Marine Biology 79, 257–267 (1984)

Marine Biology
International Journal on Life in Oceans and Coastal Waters

Diel variations in the nutritional physiology of *Calanus glacialis* from Lat. 78° N in the summer

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Abstract

Calanus glacialis (Jaschnov) from Isfjord, western Spitzbergen, showed no tendency to pronounced diurnal vertical migration or cyclic variations in feeding activity. The samples, taken regularly over a 24-h period and at three different depths in the beginning of August, did however show considerable individual variations in feeding activity. These variations, reflected in the results of gut analyses, were not related to variations in the concentrations of particulate protein, carbohydrate or algal pigments in the water. Analyses of the activities of two digestive enzymes and the electron-transport system (ETS) indicated that those few individuals always present below the photic zone were there temporarily, and showed no signs of slowing down their metabolism. The results suggest that the population of *C. glacialis,* during the Arctic summer, feeds continuously in the upper water layer, but that intermittent, non-synchronous individual feeding rhythms are the rule.

Introduction

Polar regions are characterized by an annual light cycle gradually changing from 24-h light during a short summer period to 24-h darkness in mid winter. The primary production in these regions is therefore mainly confined to a few summer months. In the marine pelagic community, where copepods dominate among herbivorous organisms, the summer is characterized by a pronounced vertical gradient in primary production. Any vertical migration by zooplankton will therefore take them through contrasting food regimes. In order to understand the dynamics of the plankton community and to quantify the energy flux it is important to know if physiological parameters of animals from such contrasting food regimes follow any diurnal cycle. The present study concerns the copepod *Calanus glacialis* from Isfjord on the west coast of Spitzbergen in a summer situation with midnight sun. This species belongs to the polar waters of the Arctic region (Grainger, 1961) and was by far the most dominant species in Isfjord, both in terms of biomass and numbers. Variables studied were: (1) population structure, (2) individual protein and lipid content, (3) ETS activity, (4) digestive-enzyme activity, and (5) gut fullness. These variables were correlated to the concentrations of particulate protein, carbohydrate and algal pigments in the water column. The motivation for the choice of the above variables is as follows. Lipid content and lipid/protein ratio are both indications of the long-term nutritional condition of the copepods, as shown by the seasonal cycles in protein and lipid content of various species from high latitudes (e.g. Båmstedt, 1978; Gatten *et al.,* 1979; Falk-Petersen, 1981). The ETS activity reflects the copepod's respiration rate (e.g. Owens and King, 1975; King and Packard, 1975). The activities of the digestive enzymes are related to the present trophic situation of the copepods and a decrease in activity reflects food deprivation (Barrington, 1962; Boucher and Samain, 1974, 1975; Boucher *et al.,* 1976). Since trypsin catalyzes protein and amylase catalyzes carbohydrate, changes in the trypsin/amylase ratio indicate changes in food composition. Gut fullness also reflects the present trophic situation. For a given developmental stage the length of filled gut is considered directly proportional to the volume of filled gut. If the gut is cleared of its content by a constant proportion per unit time, then gut content multiplied by gut clearance rate gives a good estimate of ingestion rate (Mackas and Bohrer, 1976; Boyd *et al.,* 1980; Dagg and Grill, 1980; Kiörboe *et al.,* 1982). Under the assumptions given above, it thus follows that the length of filled gut is proportional to the ingestion rate. The accuracy of this method is limited by many factors. For example, the compactness of gut content does vary and the diameter of the alimentary channel is not constant throughout its length. Furthermore, if feeding and gut evacuation are not simultaneous, then gut content at a given time may present a biased

picture of the contemporaneous feeding rate. Gut fullness is therefore not thought to be an absolute quantitative estimator of current feeding rate, but rather an indicator of significant changes in the feeding rate of the copepod.

Material and methods

Sampling

The investigation was carried out onboard R/V "Johan Ruud" of the University of Tromsö, during a cruise to the west coast of Spitzbergen in July/August, 1981. Zooplankton samples were taken in Isfjord (Lat. 78°08'N, Long. 13°48'W) every four hours with a Tucker trawl (1 m^2 opening, 0.5-mm mesh aperture) from 22.00 hrs, August 4 to 22.00 hrs, August 5. The trawl was equipped with a non-filtering cod end and a device for opening and closing. Depth was monitored using a Simrad trawl eye. Samples were taken from 10 m by 5-min trawling, from 80 m by 10-min trawling, and from 200 m by 10- to 20-min trawling. The depth of water at the sampling site was about 340 m. Salinity, temperature, density, and oxygen content in a vertical profile were measured *in situ* with a Neil Brown CTDO sonde. Water samples were taken with Nansen bottles at ten fixed depths between 1 and 200 m for determination of algal pigments, particulate protein and carbohydrate.

Analytical procedures

Calanus glacialis (Jaschnov) were sorted immediately after collection by means of a small spoon-formed sieve. Approximately 80 copepods (if available) from each sample were frozen in liquid nitrogen and thereafter kept in a deep-freeze. This material was analysed at Tjärnö marine biological laboratory after 2 to 5 wk. The frozen material was thawed and stage V copepodites separated. For each analytical sample the length of filled gut of each individual was measured under a stereomicroscope. This information was used to test the relationship between gut fullness and different physiological parameters. For lipid determinations, four replicate samples (fewer in some cases, where the number of available copepods was low) of five specimens each were homogenized in chloroform/methanol (2:1 by volume) and the extract purified according to Folch *et al.* (1957). A known proportion of this extract was evaporated in preweighed aluminum pans and the amount of total lipids determined gravimetrically. Another four replicate samples (if available) of ten specimens each were taken for homogenization in 1.5-ml distilled water. One half ml of this homogenate was analysed for amylase activity (method modified after Street and Close, 1956, with incubation temperature 37 °C, incubation time 1 h, and pH 7.0), 0.5 ml for trypsin activity (method modified after Erlanger *et al.*, 1961 with incubation temperature 39 °C, incubation time 25 minutes, and pH 8.0), and 0.1 ml for protein content (method after Dorsey *et al.*, 1977).

At the time of collection four replicate samples (if available) of five specimens each were sorted out and homogenized in 1-ml ETS reagent containing 0.04-*M* Tris, 0.08-*M* K_2HPO_4, 60-μM $MgSO_4$, 1.2-mg PVP (polyvinylpyrrolidone) ml^{-1}, 1.6-μl Triton X-100 ml, and 0.4-mg INT (p-iodotetrazolium violet) ml^{-1} in distilled water, pH 8.5. The homogenate was incubated at 40 °C for one hour whereafter 0.2-ml quench, consisting of equal parts of concentrated formalin (37% formaldehyde) and 1 M orthophosphoric acid, were added and the samples frozen. After about three-weeks storage, 1-ml chloroform/methanol (2:1 by volume) was thoroughly mixed in each reagent tube and the samples centrifuged whereby all the reduced INT was extracted in the lower of the two phases thus formed. This procedure was necessary since most of the reduced INT was bound to the fat droplets in the sample. Following centrifugation, the upper phase was discarded and methanol added to a final volume of either 2.5 or 5 ml. This solution was again centrifuged and a spectrophotometric reading taken at 490 nm, using a non-biological blank carried through the same steps as the samples. Absorbance values were converted to corresponding respiration rates by use of an appropriate conversion factor. This was separately determined from measurements on ETS activity and respiration rate in a variety of planktonic crustaceans (Båmstedt, unpublished data). The equation used in the present investigation was:

$$\mu g\ O_2 \text{ consumed } h^{-1} = 1.40 \times V \times L \times A_{490},$$

where V = ml of final sample (2.5 or 5 in this case), L = path length (cm), and A_{490} = absorbance of sample minus absorbance of blank, measured at 490 nm.

A representative sample of the remaining living copepods was preserved in 4% neutralized formalin in seawater for later stereomicroscopic determination of developmental stage and gut fullness. Twenty-five copepods, chosen randomly from each sample, were used to determine the proportional population structure. Additionally 25 stage V copepodites were examined for gut fullness. This information was used to evaluate any diel variations in stageal composition and feeding activity of stage V copepodites.

Samples of 250-ml seawater from depths down to 25 m were filtered through a 25-mm diameter GF/C glass-fibre filter. The filters were folded, wrapped in aluminum foil, and stored in a deep-freeze until analysis within three to five weeks. The filters were homogenized in 4 ml of 90% aqueous acetone and the emission spectrum recorded on a Shimadzu 510 spectrofluorometer with an excitation wave length of 425 nm. The "pigment index" was calculated as the integral area between 600 and 700 nm on the paper readout from a recorder. This section includes fluorescence caused by the main algal pigments as well as their phaeopigments (Loftus and Carpenter, 1971) and gives relative results for comparative purposes.

Additional water samples of between 500 and 1 000 ml from all sample depths were filtered through a 47-mm

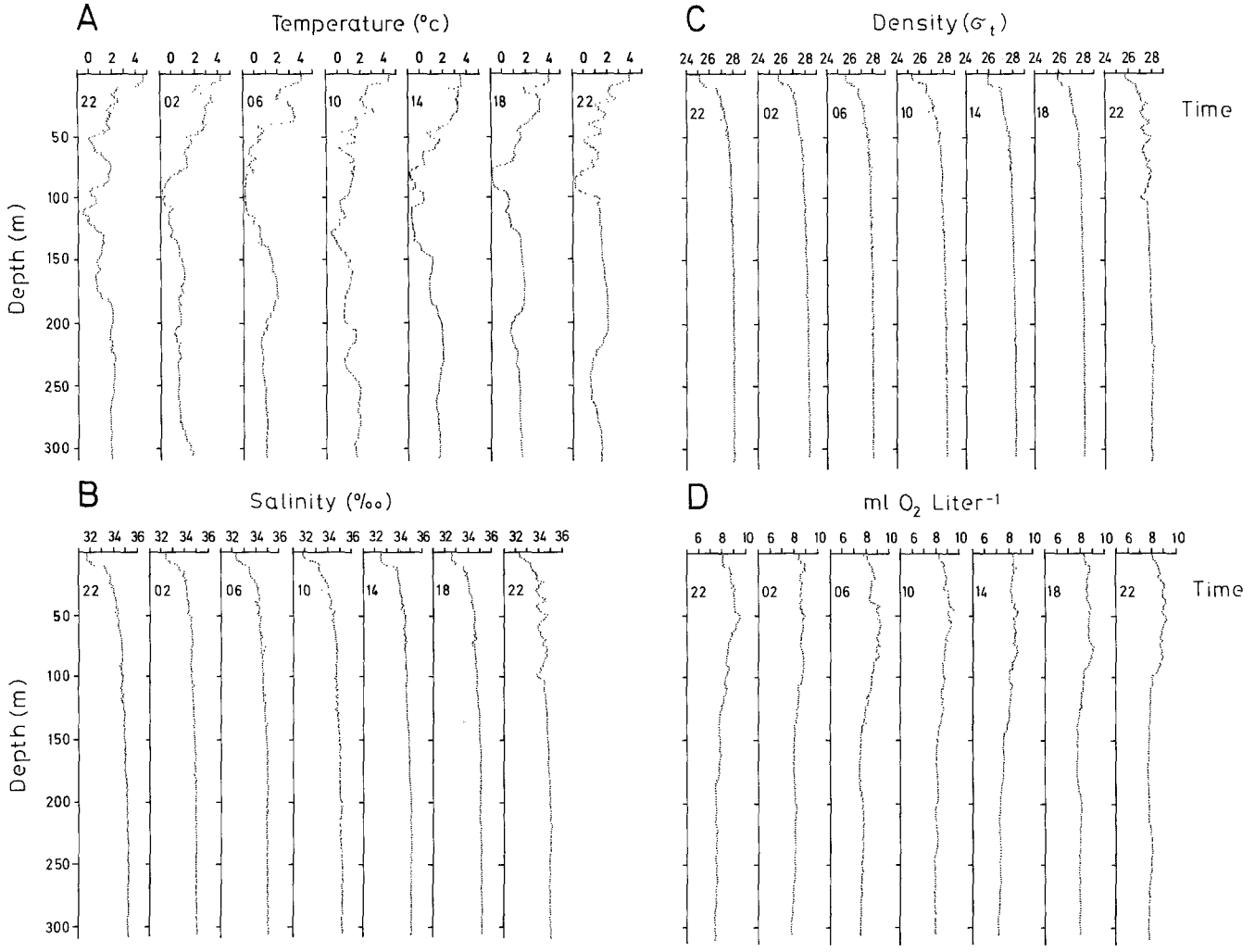

Fig. 1. Vertical profiles of hydrographical parameters. A. temperature, B. Salinity, C. Density, D. Oxygen concentration

diameter GF/C glass-fibre filter. The filters were treated as above, and, after storage for three to five weeks in a deep-freeze, two subsamples were cut out from each filter by using a punch. One subsample was used to analyse particle protein (method according to Dorsey *et al.,* 1977), the other to determine particulate carbohydrate, whereby the samples were hydrolysed in concentrated sulphuric acid (Lännergren, personal communication) and the analytical procedure by Josefsson *et al.* (1972) was followed.

Results

Environmental situation

The hydrographical situation during the sampling period (Fig. 1) was relatively stable, as best shown by the salinity and density profiles (Fig. 1 B, C). Temperature showed the greatest variation, with surface values ranging between 3.4° and 4.6 °C and minimum values between −0.5° and −1.0 °C occurring at 80 to 120 m. The alteration between lower and higher temperatures, most pronounced down to 100 m (Fig. 1 A), indicates some kind of intermediate water transport. This was not reflected in the salinity and density profiles except in the case of the final samples (Fig. 1 B, C). Salinity ranged between 31.8 and 32.6‰ S at the surface, but increased with depth to 34‰ S within the upper 20 m (Fig. 1 B). The pycnocline was always distinct and lay between 6 and 10 m (Fig. 1 C). The water was well oxygenated, with surface values ranging between 8.0 and 8.3 ml l^{-1}, and maximum values, usually at ca 50 m depth, of 8.8 to 9.5 ml l^{-1} (Fig. 1 D). These values correspond to saturations close to or, in the upper water layer, even above 100%.

Particulate protein in the upper 10 m ranged from 150 to 320 μg l^{-1} (Fig. 2 A). With a few exceptions the particulate protein then decreased gradually with increased depth to 50 to 100 μg l^{-1}.

Concentrations of particulate carbohydrate varied considerably more than those of protein, both with depth and with time (Fig. 2 B). The highest concentrations occurred in the upper 20 m, and near-surface values of ca 900 μg l^{-1} were found. The average carbohydrate concentration for the whole water column ranged from ca 190 to 700 μg l^{-1}. The corresponding protein range was 140 to 250 μg l^{-1} The

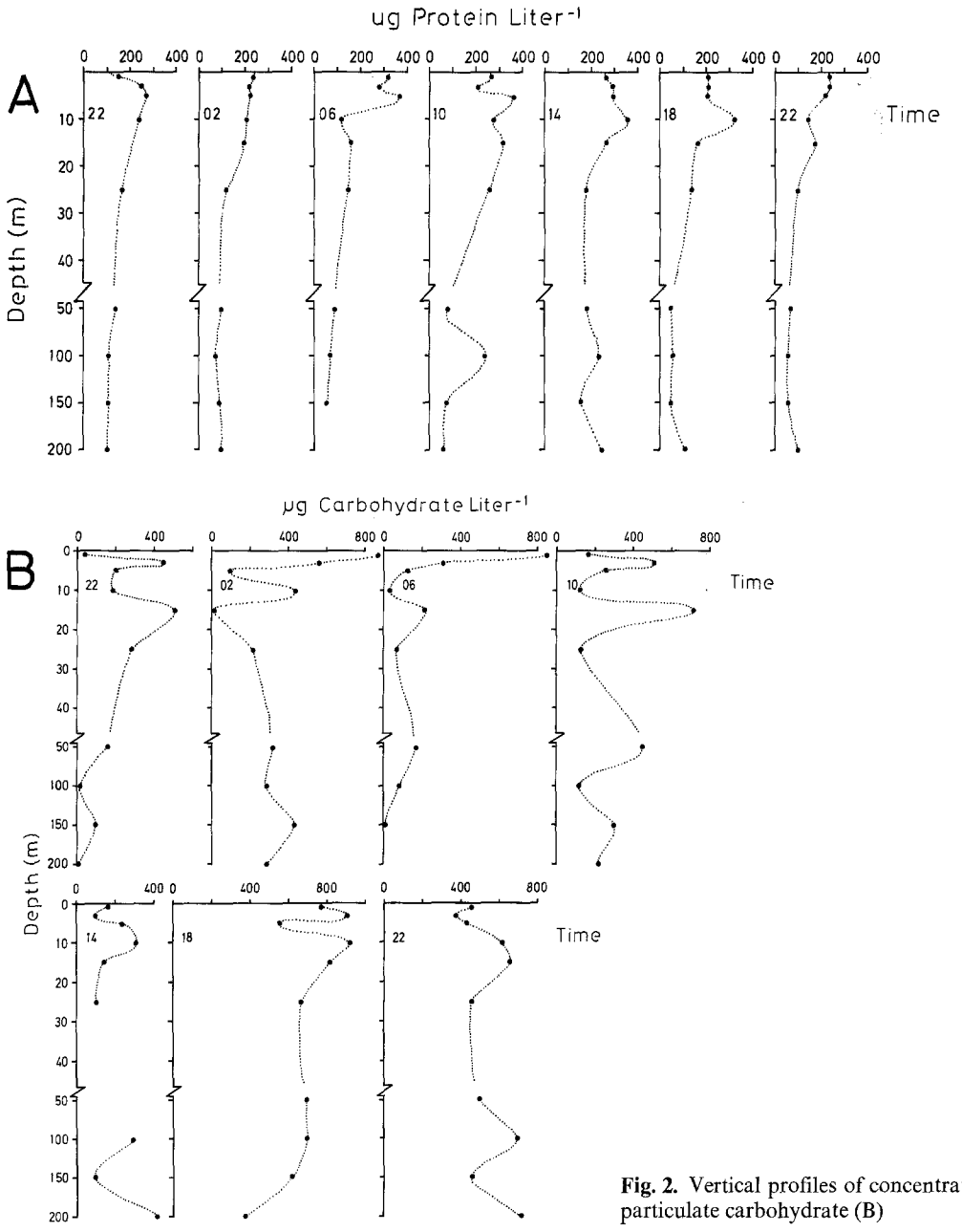

Fig. 2. Vertical profiles of concentration of particulate protein (A), and particulate carbohydrate (B)

protein/carbohydrate quotient for the whole water column ranged from 0.23 to 1.21.

The pigment index, determined down to 25 m depth, was usually highest in the upper layers (Fig. 3) with the most pronounced decrease occurring above the pycnocline depth (6 to 10 m). The highest values were recorded on the last sampling occasion, when the stratification was also the most distinct (Fig. 3). At this time, the value at the surface was eight times higher than at 15 and 25 m, indicating a high phytoplankton biomass.

Copepod population

The population structure of *Calanus glacialis* shown in Fig. 4 represents the relative composition of developmental stages among those individuals captured at the three indicated depths. Changes in the structure between depths and sample occasions do not inevitably mean changes in abundance of a given developmental stage. In reality the abundance of all stages decreased dramatically between 10 and 80 m, but less so between 80 and 200 m, as reflected in the mass of copepods captured. The decrease in abundance between 10 and 80 m was estimated to be at least 100-fold in most cases. The population structure of *C. glacialis* is therefore best described by the results from capture at 10 m. These show the dominance of stage V copepodites (64 to 96%, average 85%) with small elements of stage IV copepodites (0 to 36%, average 14%) and adult females (0 to 4%, average 1%). The figure also shows the extent to which the dominance of stage V copepodites changed with depth. From an average of 85% of the popu-

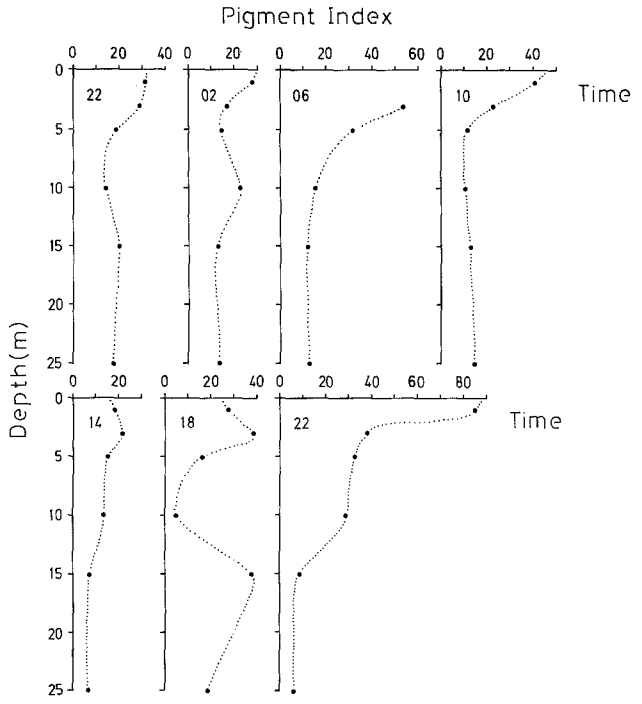

Fig. 3. Vertical profiles of phytoplankton pigments as given by the "pigment index" (see text)

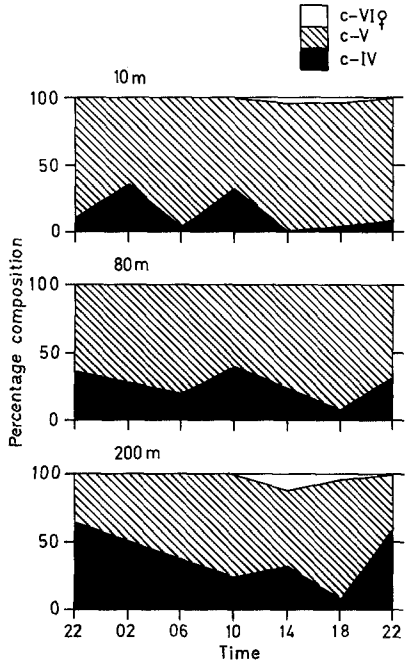

Fig. 4. *Calanus glacialis.* The population structure at three sampling depths

lation at 10 m, it decreased to 73% at 80 m and 58% at 200 m. In contrast, the relative proportion of stage IV copepodites increased with depth; 14% at 10 m, 27% at 80 m, and 38% at 200 m.

Actual *in-situ* feeding activity is indicated by the gut fullness of the copepods. The proportion of non-feeding individuals in the population is given by the percentage of

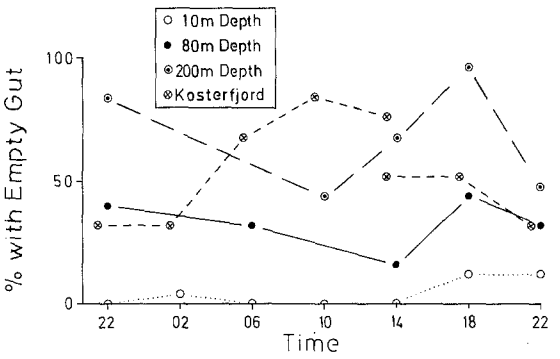

Fig. 5. *Calanus glacialis.* The proportion of copepods with empty guts taken from three depths. Results for *C. finmarchicus* from Kosterfjord, Sweden, are shown for comparison

copepods with empty guts (Fig. 5). All individuals from 10 m had food in their guts during the greater part of the day, but a small part of the population at that depth had empty guts at night (Fig. 5). A great part of the copepods captured at 80 m also had food in their guts, but most of the copepods from 200 m had empty guts (Fig. 5). The average proportion of the population with empty guts was 4% at 10 m, 33% at 80 m and 68% at 200 m. A larger proportion of the population had food in their guts during the daytime. This is the opposite trend to that found for *Calanus finmarchicus* from Kosterfjord, western Sweden, captured in early autumn (Fig. 5).

More information on relative feeding activity is shown in Fig. 6. Average gut fullness in copepods captured at 10 m showed a tendency to diel variation, with a reduction of 50% from early morning to early evening (Fig. 6 A). However, since individual variability, reflected by the large standard deviation, was always considerable, caution should be used when drawing any conclusions from this. The diel cycle of *Calanus finmarchicus* from Kosterfjord in early autumn is shown for comparison.

In the case of *Calanus finmarchicus* the cycle is reversed and more pronounced and includes a 15-fold change in average gut fullness between daytime and night-time. The average gut fullness of copepods from 80 and 200 m was always considerably lower than that of surface occurring animals (Fig. 6 B, C). The average length of guts filled with food was 744 μm for surface individuals, 299 μm for those from 80 m, and 112 μm for those from 200 m. The trend to highest feeding activity during the daytime was also found for copepods from 80 and 200 m (Fig. 6 B, C).

Average individual protein and lipid content of captured copepods is shown in Fig. 7. The average protein content did not vary significantly either with depth or time of sampling. The two samples from 200 m indicate that these copepods had considerably more lipid than those collected from 10 and 80 m (Fig. 7 C). Individuals collected at 10 m contained on average 156 μg protein and 398 μg lipid, those from 80 m 144 μg protein and 317 μg lipid, while animals from 200 m contained an average of 148 μg protein and 631 μg lipid. Average lipid/protein ratio for the three depths was 2.7, 2.0, and 3.1, respectively.

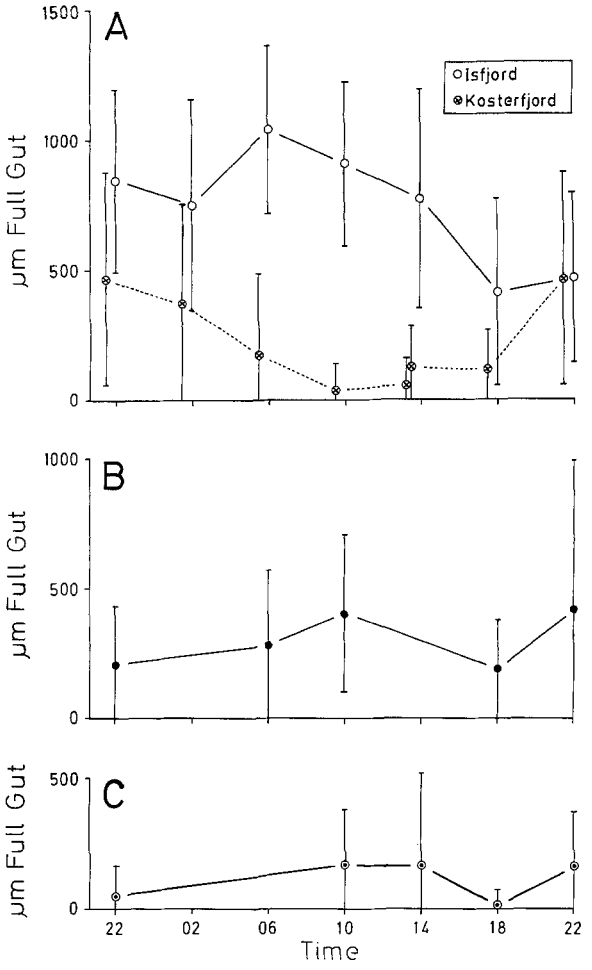

Fig. 6. *Calanus glacialis.* Average length of full guts of copepods collected at 10 m (A), 80 m (B), and 200 m (C) depth. Results for *C. finmarchicus* from Kosterfjord, Sweden, is shown in (A) for comparison. $n=25$. Vertical bars denote SD

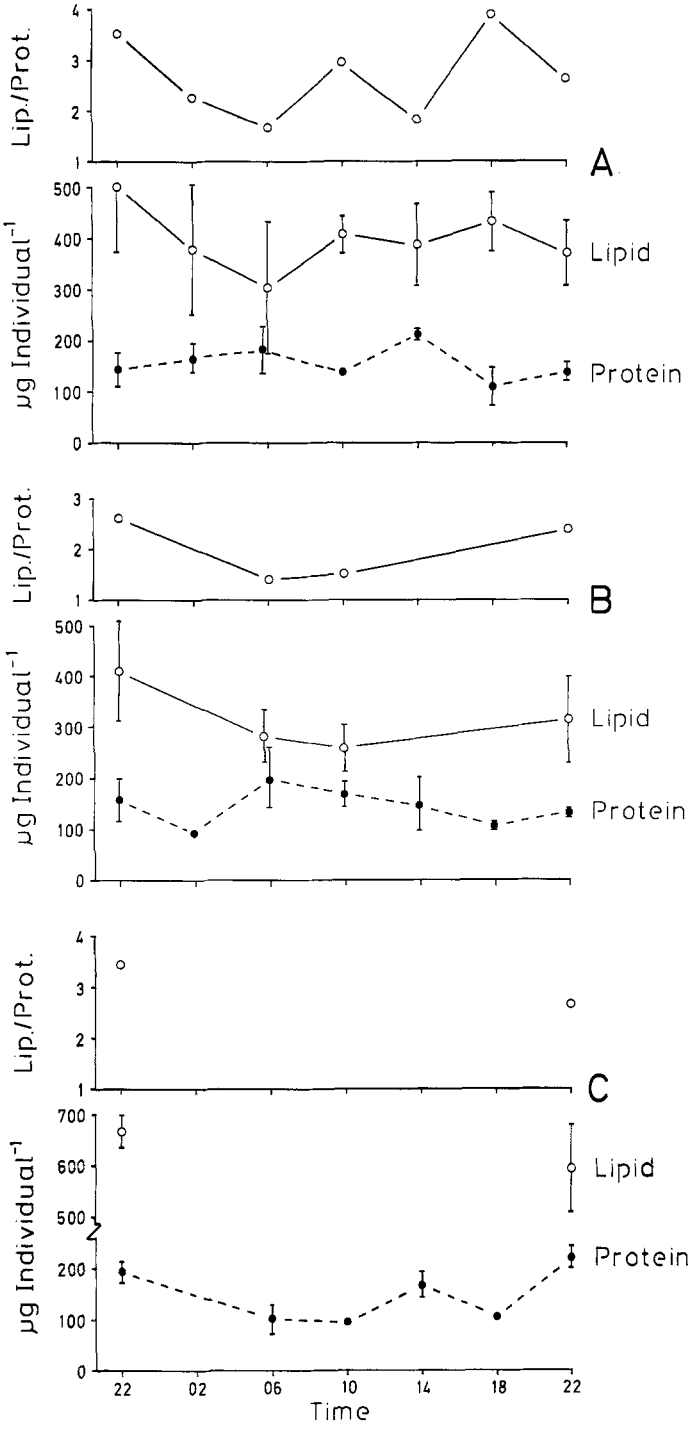

Fig. 7. *Calanus glacialis.* Average individual lipid and protein content and the lipid/protein ratio of copepods collected at 10 m (A), 80 m (B), and 200 m (C) depth. $n=4$. Vertical bars denote SD

The activities of the two digestive enzymes did not show any evident trend common to all depths (Fig. 8). Copepods captured at 10 m showed peaks in trypsin activity at 02.00 and 14.00 hrs. These peaks were also reflected in the trypsin/amylase ratio (Fig. 8 A). Copepods from 80 m showed less diel variation in trypsin activity, with the maximum, corresponding to maximum in trypsin/amylase ratio, at 10.00 hrs (Fig. 8 B). Copepods from 200 m showed one main peak in trypsin activity at 06.00 hrs, but this was not reflected in the trypsin/amylase ratio (Fig. 8 C). Average values and variability expressed as the coefficient of variation) in enzyme activities for the whole period are given in Table 1.

The activities of the two enzymes in copepods taken from 10 m showed a negative co-variation ($r=-0.82$). This situation changed in the case of copepods from 80 m ($r=-0.08$) and 200 m ($r=0.19$).

Figure 9 demonstrates that there were no clear differences in ETS activity between copepods captured at different depths. This means that individuals from the whole water column were metabolically highly active with no tendency to dormancy. Copepods from 10 m had a mean value of 0.42 $\mu g\ O_2\ h^{-1}$ individual^{-1}, those at 80 m 0.44, and those from 200 m had a mean value of 0.52 $\mu g\ O_2\ h^{-1}$ individual^{-1}. These differences were not statistically significant.

Figure 10 gives the basis for evaluating the relationship between actual feeding activity and long-term energy storage. All copepods from 200 m analysed for their lipid contents had empty guts, but contained usually more lipid

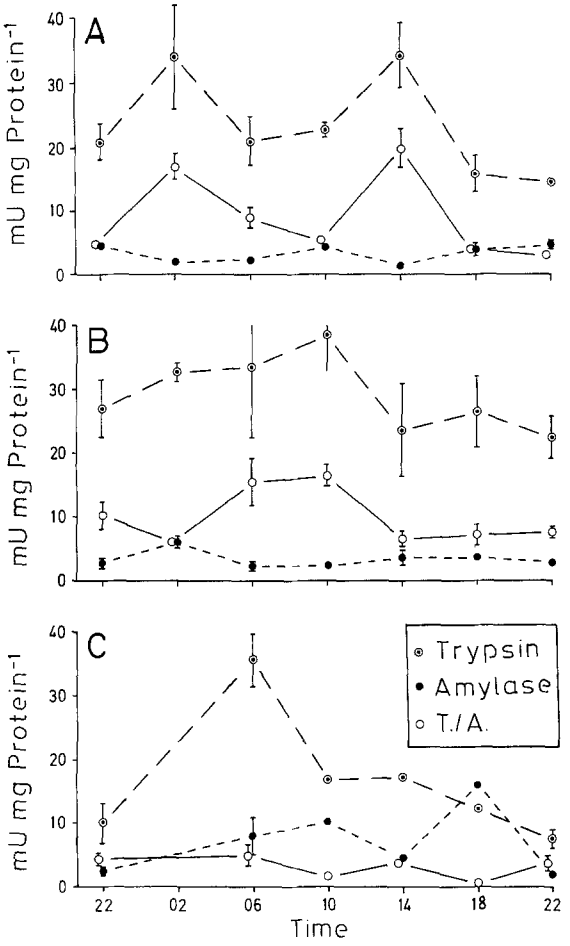

Fig. 8. *Calanus glacialis.* Average activity of trypsin and amylase and the ratio trypsin/amylase of copepods collected at 10 m (A), 80 m (B), and 200 m (C) depth. $n=4$. Vertical bars denote SD

Table 1. *Calanus glacialis.* Average activities of trypsin and amylase and the trypsin/amylase ratio of the copepods sampled over 24 h at three depths

Sampling depth (m)	Trypsin			Amylase			Trypsin/ Amylase		
	n	mean	CV	*n*	mean	CV	*n*	mean	CV
10	28	23.5	33.5	28	3.4	38.4	28	9.1	74.6
80	27	29.2	20.1	27	3.4	38.6	27	9.9	43.8
100	16	16.6	60.6	16	7.2	50.6	16	3.2	50.6
Average	3	23.1	38.1	3	4.7	42.5	3	7.4	56.3

than copepods from higher up in the water column. There was no statistically significant correlation (Student's *t*-test on the correlation coefficient, see Zar, 1974) between gut fullness and lipid content for individuals from the sampling depths 10 and 80 m ($n=28$, $r=0.229$, and $n=18$, $r=0.439$ respectively; $P>0.05$), probably an indication that all copepods were in a good nutritional state, independent of actual feeding activity.

Results shown in Fig. 11 may provide information on the relationship between ingestion activity and digestion

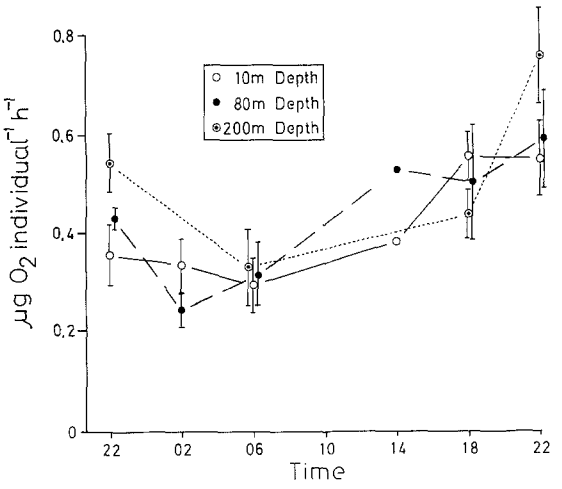

Fig. 9. *Calanus glacialis.* Respiration rate (derived from measurement of ETS activity) of copepods collected at three depths. $n=4$. Vertical bars denote SD

readiness. Out of 18 samples from 200 m analysed for amylase activity, 11 produced copepods without food in their guts. Most of these samples showed low amylase activity (Fig. 11 A) and there was no significant correlation between gut fullness and amylase activity ($n=18$, $r=0.388$; $P>0.05$). This was also the case for copepods captured at 10 and 80 m ($n=32$, $r=0.286$, and $n=31$, $r=0.290$, respectively; $P>0.05$).

Among individuals captured at 200 m, those with empty guts showed lower trypsin activity than those with food in their guts (Fig. 11 B). The same tendency was apparent in copepods from 10 m, but not in those captured at 80 m (Fig. 11 B). A Student's *t*-test on the correlation coefficient for the relationship between gut fullness and trypsin activity gave significant results for copepods captured at 10 m ($n=31$, $r=0.413$; $0.05>P>0.02$) and 200 m ($n=18$, $r=0.632$; $0.005>P>0.002$) but not for those captured at 80 m ($n=29$, $r=0.231$; $P>0.05$).

The ratio between trypsin activity and amylase activity was extremely variable, especially in copepods with relatively full guts (Fig. 11 C). Average ratios between 2.8 and 23.2 were found for individuals from 10 m having at least 500-μm filled guts, while well-fed individuals from 80 m always showed high ratios (Fig. 11 C). A Student's *t*-test on the correlation coefficient for the relationship between gut fullness and the trypsin/amylase ratio revealed significant positive correlations for copepods from 10 and 80 m ($n=31$, $r=0.375$, and $n=30$, $r=0.402$, respectively; $0.05>P>0.02$). Copepods captured at 200 m did not show any significant correlation ($n=18$, $r=0.089$; $P>0.05$).

Discussion

Species of the genus *Calanus* have life cycles which in the Arctic may exceed one year (Ussing, 1938; Digby, 1954; Dawson, 1978). Kosobokova (1980) suggested that *C. gla-*

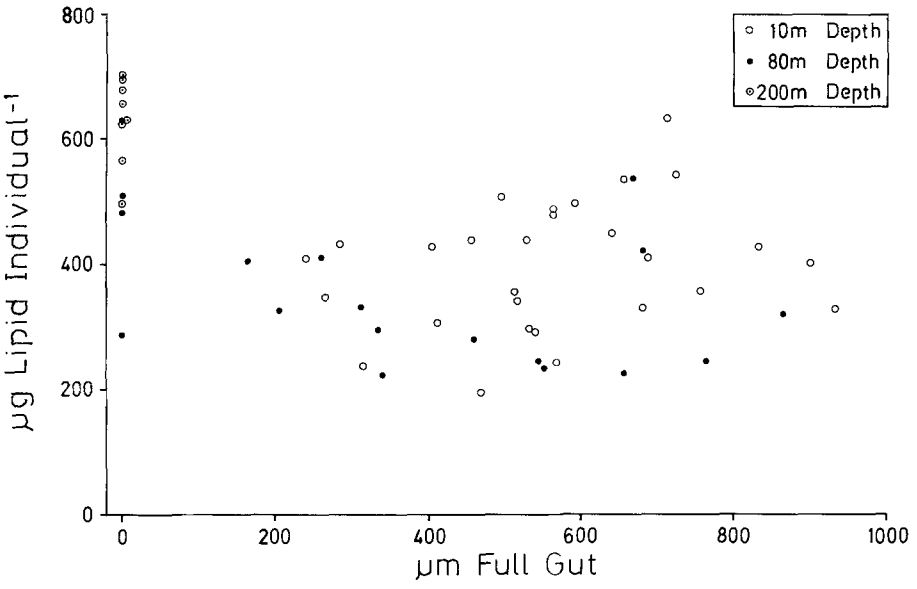

Fig. 10. *Calanus glacialis.* Relationship between average gut fullness and average lipid content of copepods collected at three depths

cialis from the Central Arctic Basin takes two years to complete its life cycle, and Grainger (1965) found that most of the population in the Arctic Ocean at Long. 120 °E became mature in the second year of life. At the time of investigation the population of *C. glacialis* from Isfjord mainly consisted of stage V copepodites with a small proportion of adult females and stage IV copepodites. It can therefore be assumed that all individuals were hatched in the preceding year and variation in age and development rate within the population was small. Variations in nutritional condition within the population were probably related to more immediate events, such as feeding activity at the time. Feeding activity at the time of investigation, as reflected by gut fullness and the proportion of copepods with food in their guts, indicates that *C. glacialis,* during the Arctic summer, feeds in the surface water over the whole day, with only minor variations for the population (Figs. 5, 6 A). At the same time, the great individual variability in gut fullness found at all times and depths sampled (Fig. 6 A, B, C) indicates that individual feeding activity is intermittent without any close synchronization. Alternatively, variations in food availability, both in time and space (see Figs. 2, 3), could influence the ingestion rate of the copepods. However, the ranges in concentration of particulate protein and carbohydrate in the upper 20 m (see Fig. 2 and p 259) indicate that the food level was always sufficient for maximum feeding rate. For other *Calanus* species, maximum feeding rate has been noted below a concentration of 500 $\mu g\ C\ l^{-1}$ (Parsons *et al.,* 1969).

Gould (1953) studied *Calanus finmarchicus* from the Firth of Clyde and interpreted that a diurnal rhythm, with the highest ingestion rate in the middle of the night occurred during periods of vertical migration. He also found that, throughout most of the year, ingestion rate was independent of time of day. He suggested that diurnal feeding rhythms occur only as a result of migration between surface water rich in food and more barren water, without any real change in filtering rate. Contradictory results by Mackas and Bohrer (1976) on some smaller zooplankton species indicate a true diel variation in filtering rates, interacting with diel vertical migration. These authors showed experimentally that the gut fullness of *Acartia clausi* was not constant even when food was continuously available, and suggested, as some earlier investigators (Conover, 1968; Pearre, 1973) that the satiation of the animals is an important factor governing feeding activity and vertical migration. My observations in Isfjord indicate the absence of vertical migration of *C. glacialis,* and this is also supported by Kosobokova (1978). From studies on Arctic freshwater zooplankton, Buchanan and Haney (1980) found that a light cycle with at least four hours of darkness was necessary to initiate a diurnal vertical migration. During the Arctic midsummer, zooplankton in general therefore seem to suppress any diurnal migration and feeding rhythms. Feeding activity is not, however, thought to be continuous, as indicated by the high variability in gut fullness of *C. glacialis* from the present study. Neither is gut fullness a direct function of the food supply since, in the present investigation, correlation analyses within each of the three depths sampled revealed that variations in the average gut fullness of *C. glacialis* were not related to variations in food supply, expressed as particulate protein, carbohydrate or pigment index ($n=6$ or 7, r varying between −0.633 and 0.653; $P>0.05$ in all cases). Insignificant correlations between gut fullness and ambient chlorophyll concentration have previously been reported for the copepods *Neocalanus plumchrus* and *N. cristatus* from the Bering Sea by Dagg and Wyman (1983). Runge (1980) has also shown in direct feeding experiments on *C. pacificus* that the past feeding condition of the copepods to a great extent determines the ingestion rate. Works by Rosenberg (1980) and Paffenhöfer *et al.* (1982) also show that the feeding processes of herbivorous copepods are by no means automatic. It thus seems probable that a copepod can interrupt feeding when

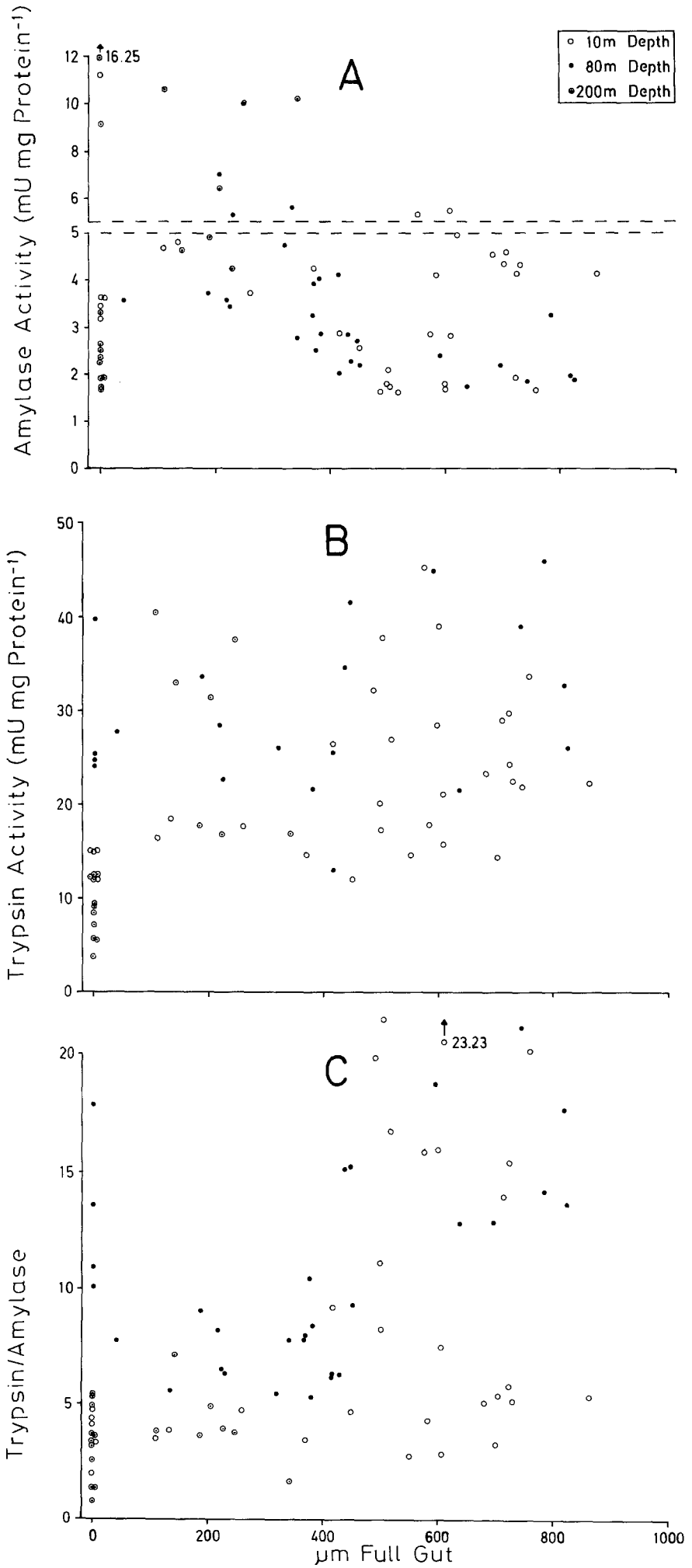

Fig. 11. *Calanus glacialis.* Relationship between average gut fullness and average amylase activity (A), trypsin activity (B), and trypsin/amylase ratio (C) of copepods collected at three depths

satiated and start feeding again when an external energy supply is required.

The copepods collected at 200 m probably exemplify the non-feeding situation very well. They frequently had empty or almost empty guts (Figs. 5, 6 C) as well as high lipid contents (Fig. 7 C), which could indicate that they were prepared for the overwintering period, but high ETS activity and digestive-enzyme activity indicated that they were not dormant and therefore might subsequently be expected to migrate up to the surface water and continue feeding. In this context the time factor for responses to variations in the food environment must be considered (Mayzaud and Poulet, 1978). In the digestion processes, digestive enzymes are continuously synthetisized and utilized, and a time lag probably exists between changes in the food intake and the response of the enzyme system. Studies on fish indicate an adaptation of the digestive-enzyme system to new feeding conditions within one week (Kawai and Ikeda, 1972), but the period is probably considerably shorter for zooplankton species, since diel variations due to a diel cycle in feeding intensity have been observed (Tande and Slagstad, 1982, for *Calanus finmarchicus;* Båmstedt, unpublished data for *C. finmarchicus* and *Metridia longa*). The relatively small differences in average enzyme activity of *C. glacialis* taken from different depths with different food supply therefore indicate a relatively short period spent below the upper, productive, water layer. The theory by Boyd *et al.* (1980) of short-term intermittent feeding of three species of copepods seems thus suitable as an explanation of high individual variability in gut fullness with an insignificant correlation with ambient food supply of *C. glacialis.*

Experimentally changed quality and quantity of food, as well as seasonally governed changes in the natural environment, have resulted in significant relationships between food quality/quantity and digestive-enzyme activities, both for fish (Kawai and Ikeda, 1972, 1973; Onishi *et al.*, 1976) and for zooplankton (Mayzaud and Conover, 1976; Mayzaud and Poulet, 1978; Hirche, 1981). In the present investigation variations in trypsin and amylase activities and in the trypsin/amylase ratio of *Calanus glacialis* from a given depth were never significantly correlated with variations in environmental particulate protein and carbohydrate or the pigment index ($P > 0.05$ in all cases). However, the results for copepods from 200 m indicate a lower trypsin activity and higher amylase activity, and consequently a considerably higher trypsin/amylase ratio than for individuals from 80 and 10 m (see Table 1). Similar effects have been observed during the initial phase of starvation of the copepods *C. finmarchicus, Metridia longa* and *Chiridius armatus* (Båmstedt and Sjöberg, unpublished data). The activities of the digestive enzymes thus indicate that copepods from 200 m were in a short-term starvation state.

The characteristics of variation in enzyme activities referred to above are in accordance with the other physiological parameters. Together they indicate that copepods sampled below 10 m were there only temporarily. The great variability in lipid storage and enzyme activities, mainly uncorrelated with the variation in gut fullness (Figs. 10, 11, pp. 262, 263) indicate that the continuous feeding activity of the population of *Calanus glacialis* in summertime is composed of individual, non-synchronous cycles.

Acknowledgements. I am grateful to the University of Tromsö, and especially to C. Hopkins, for letting me join the cruise with R/V "Johan Ruud" and for the use of their facilities onboard. I also thank B. Klefbohm at the Tjärnö laboratory for technical assistance, and C. Hopkins and K. Tande, University of Tromsö, for comments on the manuscript. The work was financed by the Swedish Natural Science Research Council (NFR).

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Date of final manuscript acceptance: February 7, 1984.
Communicated by O. Kinne, Hamburg