Physiological responses of *Calanus finmarchicus* and *Metridia longa* (Copepoda: Calanoida) during the winter-spring transition

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Abstract

Population dynamics, vertical distribution and metabolism of copepods have been related to the onset of the spring phytoplankton increase in Kosterfjorden, western Sweden, in 1983. The overwintering stages of the two marine copepods *Calanus finmarchicus* and *Metridia longa* displayed large differences in metabolic activity and behaviour. *C. finmarchicus* overwintered as Stage V copepodites in deep water and began to metamorphose to adults by the time the phytoplankton spring bloom started. Stage V copepodites did not feed, had low rates of respiration and excretion and low digestive enzyme activities, and remained in the deep water throughout the day and night. *M. longa* overwintered as adults, performed diurnal vertical migration, and had relatively high respiration and excretion rates and high digestive enzyme activities. *M. longa* fed throughout the entire water column, but feeding was most intense in the surface waters during the night. Adult female *C. finmarchicus* and *M. longa* responded rapidly to the onset of the spring phytoplankton bloom by increasing metabolic activities. Comparable results from Balsfjorden, northern Norway, indicated similar differences between the two species there, although the events in the phytoplankton and zooplankton populations in spring occur 1 to 2 mo later and *M. longa* spawns well after the culmination of the spring phytoplankton bloom. The differences due to species-specific variability and geographical locality are discussed and related to overwintering strategies.

Introduction

The problem of how zooplankton obtain nutrition during times of low phytoplankton abundance has interested a number of authors. In high latitudes during winter, phyto-plankton production is too low to fully support the nutritional requirements of zooplankton in a normal state of activity and three theories have been proposed to explain how they survive this harsh period. Experiments on *Calanus finmarchicus* and *C. helgolandicus* by Hallberg and Hirche (1980), and Hirche (1983) support the theory that this species may become dormant, whereas studies on *C. helgolandicus* by Corner et al. (1976) suggest that predation on microzooplankton by this species may give sufficient energy for survival during winter. Feeding on detritus has also been suggested as an aid to overwintering survival (e.g. by Corner et al. 1974, Lenz 1977, Chervin 1978). Particulate organic matter is often present in considerable quantities (Menzel and Ryther 1964, Menzel and Goering 1966, Lenz 1977) and could, theoretically, enable the survival of zooplankton. Experimental data, however, do not confirm this, and development on pure detrital diets is abnormal (Corner et al. 1974, Heinle et al. 1977). Many species of zooplankton, therefore, have adopted strategies of overwintering in which combinations of adaptations are used.

Recent investigations indicate that *Calanus finmarchicus* displays low activity during late autumn (Båmstedt and Ervik 1984), whereas *Metridia longa* feeds actively, although the food supply can not sustain its metabolic needs throughout winter (Båmstedt et al. 1985). The winter-spring transition is the period during which the most dramatic changes in the nutritional environment occur. A question of interest is, therefore, do these two copepod species behave differently in response to the gradually improved food conditions which are typical for such a period? In relation to this problem, we present results from copepod populations in Kosterfjorden, western Sweden, with additional data for populations from Balsfjorden, northern Norway, in order to evaluate latitudinal effects.

Materials and methods

Zooplankton samples were taken from two depth strata [from near bottom (220 to 240 m) to 50 m and from 50 m to

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the surface] in Kosterfjorden (58°52'N; 11°06'E) using a WP2 net (Fraser 1968) equipped with a closing device. Sampling was carried out during both the day (11.00 to 13.00 hrs) and night (23.00 to 01.00 hrs). Representative subsamples were preserved in 4% buffered formalin for later estimation of abundance, population structure, and gut fullness of *Calanus finmarchicus* and *Metridia longa*. Data on the population structure of the two species is given for the period end of February throughout May 1983, data for all the other measured variables is given for the period mid-February to the beginning of March.

Initially, *in-situ* feeding experiments were performed on adult female *Metridia longa*, which were first sorted from the plankton using a small spoon made of fine-meshed plankton gauze, and then promptly transferred to the experimental unit as described by Båmstedt et al. (1985). After 25 February, the salinity in the surface water where these experiments would have been incubated was so low that it would have been lethal to the copepods; subsequent to this, the feeding experiments were run in the laboratory. Unsorted zooplankton samples were brought to the laboratory, sorted within 2 h of collection, and incubated in ambient water taken from 100 m depth. The detailed experimental design for the feeding incubations has been described by Tande and Båmstedt (1987). Particle concentration and size distribution were analyzed using an Elzone Model 80 XY particle counter (Particle Data Inc., Elmhurst, Illinois, USA), equipped with 19 and 190 μm orifice tubes and covering a size spectrum from 0.7 to 98 μm equivalent spherical diameter (ESD).

Copepods collected and sorted as described above were also used for measurements of respiration and excretion rates. Sets of three to five individuals were incubated in darkness at ca. 5 °C in stoppered glass bottles, 10 to 18 ml vol. Separate experiments were run for respiration and excretion measurements. Oxygen-saturated deep water from the sampling locality was used in these experiments.

Oxygen consumption was calculated from differences between reference bottles and experimental bottles after incubation. Oxygen concentrations were measured using a Clark oxygen electrode (YSI, Model 4004) connected to an amplifier (Medelco AB, Hägersten, Sweden) and a strip recorder. Water from the bottles was drawn through the oxygen electrode chamber using a peristaltic pump, and readings were taken when the output on the strip recorder had stabilized. The system was calibrated using Winkler titration. Respiration rates of the species from Balsfjorden were measured by the micro-Winkler technique. The methods have been detailed by Tande (in press). Further information about the experimental conditions for the respiration and excretion experiments is given in Table 1.

Excretion was estimated by analysing for ammonium and inorganic phosphate. Water samples of 2 ml vol were taken using an automatic pipette, and analysed according to the method of Grasshoff (1976), but with reagent additions scaled down proportionally.

The dry weight of the individuals used in the different experiments was measured after the termination of each experiment. The copepods were briefly rinsed in distilled water and dried to constant weight at 60 °C.

The analyses of trypsin and amylase activity, and protein content (only performed on copepods from Kosterfjorden) were carried out on sets of six to ten individuals shortly after collection. *Calanus finmarchicus* was analysed on 16 February only, *Metridia longa* on 16 and 18 February. The analytical procedures followed those used by Båmstedt (1984).

Analyses of particulate matter in water samples from different depths were undertaken during the experimental period. Chlorophyll *a* concentration was measured from 2-litre samples filtered on GF/C glass-fiber filters and extracted in 90% acetone using the method of Strickland and Parsons (1968). Particle-size distribution and particle concentration were measured with a particle counter as outlined for the feeding experiments.

Table 1. Sampling and experimental conditions for *Calanus finmarchicus* and *Metridia longa* used in respiration (Resp.) and excretion (Excr.) measurements

Time of capture	Depth (m)	Incubation time (h)		Av oxygen decrease (ppm)
		Resp.	Excr.	
Kosterfjorden, 1983				
16 Feb. (02.30 hrs)	150 − 50	06 − 22	06 − 23	0.56
18 Feb. (09.30 hrs)	200 − 60	14 − 24	15 − 01	1.29
24 Feb. (12.25 hrs)	225 − 100	16 − 22	15 − 21	0.76
25 Feb. (01.00 hrs)	50 − 0	06 − 15	06 − 13	1.06
28 Feb. (23.00 hrs)	220 − 50	01 − 16	01 − 10	0.91
1 Mar. (15.30 hrs)	210 − 50	20 − 13	20 − 14	1.45
2 Mar. (23.45 hrs)	50 − 0	02⁻ − 12	02 − 09	0.99
Balsfjorden, 1985				
8 Mar. (11.00 hrs)	180 − 0	12 − 17	12 − 17	1.15
21 Mar. (14.00 hrs)	180 − 0	15 − 21	15 − 21	1.20
22 Mar. (23.00 hrs)	50 − 0	00 − 10	00 − 10	1.64
19 Apr. (13.00 hrs)	180 − 0	18 − 09	18 − 09	3.17

Results

Environmental data

The vertical distribution of chlorophyll *a* in Kosterfjorden indicated a small and relatively uniformly distributed phytoplankton population in the upper 50 m. This condition prevailed during the first part of the zooplankton investigation (Fig. 1), and a gradually developing phytoplankton bloom was first recorded on 28 February. The vertical distribution of the particle mass was well correlated with the chlorophyll *a* distribution. Before the phytoplankton increase, particles smaller than ca. 10 μm ESD made up most of the particulate matter in the water column, particles of ca. 3.5 μm ESD being especially dominant. Particles > ca. 16 μm ESD increased tenfold or more in total mass during the development of the bloom in the samples from 0 and 2 m depths. For example, on 23 February the particle mass distribution at 2 m depth showed a median at 22 μm ESD and a total

particle concentration of 0.70 ppm, whereas on 11 March the median value had increased to 52 μm ESD and a total particle mass of 6.87 ppm. Particles around 3.5 μm ESD were continuously dominant below 7 m depth.

Population structure and vertical migration

The relative composition of developmental stages of the two copepods for a three-month period in Kosterfjorden is shown in Fig. 2. *Calanus finmarchicus* overwintered as Stage V copepodites (90 to 95% in February), and Stage I copepodites of the new generation began to appear in early March. *Metridia longa* spent the winter as adults (91 to 100% in February), and a new generation began to appear in the samples somewhat earlier in March than for *C. finmarchicus*.

Information relating to vertical migration of the two copepod species is summarized in Table 2, in which the "surface aggregation index" (I_s) is defined as:

$$I_s = n_s/n_d,$$

where n_s and n_d are numbers per m³ in surface and deep waters, respectively. A surface aggregation index of 1 would indicate the same average abundance in the two vertical strata, and differences between day and night values would

indicate diurnal migration. The results presented in Table 2 show that female *Calanus finmarchicus* and female *Metridia longa* from Kosterfjorden displayed a diel rhythm, aggregating in the upper water layer at night (except on 25 February), whereas Stage V. *C. finmarchicus* remained in the deep water at all times. *M. longa* appeared to show a stronger tendency to avoid surface waters during the day than did female *C. finmarchicus* (Table 2).

Feeding activities

Field experiments on particle uptake by female *Metridia longa* at 4 m depth, using a 1 h incubation, gave a calculated daily ration of 0.5 to 9.0% (ingested particle volume as percentage of copepod volume), whereas laboratory experiments, using water from 100 m depth, gave daily rations between 1.9 and 3.4%.

Microscopic examination of *Calanus finmarchicus* and *Metridia longa* for the estimation of gut fullness indicated
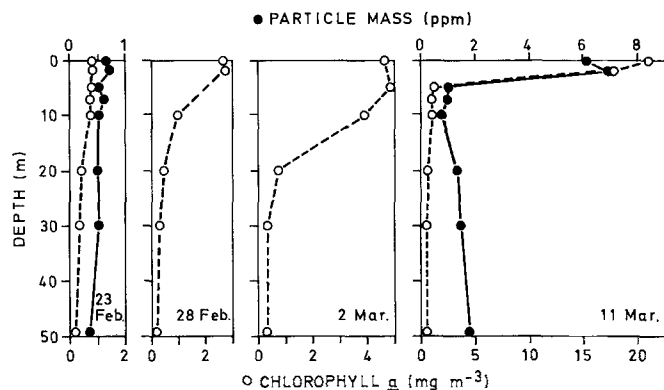

Fig. 1. Vertical distribution of suspended particulate matter and chlorophyll *a* in Kosterfjorden on four occasions between 23 February and 11 March 1983
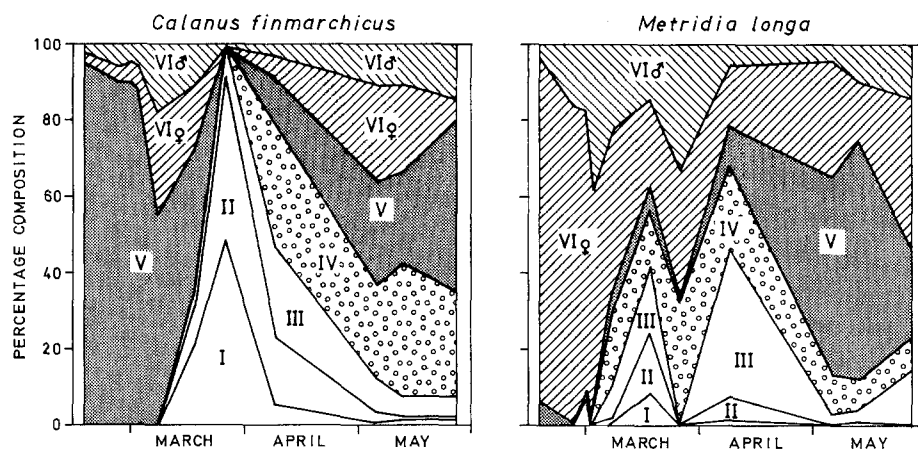
Table 2. *Calanus finmarchicus* (adult females and Stage V copepodites) and *Metridia longa* (adult females). Surface aggregation index, I_s (defined in "Results — Population structure and vertical migration") of copepods from Kosterfjorden, 1983

Time of capture	Night/ Day	Depth intervals (m)	*C. fin-marchicus*		*M. longa* ♀♀
			♀♀	CV	
16 Feb. (02.00 hrs)	N	150—50; 50—0	4.38	0.02	4.29
18 Feb. (09.00 hrs)	D	150—50; 50—0	0.12	0.01	0
24 Feb. (12.00 hrs)	D	240—50; 50—0	0.51	0.02	0.01
25 Feb. (01.00 hrs)	N	200—50; 50—0	0.95	0.05	0.49
28 Feb. (23.00 hrs)	N	220—50; 50—0	4.25	0.13	6.04
1 Mar. (15.00 hrs)	D	210—50; 50—0	1.07	0.01	0
2 Mar. (09.00 hrs)	D	210—50; 50—0	0.36	0.08	0.10
2 Mar. (23.00 hrs)	N	210—50; 50—0	2.58	0.05	2.58

Fig. 2. *Calanus finmarchicus* and *Metridia longa*. Relative composition of copepodite stages in Kosterfjorden, 1983. Collections were made at midnight from close to the bottom (220 to 240 m) to 50 m and from 50 to 0 m depth, and these data have been combined
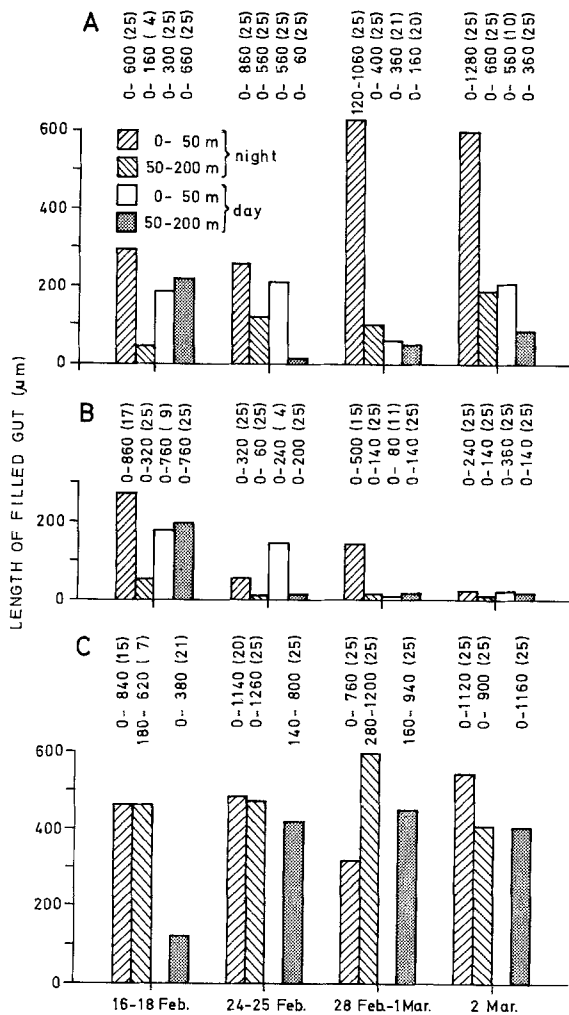
Fig. 3. *Calanus finmarchicus* (A: adult females; B: Stage V copepodites) and *Metridia longa* (C: adult females). Gut fullness (arithmetical mean) of copepods from Kosterfjorden, sampled at midday and midnight and from surface layer and deep layer. Numbers above bars: range in gut fullness and (no. of individuals analysed)

Table 3. *Calanus finmarchicus* and *Metridia longa*. Statistical comparisons (Mann-Whitney U-test) of gut fullness of copepods sampled under different light and depth conditions (see Fig. 3). upper: 0 to 50 m depth; lower: 50 to 220 m depth; day: midday samples; night: midnight samples

Conditions	*Calanus finmarchicus*		*Metridia longa*
	C V	C VI female	C VI female
16 – 18 February			
upper, day/upper, night	163.5 ***	371.5 *	ND
lower, day/lower, night	648.0 ***	85.0 *	137.5 ***
upper, day/lower, day	321.5 ***	425.5 *	ND
upper, night/lower, night	295.5 *	68.5	56.5
24 – 25 February			
upper, day/upper, night	73.0	325.5	ND
lower, day/lower, night	324.0	449.5 **	221.5 *
upper, day/lower, day	84.5 *	499.0 ***	ND
upper, night/lower, night	367.5	399.5	252.0
38 February – 1 March			
upper, day/upper, night	169.0 ***	613.0 ***	ND
lower, day/lower, night	325.5	314.0	429.0 *
upper, day/lower, day	142.5	212.0	ND
upper, night/lower, night	289.5 **	612.5 ***	215.5 *
2 March			
upper, day/upper, night	290.0	217.5 ***	ND
lower, day/lower, night	349.5	432.0 *	318.5
upper, day/lower, day	319.5	167.0	ND
upper, night/lower, night	350.0	536.0 ***	220.5 *

$*\ 0.05 \geqslant p > 0.01$; $**\ 0.01 \geqslant p > 0.001$; $***\ p \leqslant 0.001$

that feeding activity varied with depth and time of day (Fig. 3). *M. longa* was absent from the surface layer during daytime, but was apparently feeding actively in the deep layer then. This species showed less variation in gut fullness than did *C. finmarchicus*. A statistical evaluation of these observations, using a non-parametric test (Mann-Whitney U-statistic: Zar 1974) demonstrated inconsistency in these results (Table 3). For example, Stage V copepodites of *C. finmarchicus* collected from 16–18 February showed highly significant differences in gut fullness both in the surface water and the deep water when day and night samples were compared, but such differences could not be verified in the samples from 24–25 February. Table 3 also indicates that *M. longa* had less variable feeding behaviour than *C. finmarchicus*, which is in accordance with the results from Fig. 3.

Metabolic activity

The ammonium excretion rate of the two copepod species in Kosterfjorden was relatively low and stable until the end of

the period: 1 to 5 nmol mg^{-1} dry wt h^{-1} for Stage V copepodites of *Calanus finmarchicus*, and 6 to 14 nmol mg^{-1} dry wt h^{-1} for female *Metridia longa*. The ammonium excretion of *M. longa* increased abruptly at the beginning of March, when high values also were recorded for female *C. finmarchicus* (Fig. 4). Stage V copepodites of *C. finmarchicus* were not included on 3 March. Phosphate excretion followed a similar trend, although the results were more variable. The respiration rate showed no consistent pattern, but appeared to increase abruptly in *M. longa* during the last few days of the investigation (Fig. 4). Adult female *C. finmarchicus* showed a high respiration rate on the last sampling occasion, but had not been included earlier.

Based on these results, the molar O:N:P ratios were calculated. The O:N ratio showed a trend towards consistently higher values for Stage V copepodites of *Calanus finmarchicus* and lower values for *Metridia longa* as the investigation progressed (Fig. 5). Zero phosphate readings for Stage V copepodites of *C. finmarchicus* on 2 March and very low phosphate readings on 24 and 25 February for both species resulted in a few unrealistically high O:P and N:P ratios. The average N:P ratio was usually between 3 and 10 for *C. finmarchicus*, and between 10 and 20 for *M. longa*.

Measurements conducted at 2 °C on the two copepod species from Balsfjorden showed a somewhat different pattern (Fig. 6). Female *Calanus finmarchicus* displayed respi-
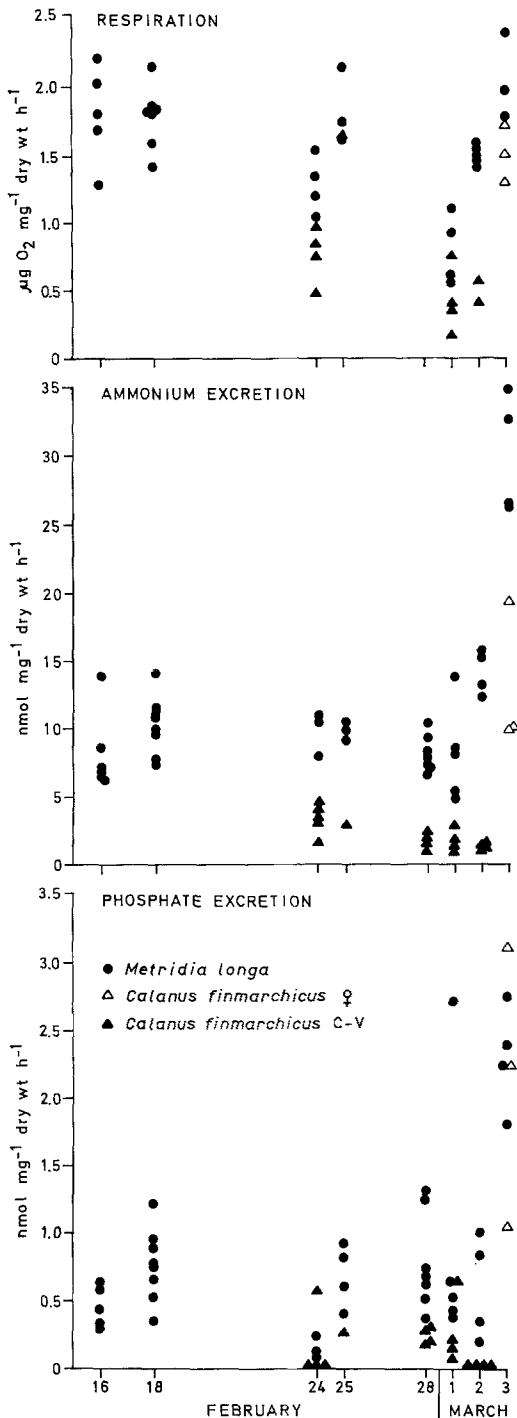
Fig. 4. *Calanus finmarchicus* and *Metridia longa*. Respiration and excretion rates of copepods from Kosterfjorden

ration and excretion rates similar to the females from Kosterfjorden, whereas *Metridia longa* excreted less ammonium but consumed oxygen at a similar rate to *M. longa* from Kosterfjorden. O:N ratios for the two Balsfjord populations were considerably higher than those for the Kosterfjord populations, especially in March (Fig. 6).

Comparisons of the two species in Kosterfjorden

Adult female and Stage V copepodites of *Calanus finmarchicus* and adult female *Metridia longa* from two sampling

occasions have been compared with respect to the physiological parameters measured (Table 4). A non-parametric test (Mann-Whitney U-test: see Zar 1974) revealed significant differences between the three groups. The results for 24 February showed that gut fullness of Stage V copepodites of *C. finmarchicus* in the surface layer was significantly lower than that of the other two groups. In the deep layer there was a significant reduction in gut fullness from adult female *M. longa* through adult female *C. finmarchicus* to Stage V copepodites of *C. finmarchicus*. Although the number of replicate measurements on respiration and excretion rates was small, the statistical test indicated significantly lower rates of Stage V copepodites *C. finmarchicus* compared to adult female *M. longa*.

Tests on the results for 2–3 March produced very similar results (Table 4), again indicating that Stage V copepodites of *C. finmarchicus* had a significantly lower excretion rate than *M. longa*, and were feeding significantly less than both adult female *C. finmarchicus* and *M. longa*.

Trypsin and amylase activities of Stage V copepodites of *Calanus finmarchicus* and adult female *Metridia longa*, measured on individuals sampled on 16 February, displayed striking differences. This was especially so for trypsin activity, which was 9 mU mg^{-1} protein ($n=3$; SD $=3$) for *C. finmarchicus* and 74 mU mg^{-1} protein ($n=3$; SD $=33$) for *M. longa*. Amylase activity was 5 mU mg^{-1} protein ($n=3$; SD $=1.0$) for *C. finmarchicus* and 9 mU mg^{-1} protein ($n=3$; SD $=1.8$) for *M. longa*. Both enzyme activities were significantly different for the two species ($p < 0.05$; Mann-Whitney U-test). A subsequent analysis on *M. longa* sampled on 18 February gave 43 mU mg^{-1} protein ($n=6$; SD $=3$) for trypsin activity and 15 mU mg^{-1} protein ($n=6$; SD $=3.2$) for amylase activity.

Discussion

In arctic-boreal waters, such as Balsfjorden in northern Norway, the herbivorous copepod *Calanus finmarchicus* spends the overwintering period in diapause until January or early February, when sexual differentiation occurs in Copepodite Stage V, and this is immediately followed by moulting to the adult stage, insemination and the onset of ovary development. These processes are entirely dependent upon internal energy reserves (Tande and Hopkins 1981, Tande 1982). On the other hand, the omnivorous copepod *Metridia longa* overwinters as physiologically active adult males and females and displays diurnal vertical migration (Tande and Grönvik 1983, Båmstedt et al. 1985). Although the final ovarian development in both *C. finmarchicus* and *M. longa* is dependent upon food obtained during the spring diatom increase, *C. finmarchicus* spawns during the peak of the spring primary production, which occurs in mid-April (Eilertsen and Taasen 1984), whereas *M. longa* does not spawn until May when the phytoplankton has levelled off (Tande 1982, Tande and Grönvik 1983, Grönvik and Hopkins 1984).
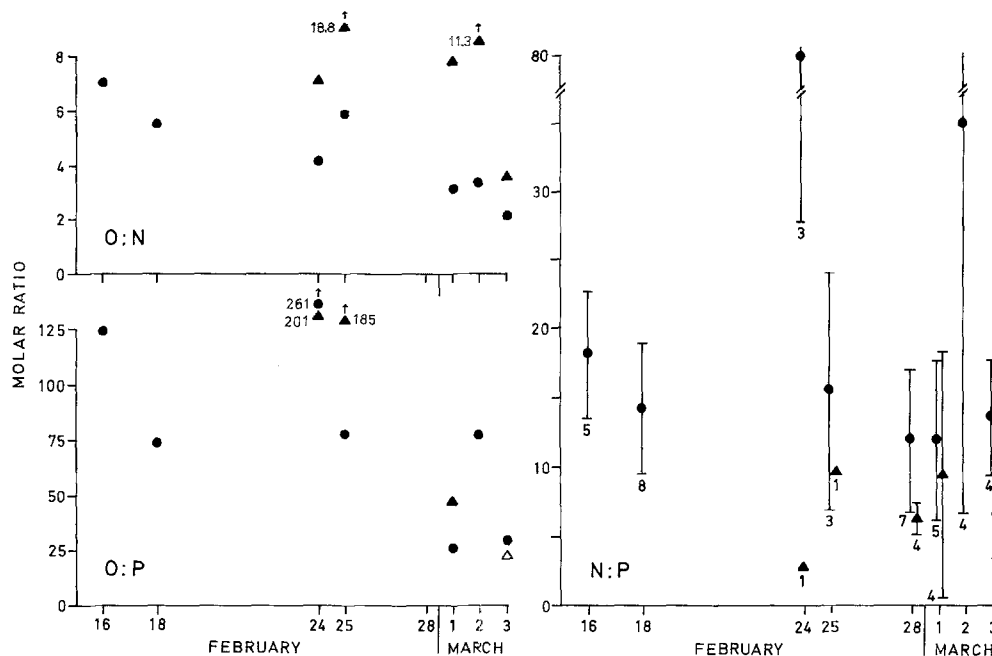
Fig. 5. *Calanus finmarchicus* and *Metridia longa*. Molar ratios of metabolic rates of copepods from Kosterfjorden; values exceeding scale are given by relevant data points. Bars on data points for N:P ratios (representing N and P measurements on same samples) are ± one standard deviation; no. of measurements is shown below each bar. Symbols as in Fig. 4

Table 4. *Calanus finmarchicus* and *Metridia longa*. Average values and statistical comparison (Mann-Whitney U-test at $p = 0.05$) of physiological parameters. Gut fullness given as percentage of prosome length of individuals captured at midnight, respiration as $\mu g \ O_2 \ mg^{-1}$ dry wt h^{-1}, excretion as nmol mg^{-1} dry wt h^{-1}. N:P ratio given on a molar basis. Values in parentheses: no. of sample units

	Gut fullness		Excretion			N:P-ratio
	0 − 50 m	50 − 220 m	Respiration	Ammonium	Phosphate	
24 February						
A: *Calanus finmarchicus* ♀♀	10.1 (25)	4.8 (25)	ND	ND	ND	ND
B: *Calanus finmarchicus* CV	2.3 (25)	0.4 (25)	0.76 (4)	3.32 (5)	0 (5)	∞ (5)
C: *Metridia longa* ♀♀	17.4 (21)	17.4 (25)	1.28 (4)	9.63 (3)	0.15 (3)	79.4 (3)
A/B U-statistic	360.5*	609.5***	16.0*	15.0**	15.0**	9.0
A/C U-statistic	457.0**	453.0**	ND	ND	ND	ND
B/C U-statistic	50.5	539.0***	ND	ND	ND	ND
2−3 March						
A: *Calanus finmarchicus* ♀♀	23.8 (25)	7.4 (25)	1.51 (3)	13.02 (3)	2.19 (3)	7.0 (3)
B: *Calanus finmarchicus* CV	1.0 (25)	0.5 (25)	0.49 (2)	1.41 (4)	0 (4)	∞ (4)
C: *Metridia longa* ♀♀	20.8 (25)	15.4 (25)	1.70 (8)	22.10 (8)	1.46 (8)	24.7 (8)
A/B U-statistic	591.0***	606.5***	16.0	34.0**	32.0**	32.0**
A/C U-statistic	608.0***	533.5***	6.0	12.0	12.0	12.0
B/C U-statistic	378.5	484.0***	16.0	20.0	17.0	32.0*

* $0.05 \geqslant p > 0.01$; ** $0.01 \geqslant p > 0.001$; *** $p < 0.001$

The present results from the populations in Kosterfjorden indicate that the two species respond differently to the seasonal change from winter to spring. The metabolic activity and diel vertical migration of Stage V copepodites of *Calanus finmarchicus* are both suppressed during winter, whereas adult female *Metridia longa* display a considerably higher activity and distinct diel vertical migration. At the onset of the spring phytoplankton bloom, *M. longa* responds immediately by increased metabolic activity and spawning, whereas the main part of the population of *C.*

finmarchicus, wich occurs as Stage V copepodites, shows no feeding activity or diel vertical migration. However, the small part of the population that occurs as adult females in the initial phase of the spring bloom does feed actively, has a high metabolic activity, migrates vertically and probably also spawns, thereby giving rise to the first cohort of the year.

It is unknown which stimuli trigger the onset of metamorphosis and reproduction in *Calanus finmarchicus*. Marshall and Orr (1972) suggested that the time of moulting is
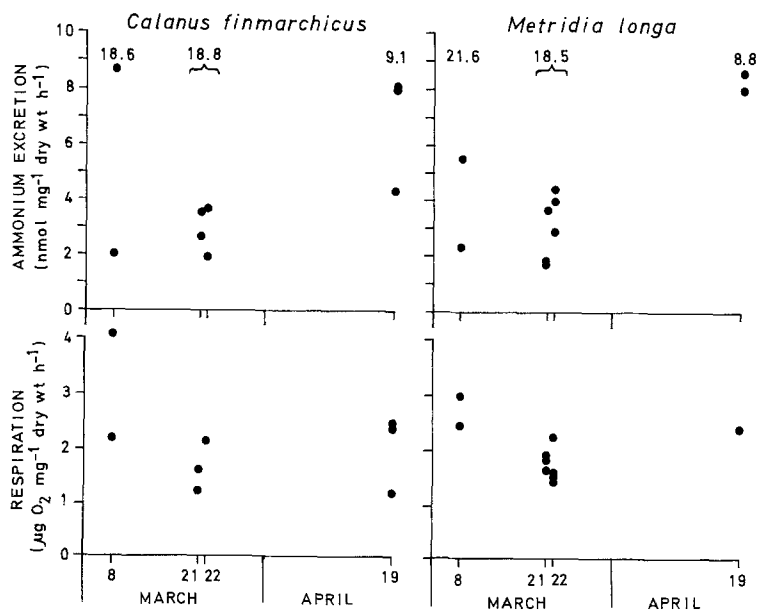
Fig. 6. *Calanus finmarchicus* and *Metridia longa*. Respiration and excretion rates of copepods from Balsfjorden. Average molar O:N ratios are indicated on top of figure

independent of latitude, and if this were true then the spawning of *C. finmarchicus* would commonly occur outside the period of the phytoplankton bloom. In some populations, the initiation of development of the genital system in overwintering Stage V copepodites occurs in mid-winter (Tande and Hopkins 1981) and can not, therefore, be governed by changes in abundance or production of phytoplankton. In Kosterfjorden, the spawning of *C. finmarchicus* in spring may vary from year to year. In 1978 and 1983, spawning occurred during the spring phytoplankton bloom, which was very intense in these years (Båmstedt 1985, and present study). In 1984, the spring phytoplankton bloom was depressed and the peak occurrence of the smaller copepodite stages indicated that spawning of both *C. finmarchicus* and *Metridia longa* occurred one month later than in 1978 and 1983 (own unpublished results). This late spawning also gave rise to only a small new generation, especially for *C. finmarchicus*. Furthermore, the population size remained small throughout the year, resulting in a small stock of overwintering individuals. A successful production season for these two large copepods therefore seems dependent upon an intense spring phytoplankton bloom; if this does not occur, they may delay reproduction for a certain time, but probably at the expense of fecundity and survival of the new generation. Because *M. longa* appears less affected by the annual differences of the spring phytoplankton bloom, we suggest that its year-round feeding activity may help to stabilize the production of this species.

Observations indicating different overwintering strategies for the two copepod species have been made on populations from the Norwegian west coast (Båmstedt and Ervik 1984) and north coast (Hopkins et al. 1985). Seasonal variations in body constituents of *Calanus finmarchicus* (Tande 1982) and *Metridia longa* (Grönvik and Hopkins 1984) support this hypothesis: in February–April adult female *C. finmarchicus* showed proportionally greater decreases in dry weight and carbon than female *M. longa*, suggesting that the

energy balance of the overwintering stages of the two species is different. An experimental investigation in Kosterfjorden on feeding in winter also indicated that *M. longa* fed more actively on naturally occurring particles and microzooplankton than did *C. finmarchicus* (Jacobsson and Nilsson 1983), although the food ration was always low for both species. A daily food ration ranging from 0.5 to 9.0% of the body mass, as estimated for *M. longa* in the current study, is low for a copepod in general (cf. Conover 1978), but within ranges reported for other boreal and arctic copepods (e.g. Tande and Båmstedt 1985, 1987, Huntley et al. 1987). Growth may persist even with these low rates of food consumption, because the daily energy loss through respiration and excretion amounted to less than 2% of the body energy in the present study. However, with our present knowledge we must suggest that overwintering *M. longa*, at least in arctic-boreal waters, can not, by food intake, fully compensate for metabolic loss throughout the winter, resulting in a slightly negative energy balance, especially during the latter part of the overwintering period. The overwintering Stage V *C. finmarchicus* copepodites, although spending less energy (lower metabolic rates, no vertical migration: see Fig. 4 and Table 2) appear to lose body constituents faster than the overwintering *M. longa* (Båmstedt et al. 1985, Hopkins et al. 1985). This is explained by their non-feeding state (Fig. 3).

A possible reason for developing a strategy whereby the overwintering period is spent as active adult animals, is that successful reproduction could presumably take place early in spring. Results from both the present study and previous ones show, however, that this does not occur. The data on maturation of *Calanus finmarchicus* and *Metridia longa* in Balsfjorden, northern Norway, indicate that *C. finmarchicus* actually spawns one month earlier than *M. longa* here (Tande 1982, Tande and Grönvik 1983). The overwintering population of *M. longa* obviously has not quantitatively or qualitatively sufficient reserves left for early reproduction, and must feed for ca. one month on the developing phyto-

plankton populations prior to spawning. In contrast, lipid-rich *C. finmarchicus* stay inactive as Stage V copepodites in the deep water until early spring, and migrate as adult females to the surface, where they immediately spawn. Synchronous spawning of the two species occurs in Kosterfjorden, although the copepods display the same differences in overwintering strategy as in Balsfjorden. We may assume that the winter conditions in Kosterfjorden are sufficient for the maturation and initiation of spawning of *M. longa* and that the phytoplankton spring bloom defines the total fecundity of both species.

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