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Moult cycle-related changes in feeding rates of larval krill *Meganyctiphanes norvegica* and *Thysanoessa* spp.

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ABSTRACT: Knowledge of crustacean moulting is derived mainly from benthic decapods, which often show profound changes in physiology and behaviour through the moult cycle. In contrast, euphausiids are suggested to be little impaired by moulting, enabling a swarming pelagic life. The aim of this study was to quantify moult cycle-related changes in the feeding activity of 2 euphausiids, *Meganyctiphanes norvegica* and *Thysanoessa* spp. Late furcilia larvae and early postlarvae were kept individually over 6 to 7 wk and fed with either a high or low concentration of *Artemia salina* nauplii or particulate fish food. The intermoult period, ~9 d for *M. norvegica* and ~8 d for *Thysanoessa* spp., increased with body weight, but did not differ with food source. Moulting was partially synchronised, with up to 50% of the individuals moulting within 48 h of each other. Daily feeding rates on *A. salina* decreased on the day before moulting, but increased during the next few days with highest values on Days 1 to 3 after moulting. The deviation from the mean feeding rate over the whole moult was more pronounced at the higher food concentration, reaching up to 40%. Likewise, the defecation volume was reduced on the moulting day and the following day to ~50% of the mean, but increased to 180% of the mean on Day 3 after moulting. Thus, the moult cycle induces significant changes in feeding rates of larval euphausiids with a similar succession of events and intensity as observed in decapods. Feeding rates, extrapolated from spot measurements on a few individuals, are unlikely to represent average values over the whole moult cycle, especially when populations moult synchronously. We propose a protocol to increase the precision of field estimates on feeding rates.

KEY WORDS: Moulting · Feeding · Defecation · Krill · Larvae · *Meganyctiphanes norvegica* · *Thysanoessa* spp.

INTRODUCTION

Being encased in a rigid exoskeleton, crustaceans have to shed their cuticle periodically to allow for growth, development and regeneration. The actual act of shedding the old exoskeleton (ecdysis) is the most obvious manifestation of the moult cycle, but the vast majority of the events related to this cycle occur internally (Skinner 1985, Roer & Dillaman 1993). Proecdysis involves the separation of the underlying epidermal cells from the old exoskeleton, resorption of organic and inorganic components, and generation of the new cuticle. At ecdysis, the old exoskeleton breaks and the new, flexible exoskeleton expands by taking up water. Postecdysis is characterised by mineralisation and further deposition of cuticle. The main tissue growth and accumulation of organic reserves usually occurs between postecdysis and the onset of the next proecdysis.

The integumentary reorganisation during the moult cycle is necessarily linked with biochemical, physiological and behavioural changes. Those modifications have mainly been studied in benthic or semibenthic decapods. These species show increased oxygen consumption and ammonium excretion rates before, during and shortly after ecdysis (e.g. Penkoff & Thurberg

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1982, Carvalho & Phan 1998, Taylor et al. 2002), suggesting high metabolic requirements during this period (Chang 1995). Shedding of the entire chitinous lining of the fore and hindgut (Passano 1960) is reflected in inhibited feeding (Chittleborough 1975, Strong & Daborn 1980, Lipcius & Herrnkind 1982). In addition, food preferences might alter around ecdysis because of different nutritional requirements during this stage (Bernardez et al. 2000, de Lestang et al. 2000). The new, soft exoskeleton often limits mobility and the use of defensive appendages in decapods, which makes them especially vulnerable to predation (Chang 1995). Therefore, moulting decapods often hide or avoid contact with conspecifics (Lipcius & Herrnkind 1982, Chang 1995).

In contrast to benthic decapods, there are few studies on moult cycle-related physiological alterations in pelagic species. Among euphausiids, the evidence is conflicting. Ecdysis happens extremely quickly in Antarctic krill *Euphausia superba*, and Buchholz (1989, 1991) suggested that their motility and feeding is little impaired by moulting. This has been interpreted as a prerequisite for a pelagic life and moving in swarms (Buchholz 1991). However, detailed measurements on another euphausiid, *Meganyctiphanes norvegica*, show that newly moulted krill have lower swimming capacity than non-moulting conspecifics (Thomasson et al. 2003). The fact that moulting *M. norvegica* do not undergo diel vertical migration but stay at depth further supports the argument that swimming performance and/or behaviour of krill is affected by ecdysis (Tarling et al. 1999). Other studies indicate reduced feeding activity (Lasker 1966, Paranjape 1967, Morris 1985) and increased oxygen consumption in moulting euphausiids (Paranjape 1967, Ikeda & Mitchell 1982). However, none of these studies has followed changes in physiological rates over the whole moult cycle and so do not allow the effect of moulting to be quantified.

A quantification of physiological alterations during the moult cycle is important, because firstly, it will help to distinguish between physiological and behavioural changes. For instance, the empty stomachs typical of moulting krill (Morris 1985) might be due to an extended physiological inability to feed or a consequence of a changed migration behaviour avoiding predation and cannibalism (Morris 1985, Tarling et al. 1999). Secondly, the environmental controls on feeding or respiration rates can only be identified accurately when internal cycles are first taken into account. In the isopod *Idotea baltica*, for instance, the moult stage causes more than 30% of the total variation in ingestion rates (Strong & Daborn 1980). Likewise, ignoring moult cycle-related changes in physiological rates might lead to errors in bioenergetic models. Metabolic rates integrated over a whole moult cycle were ~30% higher than traditional spot measurements on non-moulting shrimp (Carvalho & Phan 1998). Thus, 'average' physiological rates extrapolated from spot measurements of a few individuals might be biased, especially when moulting is synchronised as occasionally observed for euphausiids (Morris 1985, Tarling & Cuzin-Roudy 2003).

The aim of this study was to examine whether feeding rates of euphausiids are affected by the moult cycle in a manner similar to that described for benthic decapods. Northern krill, *Meganyctiphanes norvegica* and *Thysanoessa* spp. (*T. raschii* and *T. inermis*), were chosen for study. These species are central components in food webs of the northern Atlantic and fringing shelves, utilising diverse food sources and comprising important prey for fish, birds and marine mammals (Mauchline 1980, Falk-Petersen & Hopkins 1981, Dalpadado et al. 2000). However, experimental studies on their early developmental stages are rare (Le Roux 1974). Here we incubated late furcilia and early postlarvae of *M. norvegica* and *Thysanoessa* spp. individually, with various foods for a period of 6 to 7 wk to examine their moulting activity and related changes in feeding and defecation rates.

MATERIALS AND METHODS

Krill sampling. Late furcilia larvae and early postlarvae of *Meganyctiphanes norvegica* and *Thysanoessa* spp. (*T. raschii* and *T. inermis*) were collected in the deep basin of the Gullmarsfjord, west coast of Sweden (58° 19.00′ N, 11° 33.00′ E). Samples were taken on the morning of 5 September 2000 using an Isaac-Kidd midwater trawl (mesh size 1500 µm). About 200 specimens pooled from several net catches were sorted into 30 l plastic tanks of seawater and transported to the laboratory. A subsample of the freshly caught krill was immediately frozen at −80°C for later estimation of length-weight relationships, carbon and nitrogen content, and trophic position via stable nitrogen isotopes according to Peterson & Fry (1987).

Experiments. Experiments were carried out in dim blue light in a room with constant temperature (8°C). Krill were transferred individually to separate 800 ml Kautex bottles filled with 1 µm filtered fjord seawater (35 m depth) (33 PSU, O_2 > 80% saturation). The initial wet weight of each individual was measured within 1 d of capture using a Mettler microbalance. Thereafter, were divided into 3 groups, each group being fed with either 100 freshly hatched brine shrimp *Artemia salina* (L.) nauplii, 300 *A. salina* nauplii or about 5 mg of the commercial fish food 'Artemac' (Aquafauna^R). Nauplii had an atomic C:N ratio of ~6.1, and about 1.1 µg C

ind.$^{-1}$ and 0.2 µg N ind.$^{-1}$. The fish food had a particle size of 100 to 200 µm, a C:N ratio of ~6.0, and 0.42 mg C and 0.08 mg N mg^{-1} dry weight. Thus, 100 nauplii of *A. salina* comprised a total food concentration of ~0.1 mg C, while 5 mg of fish food was equivalent to 2.1 mg C.

Moulting and feeding rates on *Artemia salina* nauplii were monitored beginning on 7 September 2000. Each individual was transferred daily to a fresh bottle of filtered seawater and a new supply of food. The previous incubation water was sieved through 55 µm mesh to collect moults, faecal pellets and remaining nauplii. The daily feeding rate, F, was calculated for each individual as: $F = n_i - n_f$, where n_i is the initial number of nauplii and n_f is the number of nauplii after 24 h. Krill produced only a few very delicate faecal pellets when fed with *A. salina*, but numerous hard faecal pellets of various sizes when feeding on fish food. Over a period of about 2 wk, faecal pellets of 7 large specimens of the group fed with fish food were counted and collected on GF/F filters. The length (L) and diameter (d) of the pellets was measured under a calibrated stereomicroscope. The defecation volume (V) was calculated as: $V = (L \times \pi \times d^2)/4$.

Experiments were started with 30 individuals feeding on 100 nauplii of *Artemia salina*, 30 feeding on 300 nauplii of *A. salina* and 50 feeding on particulate fish food. However, the mortality of krill was high within the first ~8 d after capture, as has been reported from other studies (e.g. Antezana et al. 1982, Clarke & Morris 1983). Animals which survived that period usually remained alive until the end of the experiment, 6 to 7 wk later. The study includes only those individuals that underwent at least 3 moult cycles and were in good condition over the experimental period. The final wet weight was measured before animals were frozen at −80°C.

Biochemical analysis. Krill were thawed and species were identified according to Einarsson (1945). The body length was measured from the anterior lateral edge of the carapace to the posterior edge of the sixth abdominal segment (Standard length 3, Kirkwood 1982). Further treatment was according to body size: specimens <1.5 mg dry weight were dried at 60°C for 24 to 48 h and analysed whole, while larger specimens were freeze-dried, ground in an agate mortar and subsamples were analysed. Dry weight was determined using a Sartorius ultra-microbalance. The total C and N content was determined using a CHN analyser (Thermofinnigan CE 1108) calibrated with an acetanilide standard. Stable isotope ratios of freshly caught krill were analysed according to Schmidt et al. (2003).

Statistical analyses. The effect of body weight and feeding rate on intermoult period was analysed using multiple regression. Moulting synchrony was tested by assessing the goodness of fit of the observed to the expected cumulative moulting frequency distribution (Kolmogorov-Smirnov 1-sample test). A 2-way analysis of variance (ANOVA) was used to examine differences in feeding or defecation rates in relation to individual and day of the moult cycle. The null hypothesis that there was no difference between mean feeding or defecation rates over the whole moult cycle and rates on particular days of the cycle was tested with a 1-sample t-test. Differences were considered significant when $p \leq 0.05$. Mean values ±1 SD are given throughout the text and tables.

Maximum likelihood model. We used a model to investigate the implications of our findings for a hypothetical field-sampling scenario. In field situations, a population is often sampled only once to determine its *in situ* feeding rate. However, if feeding rates are biased by the moult stage and there is moulting synchrony in a population, repeated sampling and averaging may improve the approximation. This assumption was tested using a maximum likelihood model with bootstrapping (Hilborn & Mangel 1997).

The mean feeding rate over the total duration of the experiment was determined for each individual in every group. The feeding rate on any particular day was divided by this mean rate to give a percentage value for that day. The daily feeding rates were then classified according to stage of the moult cycle. Day 1 was the day of moult and the following days were labelled Day 2, 3, 4… up to the last day before moult, which was usually Day 9. Normally, Krill went through 5 moult cycles during the experiments. The value used by the model was the mean of the 5 values for each respective moult day.

The model randomly sampled the experimental population to create a new sample of 30 animals. The day of sampling for this population was then chosen randomly (this would be akin to a field situation, where the researcher would not know which moult stage dominated the population when sampled). The average feeding rate of the population on this day and also on the subsequent 5 d was determined. The average feeding rate resulting from sampling on 2 d and taking the average was calculated by combining the feeding rate on the day of sampling with that found on one of the subsequent days. This gave a total of 5 different estimates based on 2 d of sampling. A similar procedure was carried out to see the effect of sampling a population on 3 different days. The model was run 200 times and the results combined. If repeated sampling improved feeding rate estimates, then the average of 2 or more days would be closer to 100% than just 1 d alone. If the assumptions were true, the model also estimated the best subsequent days on which to sample.

Table 1. *Meganyctiphanes norvegica* and *Thysanoessa* spp. Morphometrical and biochemical characterisation of krill, either freshly caught or at the end of their incubation period. Body length (*L*) and dry weight (*W*) data were analysed using the allometric equation: $W = aL^b$., with n, the number of individuals. Carbon and nitrogen content are given as % dry weight. All *Thysanoessa* spp. from experiments were combined for length-weight regression to increase sample size (n = 14)

Species	Food	n	Length (mm)	Weight (mg)	Length-weight relationship a	b	R^2	C content (%)	N content (%)	C:N	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)
Field												
M. norvegica		20	7.7 ± 1.9	1.4 ± 1.0	0.0044	2.7684	0.91	43.6 ± 5.4	11.5 ± 1.3	4.3 ± 0.1	11.9 ± 0.3	−13.9 ± 0.4
Thysanoessa spp.		14	9.9 ± 2.6	3.1 ± 3.4	0.0006	3.6577	0.95	47.3 ± 3.0	11.0 ± 1.1	5.1 ± 0.7	12.0 ± 0.3	−15.1 ± 1.1
Experiments												
M. norvegica	100 nauplii	10	11.3 ± 1.2	3.8 ± 1.4	0.0022	3.0766	0.81	40.2 ± 2.1	11.3 ± 0.6	4.2 ± 0.2		
M. norvegica	300 nauplii	8	10.6 ± 2.1	3.7 ± 1.9	0.002	3.1456	0.95	43.4 ± 3.0	11.7 ± 0.8	4.3 ± 0.4		
M. norvegica	Fish food	28	10.2 ± 1.7	3.4 ± 1.6	0.0035	2.9251	0.96	41.5 ± 4.4	11.4 ± 1.2	4.3 ± 0.1		
Thysanoessa spp.	100 or 300 nauplii	8	9.9 ± 0.7	3.5 ± 2.5	0.0002	4.182	0.83	48.6 ± 4.4	11.5 ± 1.1	5.0 ± 0.5		
Thysanoessa spp.	Fish food	6	8.6 ± 0.8	1.3 ± 0.5				44.7 ± 1.2	11.4 ± 0.3	4.5 ± 0.1		

Table 2. *Meganyctiphanes norvegica* and *Thysanoessa* spp. Results of the Kolmogorov-Smirnov 1-sample test to assess moulting synchrony for the first 4 moult cycles (MC). The null hypothesis that moulting occurred equally over an 8, 9 or 10 d period, depending on the mean length of the moult cycle, has to be rejected if $d_i \geq d_{max}$. The difference between the observed cumulative moulting frequency and the expected cumulative moulting frequency, d_i, has been calculated for the mean length of the moult cycle, to the nearest day. The test statistic, d_{max}, has critical values depending on the number of individuals (n) and the length of the moult cycle (d). Values given in bold indicate moulting synchrony ($p \leq 0.05$)

Moult cycle	Mean length of MC (d)	Applied length of MC	d_i	d_{max}
***M. norvegica* (all, n = 49)**				
1st	8.4	8	**16.6**	9.1
2nd	8.8	9	4.6	9.5
3rd	9.1	9	7.2	9.5
4th	9.5	9	3.7	9.5
***M. norvegica* (<10 mg, n = 16)**				
1st	8.0	8	**8.0**	6.0
2nd	8.1	8	4.0	6.0
3rd	8.2	8	**6.0**	6.0
4th	9.0	9	4.9	5.5
***M. norvegica* (10–20 mg, n = 13)**				
1st	8.3	8	2.1	5.2
2nd	8.6	9	2.9	4.9
3rd	8.8	9	2.1	4.9
4th	9.1	9	1.4	4.9
***M. norvegica* (20–40 mg, n = 20)**				
1st	9.2	9	**6.1**	6.1
2nd	9.6	10	4.0	6.0
3rd	10.0	10	3.0	6.0
4th	10.3	10	2.8	6.0
***Thysanoessa* spp. (all, n = 14)**				
1st	7.9	8	4.8	5.5
2nd	7.6	8	2.5	5.5
3rd	7.8	8	3.5	5.5
4th	8.4	8	3.3	5.5

RESULTS

Morphometrical and biochemical characteristics

Freshly caught specimens of *Meganyctiphanes norvegica* and *Thysanoessa* spp. spanned a similar range of body length and dry weight (Table 1). Species differed slightly in their length-weight relationship, C:N ratio and $\delta^{13}C$ value, but the N content and $\delta^{15}N$ values were very similar. Thus, the increase in dry weight with increasing body length was more pronounced in *Thysanoessa* spp. than in *M. norvegica*. Further, *Thysanoessa* spp. had higher C content and C:N ratios but lower $\delta^{13}C$ values, which indicates a higher lipid content. The $\delta^{15}N$ values of the larvae/early postlarvae of both species were similar, while adult *M. norvegica*, sampled at the same time, had higher $\delta^{15}N$ values (13.0 ± 0.4‰, n = 20). Even though a number of factors may confound interpretation of isotope data, higher $\delta^{15}N$ values usually suggest a higher trophic position (Peterson & Fry 1987, Schmidt et al. 2003). Experimental animals did not differ from freshly caught krill in their length-weight relationship, or C and N contents (Table 1).

Intermoult periods and moulting synchrony

The intermoult periods of *Meganyctiphanes norvegica* ranged from 7 to 12 d, showing differences between individuals and between consecutive moults. The smallest individuals (less than 10 mg wet weight) mostly shed their moults after 8 (51% of occasions) or 9 d (36%). Individuals of 10 to 20 mg wet weight had an average intermoult period of 9 d (53%), but about 30% of all moults were shed after 8 d. The largest indi-

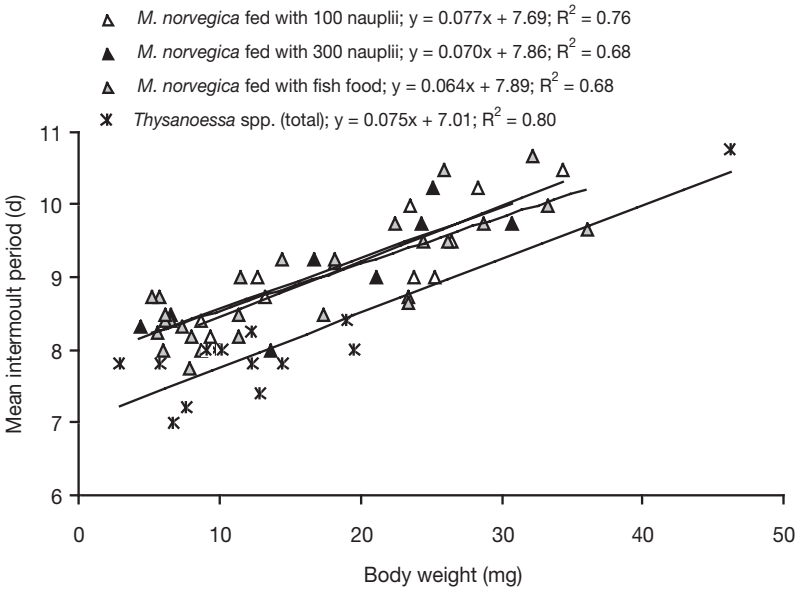

Fig. 1. *Meganyctiphanes norvegica* and *Thysanoessa* spp. Effect of body wet weight on the mean intermoult period of individual krill. All relationships were significant ($p < 0.05$, linear regression)

viduals (20 to 40 mg wet weight) usually moulted after either 9 or 10 d (80%) and sometimes after 11 d (15%). Although intermoult period varied with body size (Fig. 1), diet did not have any further effect. The same held true for the feeding rate: for *M. norvegica* fed with *Artemia salina* nauplii, 44% of the variability in the intermoult period was explained by body weight ($p < 0.001$) but none of it by different daily ration ($p = 0.613$, multiple regression).

The mean intermoult period of *Thysanoessa* spp. was about 1 d shorter than for similar sized *Meganyctiphanes norvegica* ($p = 0.0012$, Tukey's HSD test). Moulting usually occurred after 8 d (52% of occasions), but 23% of all moults were shed after 7 d. In line with results for *M. norvegica*, the average intermoult period of *Thysanoessa* spp. increased with body weight (Fig. 1).

The moulting activity did not show a directional change over the experimental period, but varied on a day-to-day basis. Both *Meganyctiphanes norvegica* and *Thysanoessa* spp. showed peaks of moulting activity every 7 to 10 d, with 30 to 55% of the individuals moulting within 48 h of each other (Fig. 2). It was mainly during the first moult cycle that the distribution of moulting events was significantly (*M. norvegica*) or nearly significantly (*Thysanoessa* spp.) different from a random distribution (Table 2). Synchrony was strongest in the smallest size fraction of *M. norvegica* (Fig. 3, Table 2).

Feeding rates in treatments with *Artemia salina* nauplii

Overall, feeding rates of *Meganyctiphanes norvegica* and *Thysanoessa* spp. remained fairly constant over the experimental period covering 5 to 6 consecutive moulting events, but differed among treatments, individuals and days of the moult cycle (Fig. 4, Table 3). Both *M. norvegica* and *Thysanoessa* spp. showed higher feeding rates when 300 instead of 100 nauplii were offered every day; rates were 113 ± 22 nauplii ind.$^{-1}$ d^{-1} versus 69 ± 13 nauplii ind.$^{-1}$ d^{-1} for *M. norvegica* and 92 ± 48 nauplii ind.$^{-1}$ d^{-1} versus 33 ± 10 nauplii ind.$^{-1}$ d^{-1} for *Thysanoessa* spp. (Fig. 4).

There was a significant positive relationship between mean feeding rate of individual *Meganyctiphanes norvegica* and body weight in the treatment with 300 nauplii ($R^2 = 0.5911$, $p = 0.026$, $y = 1.8298x + 80.431$). This was not the case with 100 nauplii offered every day, and the lower mean feeding rates suggest food limitation at this food concen-

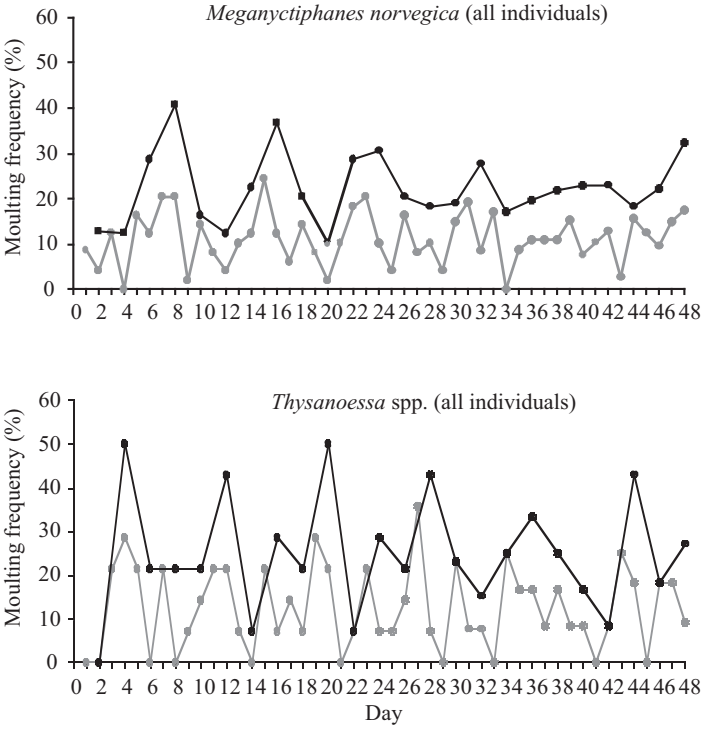

Fig. 2. *Meganyctiphanes norvegica* and *Thysanoessa* spp. Moulting activity (% of total individuals) over the experimental period. Data are plotted on a daily basis (grey) and added for 2 consecutive days (black)

tration (R^2 = 0.0919, y = 0.4506x + 59.754). *Thysanoessa* spp. had lower feeding rates than *M. norvegica* of similar size, but the number of individuals was too small for statistical analyses.

Moult cycle–related changes in feeding rates

Feeding rates changed depending on the day of the moult cycle. This pattern of variation was consistent, irrespective of food concentration and krill species (Fig. 5). Compared to the mean feeding rate over the whole moult cycle, rates were reduced on average to 60–75% on the day before moulting ($p < 0.03$, 1-sample t-test) and to about 90% on the moulting day. During the next 2 to 3 d, feeding rates increased on average to 110–120% ($p < 0.05$, 1-sample t-test), but were similar to the mean for the rest of the moult cycle. The drop in feeding rate on the day before moulting was common to all individuals, but they differed in the length of time the reduction lasted for. Some individuals also had low feeding rates on the moulting day, while others showed moderate or even sharply increased food intake during the moulting day.

Moulting-induced differences in feeding rates of *Meganyctiphanes norvegica* were more pronounced in the treatment with 300 nauplii than in that with 100 nauplii ($p = 0.0159$, Tukey's HSD test). Before and after moulting, feeding rates differed by 74 ± 25% of the mean in the treatment with 300 nauplii and by 46 ± 14% in the treatment with 100 nauplii.

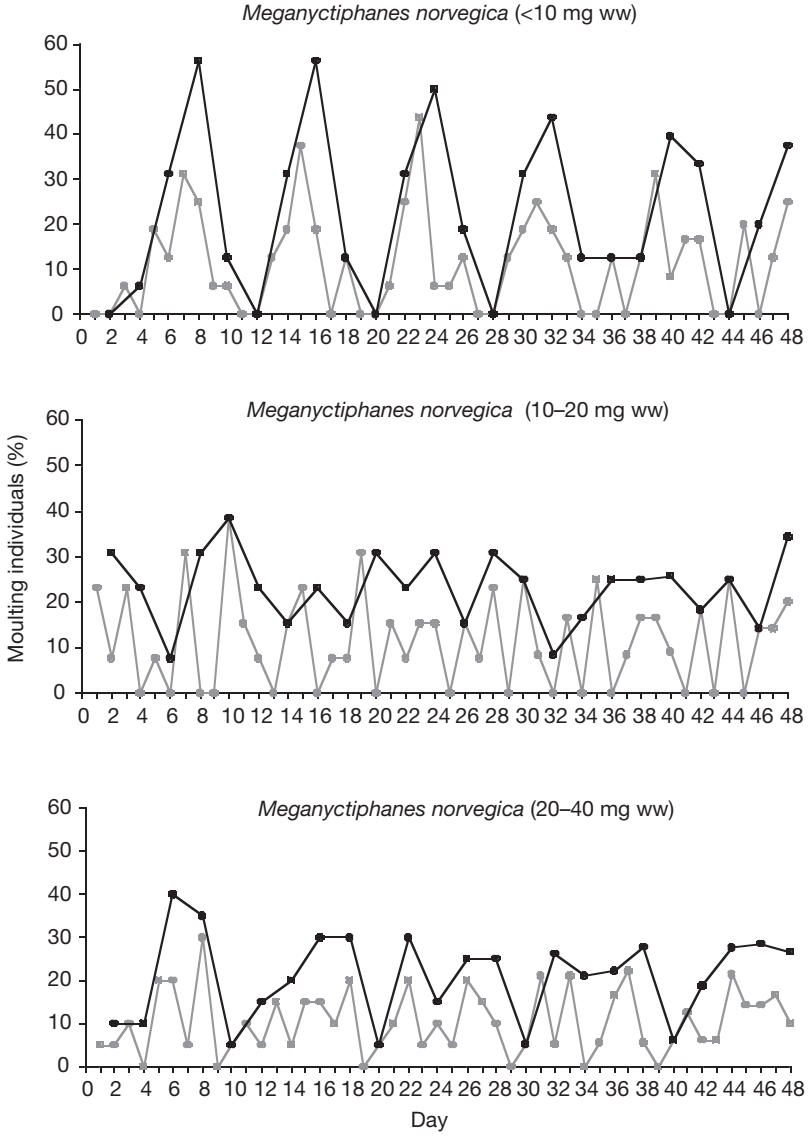

Fig. 3. *Meganyctiphanes norvegica*. Moulting activity (% of individuals within a given size class) over the experimental period. Data are plotted on a daily basis (grey) and added for 2 consecutive days (black); ww: wet weight

Faecal pellet production in treatments with particulate fish food

Meganyctiphanes norvegica feeding on particulate fish food produced on average 149 ± 38 pellets ind.$^{-1}$ d^{-1} of 0.38 ± 0.05 mm length, which resulted in a mean defecation volume of 0.16 ± 0.04 mm^3 ind.$^{-1}$ d^{-1}. Significant differences between individuals were seen in the length of faecal pellets, which increased with body size (R^2 = 0.4875, $p = 0.0081$, y = 0.0365x + 1.5951), but not in number of pellets and defecation volume (Table 4). Faecal pellet production was consistent over 2 consecutive moult cycles, but varied with the day of the moult cycle (Fig. 6, Table 4). The number of faecal pellets and the defecation volume dropped on the moulting day and day after to about 50% of the mean value, but increased on average to 140–180% of the mean on Days 3 and 4 after moulting (Fig. 7). Differences in the length of faecal pellets were less pronounced, with a reduction to 75–90% of the mean value during the moulting day and day thereafter, and an increase to about 110% after moulting.

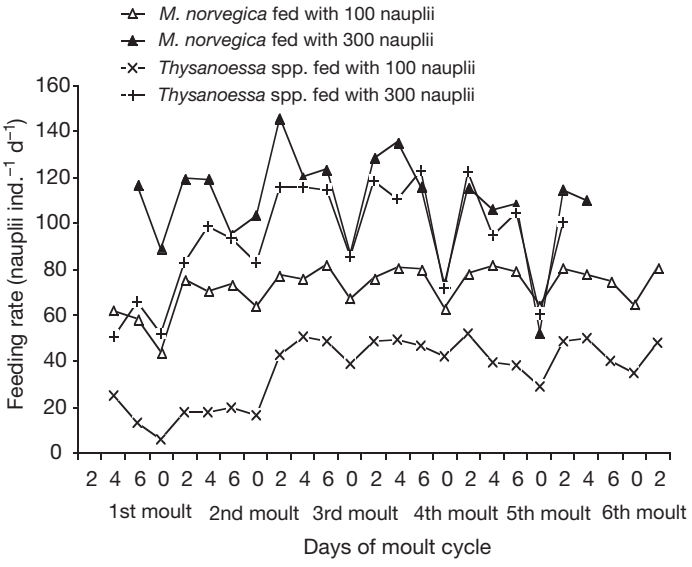

Fig. 4. *Meganyctiphanes norvegica* and *Thysanoessa* spp. Mean feeding rates over the experimental period of about 6 to 7 wk. The moult cycle was divided in 4 periods: day before moulting and moulting day (0), Days 1 and 2 after moulting (2), Days 3 and 4 after moulting (4) and Days 5 and 6 after moulting (6). If the moult cycle was longer than 8 d, additional days were included in the last 2 periods

Maximum likelihood model; the effect of repeated sampling

The potential error in feeding rates that would be made when sampling a synchronously moulting population depends on the prevailing moult stage within the population. Rates might deviate from the mean feeding rate over the whole moult cycle by up to 40% on the day before moulting and up to 25% on the day after moulting, but will match the mean feeding rate on other days (Fig. 5). In field situations, an investigator is often unaware of the dominant moult stage since its determination is time consuming and requires some practice. In these instances, an accuracy of, on average, no more than ±10 to 16% of the average feeding rate over the whole moult cycle can be expected, depending on food concentration (Table 5). However, if the same population is sampled twice on non-consecutive days, the potential error can be reduced by at least ⅓. Visiting a population 3 times can reduce the potential error by half.

DISCUSSION

Feeding studies of pelagic crustaceans have frequently addressed diurnal cycles and vertical migration, but very few have looked at the longer moult cycle. This is partly because pelagic crustaceans, such as euphausiids, are highly mobile, swim constantly to avoid sinking and move in swarms, and are thus expected to be little impaired by moulting. However, this study has shown that feeding rates of euphausiids vary clearly with the moult cycle. Together with the fact that moulting can be partially synchronised, this has consequences for the interpretation both of field data on gut content and laboratory feeding experiments. The target organisms of this study were the important, but rarely examined, early developmental stages of *Meganyctiphanes norvegica* and *Thysanoessa* spp. We therefore (1) discuss basic data on their intermoult period, (2) compare moult cycle related changes in feeding rates of euphausiids with those of decapods, (3) discuss the phenomenon of moulting synchrony, and finally (4) give some implications of our findings for field sampling.

Intermoult period

The 2 components that determine the pattern of crustacean growth are the intermoult period and the growth increment per moult. An effect of temperature and body size on the intermoult period has been shown repeatedly, but there are conflicting results on the effect of food (reviewed in Hartnoll 1982). Some studies on euphausiids suggest that a deficit in food quality or quantity reduces the increment per moult but does not affect the intermoult period (Lasker 1966, Fowler et al. 1971), while others also found a lengthening of the intermoult period (Le Roux 1974, Pillar 1985, Buchholz 1991).

Table 3. *Meganyctiphanes norvegica* and *Thysanoessa* spp. Comparison of differences in feeding rates (nauplii ind.$^{-1}$ d^{-1}) between individuals and days of the moult cycle. Rates of *M. norvegica*, feeding on 100 and 300 nauplii d^{-1}, were analysed separately, while for *Thysanoessa* spp. data from both treatments were combined to increase sample size

Source	*M. norvegica* (100 nauplii) df	*F*	p	*M. norvegica* (300 nauplii) df	*F*	p	*Thysanoessa* spp. (100 and 300 nauplii) df	*F*	p
Individuals	9	13.03	0.0001	7	5.00	0.002	7	21.79	0.0001
Days of moult cycle	3	16.54	0.0001	3	6.45	0.003	3	4.00	0.024

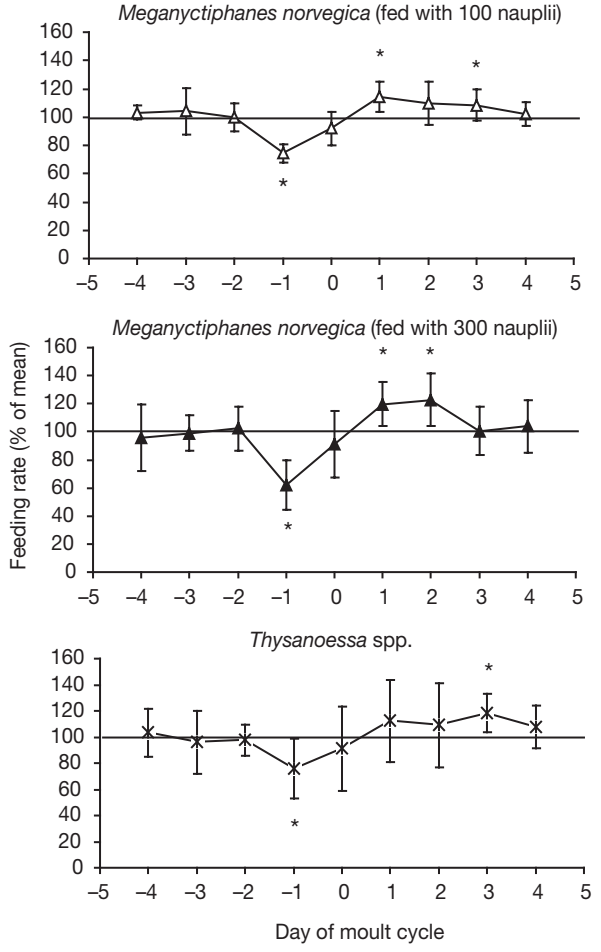

Fig. 5. *Meganyctiphanes norvegica* and *Thysanoessa* spp. The effect of moulting on feeding activity. For each krill the mean feeding rate on a particular day of the moult cycle was compared with that over the whole experimental period. The values (mean ±1 SD) represent all individuals per treatment for *M. norvegica* and combined results from treatments with 100 and 300 nauplii for *Thysanoessa* spp. *: significant reduction or increase in feeding rates ($p < 0.05$, 1-sample *t*-test)

In the present study, the intermoult period of larval *Meganyctiphanes norvegica* increased with body weight, but was not sensitive to the food regime. This suggests that the quantitative difference between 100 and 300 *Artemia salina* nauplii, and the qualitative difference between *A. salina* and particulate commercial fish food were of minor importance in determining the intermoult period in our experiments. Likewise, Le Roux (1974) found that larval *M. norvegica* from the Mediterranean had an intermoult period of 4 to 5 d when fed either with a pure diet of *A. salina* nauplii or a mixture of *A. salina* nauplii and 2 algae species. However, the intermoult period increased when only algae were given, underlining the value of an animal component in the diet of early developmental stages of *M. norvegica* (Le Roux 1974). Larvae of another euphausiid, *Nyctiphanes capensis*, had a slightly longer intermoult period when fed with pure algae *Phaeodactylum tricornutum* or copepod nauplii, while no differences were seen with pure *A. salina* nauplii, the algae *Tetraselmis chuii* or various mixtures (Pillar 1985). The effect of food concentration seems to be similar to that of food quality, altering the intermoult period only when in a clear deficit (Ikeda & Thomas 1987). This might explain why temperature and body size, but not food, are usually assumed to be the major factors determining the intermoult period (Mauchline 1980, Nicol 2000).

Our observations that intermoult periods were ~8 d for larvae/early postlarvae of *Thysanoessa* spp. and ~9 d for *Meganyctiphanes norvegica* agree well with results from previous studies, when accounting for different temperature or body size (Paranjape 1967, Fowler et al. 1971, Le Roux 1974, Sameoto 1976, Dalpadado & Ikeda 1989).

Moult cycle-related changes in feeding rate

There is conflicting evidence on the effects of moulting on the feeding activity of euphausiids. Lasker (1966) first noted that *Euphausia pacifica* ingested fewer nauplii on the day of ecdysis and suggested that moulting impairs feeding. Likewise, Paranjape (1967) concluded from faecal pellet production of euphausiids that feeding decreases on the days before and during ecdysis, but increases sharply afterwards. On the other hand, Buchholz (1989) found no reduction in the diges-

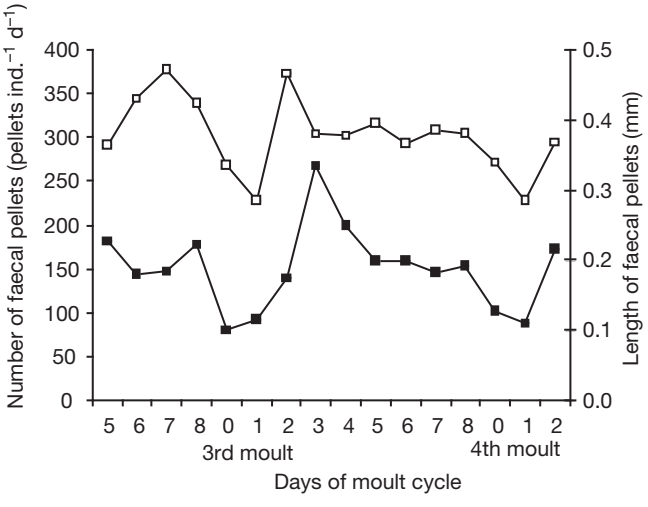

Fig. 6. *Meganyctiphanes norvegica*. Mean number (■) and length of faecal pellets (□) over an experimental period of about 2 wk

Table 4. *Meganyctiphanes norvegica*. Comparison of differences in number of faecal pellets (ind.$^{-1}$ d^{-1}), length of faecal pellets (mm) and defecation volume (mm^3 ind.$^{-1}$ d^{-1}) between individuals and days of the moult cycle

Source	Number of faecal pellets df	*F*	p	Length of faecal pellets df	*F*	p	Defecation volume df	*F*	p
Individuals	7	2.18	0.093	7	3.39	0.02	7	1.58	0.210
Days of moult cycle	3	7.61	0.002	3	4.61	0.015	3	8.78	0.001

tive enzyme activity of *Euphausia superba* around ecdysis, which led him and Priddle et al. (1990) to conclude that krill behave differently from benthic decapods in that their activity is little affected by moulting and their feeding is only interrupted for a very short time. However, none of the above studies quantified changes in feeding or defecation rates over the whole moult cycle.

Our results for late furcilia and early postlarvae of *Meganyctiphanes norvegica* and *Thysanoessa* spp. suggest that daily feeding rates of krill can be significantly affected by the moult cycle. The succession of events, with lowest feeding rates before ecdysis and highest rates soon afterwards, mirrors the pattern in decapods and isopods (Chittleborough 1975, Strong & Daborn 1980, Lipcius & Herrnkind 1982, Hill & Wassenberg 1992, Anger 2001). Forming the new and detaching the old exoskeleton will, to some extent, affect peripheral, sensory neural pathways and muscular insertions, and therefore the ability to catch, handle and macerate food items. Shedding of the entire chitinous lining of the foregut has been described for decapods (Passano 1960) and euphausiids (Ikeda et al. 1984), and essentially stops food passage and digestion. Elevated ingestion rates directly after moulting might represent compensation for previous metabolic losses and uptake of minerals to harden the exoskeleton rapidly (Hill & Wassenberg 1992, de Lestang et al. 2000).

Thus, euphausiids and decapods do not differ in their basic responses during moulting, but might vary in the actual duration of events. For example, in a subadult lobster *Panulirus argus* with an intermoult period of ~63 d, the drop in the feeding rate started ~8 d before ecdysis, no feeding was observed for at least 1 d around ecdysis and the period of increased feeding after ecdysis lasted for ~10 d (from data in Lipcius & Herrnkind 1982). By comparison, the intermoult period of larval *Meganyctiphanes norvegica* was only 9 d, of which 1 d was characterised by reduced feeding rates and 2 d by enhanced feeding rates. Thus, the 24 h period over which feeding rates are usually integrated, represents a shorter proportion of the total moult cycle in *P. argus* than in *M. norvegica*. As a consequence, daily feeding rates of *P. argus* can differ greatly from the mean feeding rate (up to 100%), while those of *M. norvegica* differ much less (~30%). On the day of ecdysis, the feeding rate of *M. norvegica* was not zero but close to the mean, probably because feeding only stopped for a fraction of that day and thereafter a period of high feeding activity started.

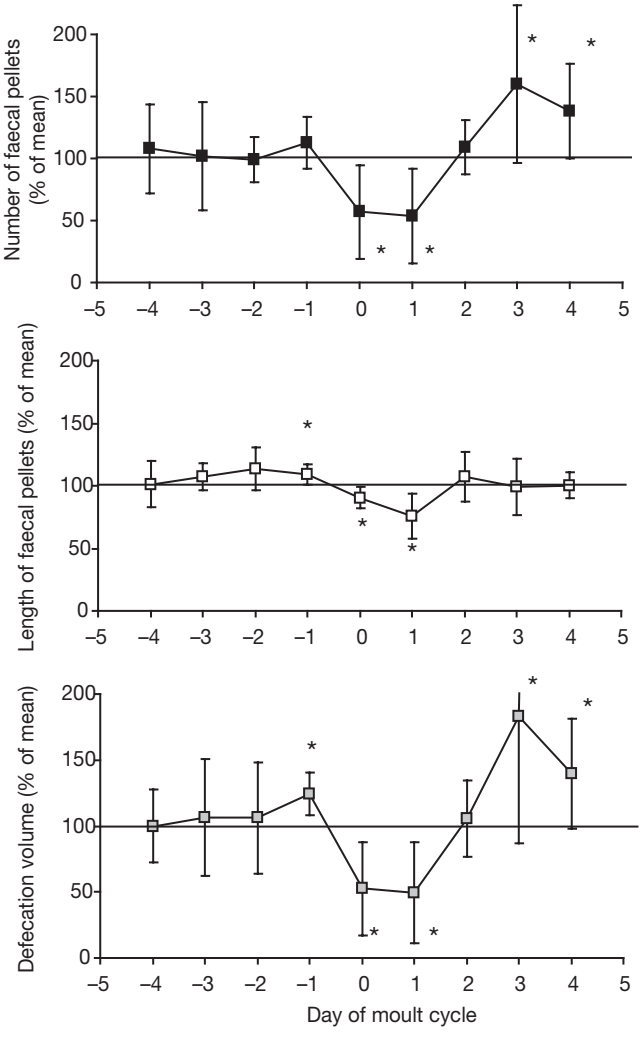

Fig. 7. *Meganyctiphanes norvegica*. The effect of moulting on the number and length of faecal pellets, and the defecation volume. For each krill the mean number, length and volume of faecal pellets on a particular day of the moult cycle was compared with the mean values over 2 moult cycles. Values represent all individuals (mean ±1 SD). *: indicate significant reduction or increase in parameters ($p < 0.05$, 1-sample *t*-test)

A synthesis of data across euphausiids, decapods and isopods confirms that moulting events are more strongly reflected in daily feeding rates when the intermoult period is longer (Table 6). This is not only true for different species and developmental stages, but also for the same stage reared at different temperatures. The feeding rate of megalopa larvae of the crab *Carcinus maenas* was zero on the day before ecdysis when the intermoult period was long (21 d at 12°C), but dropped to only 60% of the mean when the intermoult period was short (8 d at 25°C) (Dawirs & Dietrich 1986). Food concentration is another factor that alters the reduction and subsequent increase in feeding rates around ecdysis. Our experiments showed that, with excess food, daily feeding rates of *Meganyctiphanes norvegica* before and after moulting differed by about

Table 5. *Meganyctiphanes norvegica* and *Thysanoessa* spp. The probable error (coefficient of variation) in feeding rates that would be made when sampling a synchronously moulting population once, twice or on 3 occasions. Where a population was theoretically sampled either twice or 3 times, the best estimate of feeding rate was assumed to be the average of these particular observations

	Sampling frequency (d)			
	1	2 consecutively	2 non-consecutively	3 consecutively
***M. norvegica* larvae**				
100 nauplii ind.$^{-1}$ d^{-1}	10.5%	8.9%	6.8%	4.8%
300 nauplii ind.$^{-1}$ d^{-1}	15.9%	12.6%	10.5%	5.7%
***Thysanoessa* spp. larvae**				
100 or 300 nauplii ind.$^{-1}$ d^{-1}	11.6%	8.4%	6.7%	6.7%

Table 6. Comparison of moult cycle-related changes in daily feeding rates for various species of euphausiid, isopod and decapods. Minimum and maximum feeding rates (% of mean feeding rate over the whole moult cycle) were calculated from data given in literature searched. The feeding rate on a particular day of the moult cycle was classed as differing significantly from the mean feeding rate over the whole moult cycle, when its standard deviation (SD) did not cover the mean value. n; number of replicates, IMP; intermoult period

Species/Stage	n	IMP (d)	Food source/ concentration/Temp. (°C)	Feeding rate (%) (min)	(max)	Values differing from mean
Euphausiid *Meganyctiphanes norvegica* (present study)						
Late furcilia larvae	10	9	*Artemia* sp./low conc.	75	115	33%
Late furcilia larvae	8	9	*Artemia* sp./high conc.	60	123	33%
Euphausiid *Thysanoessa* spp. (present study)						
Late furcilia larvae	8	9	*Artemia* sp.	76	118	22%
Crab *Hyas araneus* (Harms et al. 1991)						
Zoea II larvae	20	13	*Artemia* sp.	46	137	~50%
Megalopa larvae	20	28	*Artemia* sp.	48	192	~50%
Crab *Carcinus maenas* (Dawirs & Dietrich 1986)						
Megalopa larvae	10	8	*Artemia* sp./25°C	60	147	~25%
Megalopa larvae	10	10	*Artemia* sp./18°C	21	240	~90%
Megalopa larvae	10	16	*Artemia* sp./15°C	8	279	~70%
Megalopa larvae	10	21	*Artemia* sp./12°C	0	250	~60%
Rock lobster *Jasus edwardsii* (Tong et al. 1997)						
Phyllosoma VI larvae	10	16	*Artemia* sp./low conc.	58	104	no SD
Phyllosoma VI larvae	10	15	*Artemia* sp./medium conc.	50	110	no SD
Phyllosoma VI larvae	10	14	*Artemia* sp./high conc.	52	118	no SD
Spiny lobster *Panulirus longipes* (Chittleborough 1975)						
Juvenile	2	~50	Abalone muscle	0	325	no SD
Spiny lobster *Panulirus argus* (Lipcius & Herrnkind 1982)						
Subadult	6	63	Fiddler crab	0	213	~30%
Isopod *Idotea baltica* (Strong & Daborn 1980)						
Adult	17	24	Algae material	19	146	~50%
Prawn *Penaeus esculentus* (Hill & Wassenberg 1992)						
Adult	34	24	Greentail prawn	0	203	~50%

±30% from the mean, while with lower food, rates differed by only ±20%. A similar tendency was seen for phyllosoma larvae of a lobster, *Jasus edwardsii*, also fed with different concentrations of *Artemia* sp. (Tong et al. 1997). Daily food consumption of decapod larvae did not alter over the moult cycle when food concentration or quality was limited (Harms et al. 1991, Tong et al. 1997). Furthermore, we found clear individual differences in response to moulting. Some krill, for instance, had reduced feeding rates on 3 consecutive days before ecdysis, while others only on 1 d. Such individual variability has also been seen in lobster and prawns (Lipcius & Herrnkind 1982, Wassenberg & Hill 1984). About 30% of the prawns *Penaeus esculentus* continued feeding on the night of ecdysis (Wassenberg & Hill 1984).

Comparing minimum and maximum feeding rates of various crustacean species (Table 6), it is clear that the effect of moulting on average daily feeding rates is less pronounced in larval *Meganyctiphanes norvegica* and *Thysanoessa* spp. than in juvenile and adult decapods, but is very similar to that in some decapod larvae and in an isopod species. Thus, there is no fundamental difference in feeding behaviour between euphausiids and decapods around ecdysis. This seems to be true not only for feeding, but for their general activity. Ecdysis within seconds has not only been observed for *Euphausia superba* (Buchholz 1991), but also in several prawn species, while lobsters often take more time (reviewed in Wassenberg & Hill 1984). The prawn *Penaeus esculentus* is able to swim immediately after ecdysis (Wassenberg & Hill 1984) and the lobster *Panulirus argus* also retains its neuromuscular coordination around ecdysis (Lipcius & Herrnkind 1982). Sustained agility seems to be a critical feature of the moult cycle, not only in pelagic crustaceans but also in those decapods that moult in the presence of conspecifics and mate in the soft-shelled postmoult condition (Atema et al. 1979, Lipcius & Herrnkind 1982).

Synchronous moulting

Synchronous moulting of euphausiids has been observed frequently, but authors debate whether it is an artefact caused by their capture (Clarke & Morris 1983, Nicol 1989) or a common strategy in the field (Morris 1985, Tarling et al. 1999). However, an induction of moulting synchrony during capture of the animals seems unlikely, as spontaneous shedding of the exoskeleton as a fright response (Hamner et al. 1983) is only possible in those krill which are very close to ecdysis (Buchholz 1985).

In the present study, peaks of moulting activity were observed every 8 d for the smallest size class of *Meganyctiphanes norvegica* — which clearly suggests moulting synchrony. Larger *M. norvegica* and *Thysanoessa* spp. showed some tendency towards synchronous moulting during their first moult cycle in the laboratory, but lost this pattern later in the experiment. Unfortunately, we did not have enough freshly caught krill larvae to perform a moult-stage analysis; the ultimate proof of moulting synchrony in the field (Buchholz 1985, Nicol & Stolp 1990). Applying this moult-stage technique, Tarling & Cuzin-Roudy (2003), observed that female *M. norvegica* in the Clyde Sea spawn and moult synchronously throughout the reproductive season. Thus, eggs are released in pulses and distinct cohorts can develop. Such a mass occurrence of vulnerable developmental stages (egg, early larvae) might satiate the predator population and thereby reduce total losses in the prey population (Ims 1990). Similarly, synchronised moulting of the larvae might minimise predation and cannibalism during vulnerable stages of the moult cycle (Reaka 1976). Even though moulting or spawning synchrony seem to be most persistent in isolated *M. norvegica* populations inhabiting the Clyde Sea (Tarling & Cuzin-Roudy 2003), Kattegat (Tarling et al. 1999) or Gullmarsfjord, it has also occasionally been found in *Euphausia superba* swarming in open waters (Buchholz et al. 1996, G. A. Tarling et al. unpubl. data).

Implications for field studies on gut content and feeding rate

Among the many factors that might dictate the feeding rates of euphausiids in the field, the effect of the moult cycle stage has rarely been examined. Only Priddle et al. (1990) linked variations in gut fullness of *Euphausia superba* swarms to individual characteristics such as body length, maturity stage and moult stage. Empty guts characterised 60% of krill just before moult and 30% of those just after, resulting in lower average gut fullness in these groups compared to other moult stages (Priddle et al. 1990). However, these groups comprised a small fraction of the population, and so moult stage accounted for only 4.2% of the total variation in gut fullness (Priddle et al. 1990). Our study suggests that moulting does not only cause an empty gut around ecdysis, but has an extended and rather complex effect on feeding. Thus, feeding rates might be significantly reduced or increased over a longer proportion of the moult cycle (Table 6), and the strength of the effect varies with food concentration and intermoult period.

Measuring ingestion rates is another method used to study krill feeding activity and food preferences (e.g. Atkinson et al. 2002). A common assumption here is

that experiments with a few individuals chosen randomly from the field will provide a satisfactory estimate of energy consumption for an average member of the population. In some studies, moulting krill were excluded to reduce the variability of the results (Heyraud 1979, Ikeda & Mitchell 1982). However, our study suggests that feeding rates could be biased even though ecdysis may not occur during the experiment. We found that, with a short intermoult period, rates deviated from the mean value mainly on the day before and after ecdysis.

Over- or underestimation of population feeding rates of up to 40% might occur when most of the krill are in the same moult stage and the population is sampled during a few days around moulting. Accurate moult staging requires time and practice, so the dominant moult stage in a population on the day of sampling is usually not determined. In these cases, measurements of feeding rates can be no more accurate than ±15% (Table 5). Such an error in feeding rates might be of minor relevance compared to those inherent in experimental manipulation or carbon-conversion factors (Båmstedt et al. 2000). However, errors may be greater for synchronously moulting adults due to their longer intermoult period. If repeated sampling of a population is possible, ideally on 2 non-consecutive days, this will reduce the effect of the moult cycle by one-third and, therefore, help to gain more precise population feeding rates or bioenergetic models for individual krill.

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