	4.2	17.6	88.9
	7/5	28.2	53.6	25.6	1.2	2.9	11.2	94.5
	7/7	29.5	52.7	8.7	1.7	3.6	18.4	83.7
	30/9	52.9	55.7	16.9	1.5	3.7	16.3	94.1
	26/11	64.4	49.0	44.2	2.1	3.0	13.8	112.1
	16/2	53.2	52.9	10.7	1.9	3.0	17.6	86.2
II	31/3	53.0	47.6	26.2	1.7	3.7	16.7	95.9
	7/5	49.9	53.8	21.7	1.2	3.8	11.1	91.5
	7/7	59.8	46.2	12.8	1.2	4.1	19.8	84.2
	30/9	68.7	50.1	17.1	1.6	3.6	16.2	88.7
Juveniles 0	30/9	3.8	54.4	14.7	2.0	5.3	29.1	105.5
	26/11	13.9	51.3	21.6	2.0	3.8	18.4	97.0
	16/2	12.1	56.9	10.5	1.5	2.4	20.0	91.3
Mean		–	53.7	19.4	1.6	3.8	17.2	–
	CV%	26.2	11.0	18.6	15.8	15.5	6.9	
	n	12–38	3–7	3–7	2–7	2–8	2–7	

variations in the composition of *M. norvegica* in the Läsö-Deep, the amount of each biochemical component is expressed as a percentage of the dry weight. This avoids any errors caused by variation in water content, and conveys information which helps distinguish the accumulation of a certain component due solely to growth from the storage as a reserve substance (Table 1).

For comparison, graphs (Figs 2 and 3) were added to give an impression of the development in absolute amounts. A sample size of generally 5 specimens per data point seem sufficient as standard deviations are low. For technical reasons, a two-month interval between data points is taken in contrast to the roughly monthly interval of the population analysis conducted by Boysen & Buchholz (1984).

Carbohydrates stay low throughout the year and show no differences in relation to sex and year-class ($p = 0.05$). Accordingly, these compounds are insignificant as a metabolic store, in contrast to other invertebrates, e.g. molluscs, where glycogen depots can constitute over 30 % of the dry weight (Walne & Mann, 1975).



Figs 2 and 3. *Meganyctiphanes norvegica*. Annual development of mean biochemical content (mg · individuum^{-1}) of protein (prot) and lipid (lip) in year-class I (straight lines) and year-class II (dashed lines). Standard deviations indicated as bars (partly shown one-sided or inside symbols)

A slight decrease in the chitin proportion over the year reflects the changing surface to weight ratios in growing animals. The same applies to ash content, although a depression is evident in the latter in May when lipid and protein show peak values. Therefore, the apparent drop in ash percentage is generated by a proportional effect.

Protein and lipid are the most important body components and also show the most distinct seasonal changes. These variations can be linked to the availability of food (see Figs 1–3).

Protein and lipid-levels (in mg/individual: Figs 2 and 3) are generally low and/or decrease after the spring plankton bloom in the two sexes as well as year classes. Towards autumn, parallel to rising plankton values, lipid and protein values increase steeply to a maximum in November. Until February, protein values change little due to the weight decrease (Fig. 1), whereas the marked decrease in lipid can be associated with its use as energy source during winter. Consideration of proportions (Table 1) rather than of absolute amounts (Figs 2 and 3) makes this even clearer:

The protein proportions in both sexes in year class I do not show marked changes but oscillate slightly around a value of 53 ± 2 % in females, and 57 ± 8 % in males (data calculated from Table 1). Accordingly, the proportion of protein as a structural body component stays the same in a growing animal, whereas lipid proportions change as energy reserves are built up and utilized again in relation to the prevailing food supply. The weight loss during winter (Fig. 1) is therefore a consequence of lipid depletion.

Protein and lipid amounts are naturally higher in year-class II krill ($p = 0.05$; see also Table 1), but the annual pattern is similar to year-class I (Figs 1 and 2), until animals disappear in autumn, presumably due to senescence and predation.

In relative and absolute amounts, the winter peak in lipids is marked. In year-class I, it constitutes 48 % of the dry weight of males and 44 % of that of females. This would mean a difference of 40 % and 36 % respectively between the summer minimum and the winter maximum. In summary, it can be stated that the major components of the Northern krill, i.e. protein and lipid, show seasonal changes closely related to the standing stock of surrounding plankton. The major physiological role of protein is connected to growth, whereas lipid is used mainly as a metabolic depot.

A second, much discussed interrelationship with sexual maturation is not substantiated by our data of the Kattegat-krill. Falk-Petersen (1981) concludes that lipids show variations linked to gonad maturation mainly during winter in a Norwegian fjord. Båmstedt (1976) comes to the same conclusion but contends that the loss in lipids during winter cannot be explained solely on the grounds of gonad maturation but to a greater extent by catabolism of internal reserves. In the case studies here, neither maturation nor spawning coincided with the observed lipid decrease. In August, approximately 60 % of the females have laid their eggs and by October virtually all the females have spawned (Boysen & Buchholz, 1984). At that time, the lipids are still increasing. Thus, they are out of phase with gonad activity and reach their peak in late autumn. At the same time, the number of spermatophore-carrying males is reduced to a minimum. On the other hand, ovary maturation starts in January and continues until the end of July. It must therefore be concluded that the main function of the lipids stored in late September and November is to fuel the metabolism during winter, i.e. they are an overwintering reserve.

The values presented here do not allow fine temporal resolution, but quite obviously

in May, halfway through the maturation cycle, the lipid content is approx. 1.4 times higher in females than in males (Table 1) apparently due to egg production. The latter data accord well to the work of Bachler (1984), who found a factor of 1.3 in lipids of gravid females versus males in *M. norvegica* from the Läsö-Deep. The lipid proportion drops off in females towards July as eggs are released, and the values equal those of the males ($p = 0.05$). The clear correlation of the lipid content with phases of sexual maturation was only possible on the basis of the previous detailed population study (Boysen & Buchholz, 1984).

M. norvegica in the Kattegat shows similar spawning times to the Antarctic *E. superba:* both species spawn between mid and late summer (Boysen & Buchholz, 1984; Everson, 1977). Accordingly, it would be of great interest to know if lipids also constitute an overwintering store in *E. superba.* So far, no extensive seasonal data on lipid composition are published although some are in preparation (A. Clarke, W. Hagen, pers. comm.)

The two euphausiid species correspond in another respect: in *M. norvegica* the predominant lipid class is triacylglycerol (= TAG; Bachler, 1984; Clarke, 1984b; Saether et al., 1986). In *E. superba* a high percentage of this compound is also found, although accompanied by a considerable amount of phospholipids (Clarke, 1980; Ellingsen, 1982; Reinhardt & Van Vleet, 1986). The lipid class composition does not change substantially in relation to season in the Northern krill (Sargent & Falk-Petersen, 1981). Accordingly, the data presented here suggest that TAG can function as the overwintering reserve in *M. norvegica.* Whether TAG also constitutes part of the depot lipids for overwintering in *E. superba* remains to be elucidated. Apart from a single report by Reinhardt & Van Vleet (1986) on *E. superba,* neither of the species regularly contain wax esters, which form the major and typical depot lipid in other zooplankton species such as copepods and some other smaller euphausiids (Lee et al., 1971; Sargent, 1976; Bachler, 1984; Clarke, 1984a; Saether et al., 1986).

In comparison to the literature, the data of the current investigation correspond well to values given by Båmstedt (1976). The latter author compares the overall means of the annual study irrespective of sex and season (see Table 1 for present data). As the biochemical composition changes considerably within the year, it is favourable to differentiate into seasonal values. In Table 2, this is done by grouping together spring and summer data, where available, or spring data, contrasted with the maximum winter-value, if given. The results on *M. norvegica* are further grouped according to latitude and compared with *E. superba,* in order to be able to deduct different composition due to possible adaptations to the environment, whether boreal, subarctic or truly polar.

Considering the lipid/protein ratios in Table 2, the lipid percentage (15 %) of the present study is lowest in *M. norvegica.* Accordingly, it can be argued that the lipid content increases with latitude in that species. Falk-Petersen (1981) in fact states that the higher lipid values in the subpolar population (spring/summer, 35 %) are a consequence of cold water adaptation. Such dependency has been clearly demonstrated in other zooplankton species (Clarke, 1983). On the other hand, the value given by Saether & Mohr (1987) for *M. norvegica* from the same subarctic region is lower by 9 % than in the former study. *E. superba* as a true polar species has relatively low lipid values (summer, 16 %: Ellingsen, 1982; 21 %: Clarke, 1980) which also indicates that the high value given by Falk-Petersen is unusual. We feel therefore that the otherwise close range of the lipid

Table 2. Comparison of biochemical composition of *M. norvegica* and *E. superba* in relation to latitude. The given values include data, if differentiated, of year-class I animals (♂♂ and ♀♀) as recalculated from the literature. Data are in percent/dry weight. S = spring, SS = spring/summer, SU = summer, W = winter peak value; months are indicated as figures; *singular value

Species/ Region	Latitude	Season	Protein	Lipid	CH_2O	Chitin	Ash	Reference
Meganyctiphanes norvegica								
Kattegat	57 °N	SS 3, 4, 7	55.9	14.9	1.5	4.1	17.2	current study
		W 11	48.2	46.5	2.1	3.0	13.9	
Bals Fjord	69 °N	SS 4–7	36.8	35.4	–	–	15.8	Falk-Petersen (1981)
		W 10	36.1	42.4	–	–	13.4	
Bals/Ulls Fjord	69 °N	S 2–4	44.2	25.8	–	–	12.8*	Saether & Mohr (1987)
Euphausia superba								
South Georgia	53–59 °S	SU 1–3	48.5	20.5	2.3	9.3	15.5	Clarke (1980 and pers. comm.)
Weddell Sea	60–73 °S	SU 1–2	44.8	15.9	–	2.3*	17.0	Ellingsen (1982)

values – including the boreal to subarctic Northern as well as the Antarctic krill – does not clearly point to a geographical correlation in respect to lipid contents. More information, in particular on *E. superba*, is needed to come to a more definite conclusion.

Carbohydrate, chitin and ash values compare well in the two krill species. The relatively high chitin value found by Clarke (1980) in *E. superba* is presumably due to the mild extraction procedure in relation to other work. As a consequence, the close similarity in proximate biochemical composition of the Northern and Antarctic krill supports the above suggested good comparability in terms of general physiology. On the other hand, the relatively simple but widely used methods of biochemical determination as presented here may be too crude to detect slight but important differences. A more sophisticated biochemical analysis of other body components, particularly in relation to the moulting processes, is currently in press (Spindler & Buchholz, 1987) and a further paper is being prepared for publication.

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