OPHELIA, 22 (1): 15-31 (June 1983)

ALGAL GRAZING BY THE PLANKTONIC COPEPODS *CENTROPAGES HAMATUS* AND *PSEUDOCALANUS* SP.: DIURNAL AND SEASONAL VARIATION DURING THE SPRING PHYTOPLANKTON BLOOM IN THE ØRESUND

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ABSTRACT

Seasonal and diel variation in rate of algal grazing were estimated from measurements of gut content (plant pigments) and gut turnover in the copepods *Centropages hamatus* and *Pseudocalanus* sp. during spring (Januar-May) in the Øresund. Both species exhibited significant diel variation in gut content and ingestion rate at the three depths studied (5, 10 and 22 m), with the highest ingestion rates and gut contents during night. The variation was most pronounced in March, but almost insignificant in April. Since the copepods did not migrate vertically, the observed pattern is due to a variable feeding activity rather than caused by continuous feeding at varying food concentrations. We found a positive correlation between ambient algal concentration and algal ingestion rate and gut content for both species in weekly morning samples. The results indicated satiation of the ingestion rates at high algal concentrations. Maximum algal ingestion rates measured in the field were similar to maximum ingestion rates measured in the laboratory in C. *hamatus* at the same temperatures. However, due to the circadian feeding rhythm, the daily rations estimated in the field were considerable less than corresponding maximum daily laboratory rations, and were in addition relatively constant ($\sim$ 6-12 ng chlorophyll-*a* $\cdot$ ind^{-1} $\cdot$ d^{-1}) and independent of depth and ambient algal concentration. An assessment of the total mesozooplankton algal grazing pressure, based on measured zooplankton densities and estimated algal rations, showed that less than 1-5 % of the phytoplankton primary production was channeled through mesozooplankters in the Øresund during the period studied.

INTRODUCTION

Much has been learned about feeding behaviour and energetics of planktonic copepods from laboratory experiments. In order to assess the quantitative role of copepods as phytoplankton grazers, several workers have focussed upon the relationship between algal concentration and feeding rate in the laboratory (e.g.

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Frost 1972, Harris & Paffenhöfer 1976). However, the complexity of the environment in the sea, e.g. with respect to type, quality and size distribution of the particles available to the suspension feeding copepods, as well as to micro-scale variation in phytoplankton abundance, makes the application of laboratory measured feeding rates to the field questionable. In addition, a number of aspects of copepod feeding behaviour, essential to the understanding of their quantitative role as phytoplankton grazers in the sea, are very difficult or impossible to study in the laboratory. For example, what is the diel variation in feeding rate? To what extent does feeding rate vary with depth? Or with season? How does vertical migration influence the daily algal ration? Such questions are probably most properly elucidated by studies of copepod feeding behaviour *in situ*.

Mackas & Bohrer (1976) studied copepod algal grazing *in situ* by measuring the quantity of plant pigments (i.e. chlorophyll-*a* and phaeopigments) in the guts of copepods caught at various depths and times. Several workers have applied this method to copepods from various geographical areas (e.g. Boyd *et al.* 1980, Dagg & Grill 1980, Dagg *et al.* 1980). In a previous study (Kiørboe *et al.* 1982) we measured the turnover rate ('gut clearance') of plant pigments in the guts of the copepod *Centropages hamatus* at various temperatures in the laboratory, thus allowing an approximate estimation of algal grazing rate *in situ* from measurements of gut content. Comparison in the laboratory of ingestion rates estimated by this method with estimates derived from observed decreases in algal concentration in experimental bottles, showed the gut content method to yield reliable results. This method has the obvious advantage that the copepods have been feeding in their natural environment, and that all the factors that influence feeding are unaffected by the researcher. An important limitation of the method is, however, that only the algal part of the diet is included in the estimate, thus ignoring feeding on particles of non-algal origin. The method therefore focusses upon the functional relationship between phytoplankton and zooplankton grazing.

In the present paper we have applied this method to investigate seasonal and diel variation in algal grazing of the copepods *C. hamatus* and *Pseudocalanus* sp. in the Øresund (Denmark) during spring 1981. (Due to confusion whether *Pseudocalanus* should be classed with *P. elongatus* or *P. minutus*, cf. Corkett & McLaren (1978), we here refer to it as *Pseudocalanus* sp.) During this period there is a marked variation in phytoplankton abundance. Øresund is characterized by a permanent, steep halocline in 10-15 m depth. This probably prevents the zooplankters from making vertical excursions across the halocline, since neither *Pseudocalanus* sp. nor *C. hamatus* survive transfer from surface to bottom water (or reverse) in the laboratory (unpubl. obs.). Diel migration was therefore only studied superficially. Variation in algal grazing with time of day and depth have been integrated to arrive at estimates of daily algal rations, and the field estimates have been compared to measurements of algal grazing rate in the laboratory, and to estimates of phytoplankton primary production in the Øresund.

Thanks are due to the crew of R/V 'Ophelia', B. Thrue and B. Jørgensen for assistance during cruises. Dr. W. Nicolaisen criticized the manuscript.

MATERIALS AND METHODS

Investigations were carried out at Ellekilde Hage (northern part of Øresund) from 15th of January to 27th of May 1981. Water depth at the station is 30 m. In the northern part of Øresund a halocline separates a surface layer of brackish water (10-15 ‰ S) originating from the Baltic Sea from high saline (30-33 ‰ S) North Sea water at bottom. During spring and autumn blooms, the highest algal biomass is found in the halocline in a narrow layer of about 22 ‰ S, probably Kattegat surface water in origin (Nicolaisen & Christensen, pers. comm.). During the investigation period weekly sampling in this water body was carried out, all between 10:00 and 11:00 a.m. In addition to the weekly sampling, four diurnal investigations on 17-18 February, 16-17 March, 7-8 April and 26-27 May were carried out. They included sampling every second hour at three depths: above (3-5 m), within (9-13 m, 22 ‰ S) and below (20-22 m) the phytoplankton maximum layer.

Sampling

Zooplankton were collected from discrete depths with an opening-closing 200 μm mesh size WP2 net (Tranter 1968). Horizontal towing was not necessary because the current would stream the net. Depending on the current velocity and copepod concentration, sampling time varied between 2 and 10 min. After sampling, the cod-end content was diluted in filtered sea water from the collection depth. Subsamples containing 50-200 copepods were filtered on Whatman GF/C filters that were instantaneously deep-frozen with carbonic acid from a spray-can (Kälte spray 75). Less than 5 min. elapsed from closure of the plankton net till freezing of the copepods. The filters were kept frozen until further treatment. Prior to zooplankton sampling, the depth for 22 ‰ S was located and water was collected from the three depths with a hose connected to a monopump. Salinity and temperature were measured by means of a Salinity Temperature Bridge Type MC5 (Electronic Switchgear (London) LTD) with the transducer carried by the hose end. Algal concentrations were measured fluorometrically in water samples as chlorophyll-*a* after acetone extraction (Strickland & Parsons 1968). To identify the dominating algal species, phytoplankton was collected on a 20 μm plankton gauze and preserved in 4 % formaldehyde. Collections were carried out once during each of the diurnal investigations from the three depths.

On March 16-17 diel migration of the copepods was investigated. Using the pump, zooplankton from 230 l of water was collected on a 200 μm plankton gauze at two hour intervals from the three depths. The samples were stored in 4 % formaldehyde until identification and counting in the laboratory.

Gut content and ingestion rate

In the laboratory adult *Centropages hamatus* and *Pseudocalanus* sp. females were picked from the frozen filters under the dissecting microscope. To prevent thawing during sorting cool light was used and the frozen filter was immersed in a salt-ice mixture. The copepods were cleaned for adherent algae with a small brush, and 15-40 specimens were tranferred to 5 ml of 90 % acetone. The plant pigments (chlorophyll-*a* + phaeopigments) in the guts were determined according to Kiørboe *et al.* 1982. Whenever possible 5 replicates from each sampling were measured.

To measure the effect of freezing on the plant pigment content of the copepods a separate experiment was set up in the laboratory. Adult *C. hamatus* and *Pseudocalanus* sp. females, fed a mixture of the algae *Isochrysis galbana, Dunaliella marina* and *Phaeodactylum tricornutum* during 4 hours, were gently collected on a plankton gauze and transferred to filtered sea water. As in field sampling subsamples were filtered on Whatman GF/C filters. Some were immediately transferred to acetone and analysed for plant pigments, while others were deep-frozen. The effect of freezing was a lowered content of algal pigments as found by fluorometric analysis. The 'loss' of pigment (chlorophyll-*a* + phaepigments) was not correlated with duration of freezing and averaged 33 % $\pm$ 7 % (SD), n = 21. This loss due to freezing was corrected for in the field samples. Further, all values were corrected for background fluorescence of the copepods. This was obtained by measuring the fluorescence of specimens starved for 24 h. Background fluorescence did not differ between the two species (*C. hamatus*: 0.059 ng pigm. · ind^{-1}, SD = 0.013; *Pseudocalanus* sp.: 0.063 ng pigm. · ind^{-1}, SD = 0.03). A common value of 0.06 ng pigm. · ind^{-1} was used for both species.

Ingestion rate of plant material was estimated by multiplying the corrected gut content by the gut clearance rate and was expressed as ng chlorophyll-*a* · ind^{-1} · h^{-1}. In a previous study we measured the gut clearance rate in *C. hamatus* at 4 temperatures (1,5, 10, and 15 °C) (Kiørboe *et al.* 1982). Linear regressions of the log transformed values were used to calculate the gut clearance rate at ambient temperature. In the calculations *Pseudocalanus* sp. was assumed to have the same gut clearance rate as *C. hamatus*.

Possible methodological biases that must be considered include defaecation prior to freezing, inclusion of algae attached to the copepods in the gut pigment analyses and physiological variation in gut clearance rate. However, none of these seem to be serious. Compared to the short time elapsed from capture to freezing, gut clearance rate is very slow at the low ambient temperatures (0.6 % ·

min^{-1} for *C. hamatus* at 5 °C, Kiørboe *et al.* 1982). Likewise, accidental defaecation due to handling is probably insignificant, judging from comparison of maximal gut contents in field-collected *C. hamatus* with maximal gut content in laboratory-fed specimens (see Discussion, and c.f. also Gauld (1953) and Mackas & Bohrer (1976)). A significant diel variation in gut content at a constant algal concentration (c.f. Fig. 4) precludes that attached algae are included in gut pigment analyses to any significant degree. Finally, gut clearance is strongly influenced by temperature (Kiørboe *et al.* 1982), but may vary with food quality as well. However, gut clearance was estimated on a diatom diet in the laboratory (*Ditylum brightwellii*), and diatoms dominate the phytoplankton in the Øresund during spring.

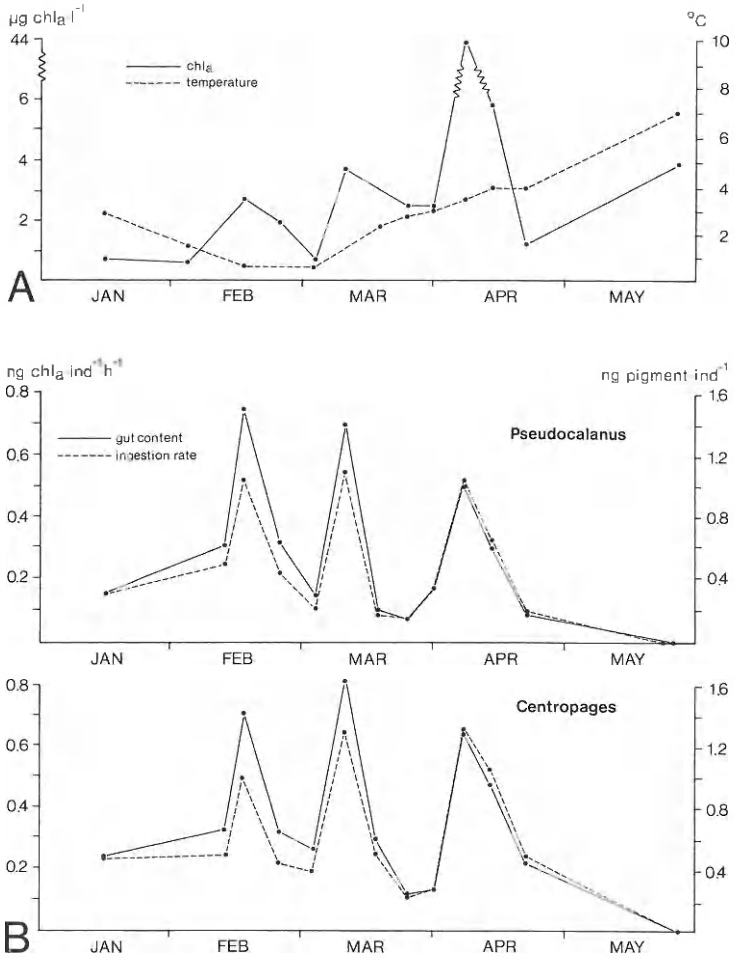

FIG. 1. A, temperature and chlorophyll-*a* concentration (µg chlorophyll-*a* · l^{-1}) in 22 ‰ S water (depths 9-13 m) during spring 1981 at Ellekilde Hage in northern Øresund. B, gut content (ng pigment · ind^{-1}) and ingestion rate (ng chlorophyll-*a* · ind^{-1} · h^{-1}) in *Pseudocalanus* sp. and *Centropages hamatus* collected at 10:00 a.m. in 22 ‰ S water.

RESULTS

During the sampling period the chlorophyll-*a* concentration in the 22 ‰ S water body rose from 0.6 μg chlorophyll-*a* · l^{-1} in January to a peak of 44 μg chlorophyll-*a* · l^{-1} in the beginning of April. In May after the spring bloom the chlorophyll-*a* concentration remained relatively high (Fig. 1). Unlike chlorophyll-*a* the concentration of phaeopigments in the 22 ‰ S water showed only little variation during the sampling period (range: 0.2-0.6 μg phaeopigment · l^{-1}). From February through April the diatoms *Skeletonema costatum, Thalassionema nitzchioides* and various *Chaetoceros* species dominated the phytoplankton. On 26th May very few algae were present in the preserved samples in spite of a relatively high chlorophyll-*a* concentration in the 22 ‰ S water.

Gut content and ingestion rate

The variation in the uncorrected gut content in the 2-5 replicates from each sampling usually was small (SD less than 20 % of the mean in 85 % of the samples). In a few samples with a low mean content, however, it was substantially higher (SD up to 80 % of the mean).

For both copepod species gut content and ingestion rate in the weekly morning samples from the 22 ‰ S water varied markedly (*Pseudocalanus* sp.: 0-1.45 ng pigment · ind^{-1}, 0-0.56 ng pigment · $ind^{-1} \cdot h^{-1}$; *C. hamatus*: 0-1.62 ng pigment · ind^{-1}, 0-0.65 ng pigment · $ind^{-1} \cdot h^{-1}$; gut content and ingestion rate, respectively). Three distinct peaks in gut content for both species were found, coinciding with peaks in the phytoplankton biomass (Fig. 1). In May almost no pigment was found in the copepods in spite of a relatively high chlorophyll-*a* concentration. Omitting the May samples, corresponding values of ingestion

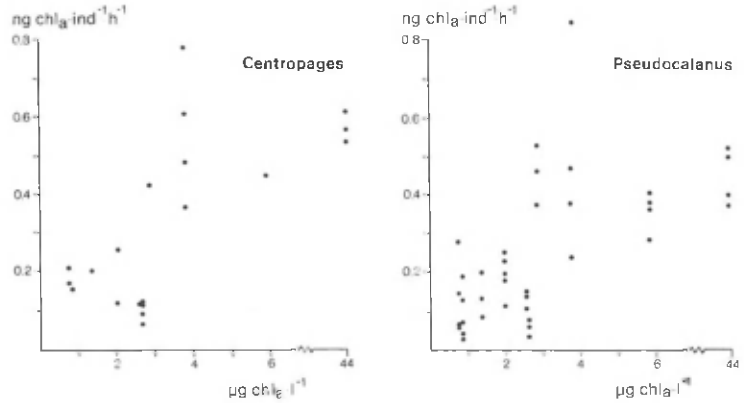

FIG. 2. Ingestion rate (ng chlorophyll-*a* · $ind^{-1} \cdot h^{-1}$) in *Centropages hamatus* and *Pseudocalanus* sp. as a function of algal concentration in water. Data from Fig. 1.

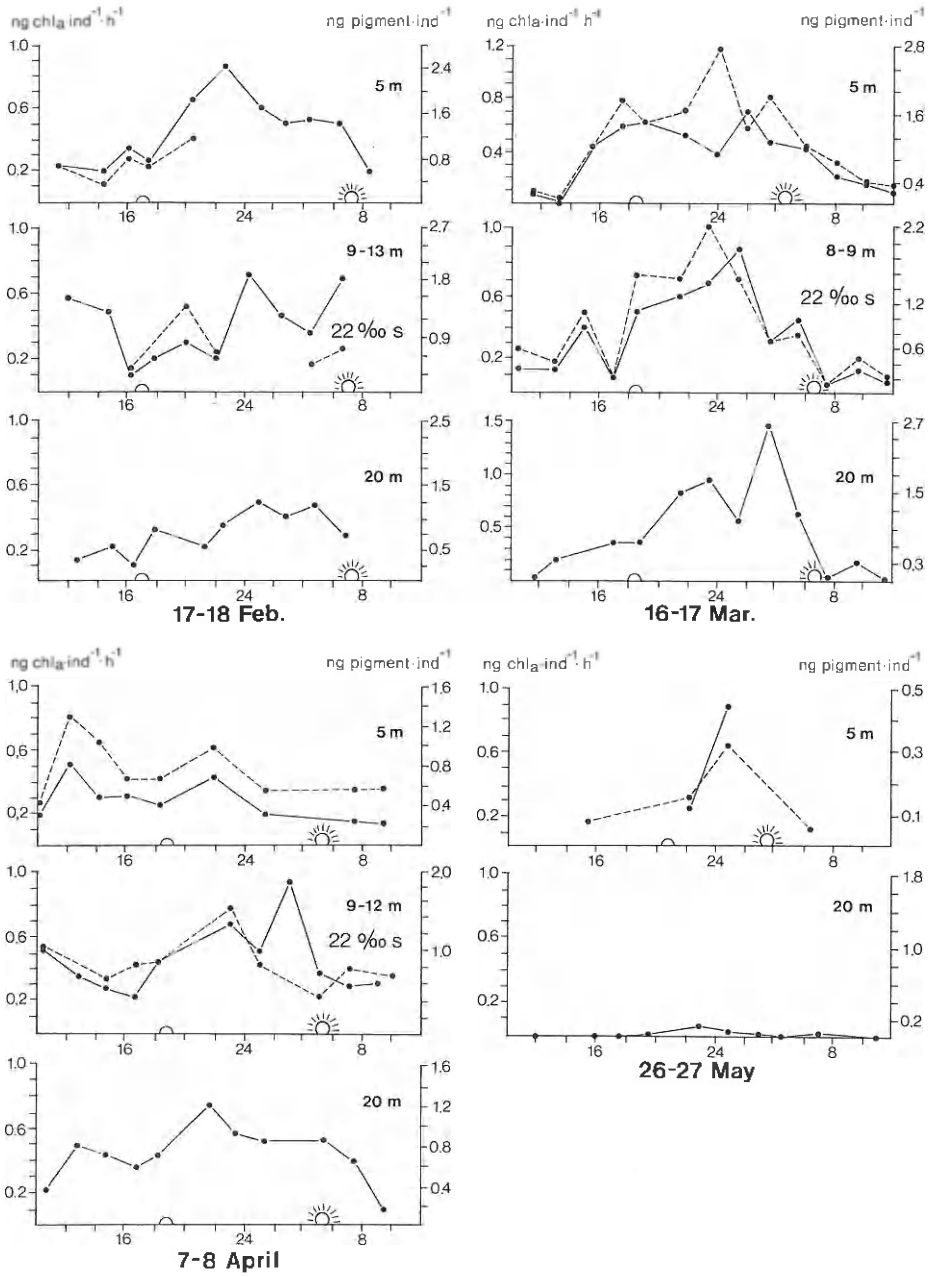

FIG. 3. Gut content (ng pigment · ind^{-1}) and ingestion rate (ng chlorophyll-*a* · ind^{-1} · h^{-1}) in *Pseudocalanus* sp. (●———●) and *Centropages hamatus* (●– – – –●) at two hour intervals during 17-18 February, 16-17 March, 7-8 April and 26-27 May. In May, measurable amounts of pigment were not present in the copepods from 22 ‰ S.

rate and chlorophyll-*a* content have been plotted in Fig. 2. Ingestion rate and algal concentration were positively correlated (*Pseudocalanus* sp.: Spearman's rank correlation coefficient $r_s = 0.71$, $p < 5\,\%$; *C. hamatus*: $r_s = 0.62$, $p < 5\,\%$). Due to a large scatter no curve fitting was done. However, the plots indicate satiation of the ingestion rate in both *C. hamatus* and *Pseudocalanus* sp.

Fig. 3 shows the gut content and ingestion rate during the four diurnal investigations. In samples from 20 m depth numbers of *Centropages hamatus* were too low to measure gut content. Diel variation in ingestion rate was found at all three depths in February and March, with the highest gut contents and ingestion rates during the night. The variation was most pronounced in March, but almost insignificant in April. Integrating the ingestion rates shown in Fig. 3 gives the daily rations in Table 1. In spite of different circadian rhythms in ingestion rates and the varying algal concentrations, daily rations show little variation, both temporarily and with depth. In *Pseudocalanus* sp. it ranged between 6.8-11.8 ng pigment · $ind^{-1} \cdot d^{-1}$ and in *C. hamatus* 10.8-12.1 ng pigment · $ind^{-1} \cdot d^{-1}$, ignoring the May samples.

Chlorophyll-*a* constituted a constant proportion of the total plant pigment in the water during each of the diurnal investigations. However, in *Pseudocalanus* sp., but not in *C. hamatus*, diel variation in the ratio $\frac{\text{phaeopigment}}{\text{phaeopigment} + \text{chlorophyll-}a}$ was found. The ratio was high during night and fell during day (Fig. 4, only 22 ‰ S depth shown).

TABLE 1. *Pseudocalanus* sp. and *Centropages hamatus*. Daily algal rations (ng chlorophyll-*a* · $ind^{-1} \cdot d^{-1}$) at various depths and dates in the Øresund during spring 1981. –, no measurements.

Date	Depth, m	chl-*a*, $\mu g \cdot l^{-1}$	Ration, ng chl-*a* · $ind^{-1} \cdot d^{-1}$	
			Pseudocalanus	*Centropages*
Feb. 17-18	5	2.3	10.2	–
	9-13	2.6	10.6	–
	18-25	1.0	7.4	–
Mar. 16-17	3- 5	0.6	9.5	12.1
	8- 9	4.6	9.1	10.8
	21-22	0.8	11.8	–
Apr. 7-8	3- 5	3.5	6.8	11.7
	9-13	28.5	10.9	10.8
	21-22	0.3	11.6	–
May 26-27	5	0.7	–	5.9
	7-10	3.0	0	0
	22	0.2	0.3	–

There was found no evidence of diel vertical migration on 16th March, as the depth distribution of *Pseudocalanus* sp. and *C. hamatus* did not change during the 24 hours.

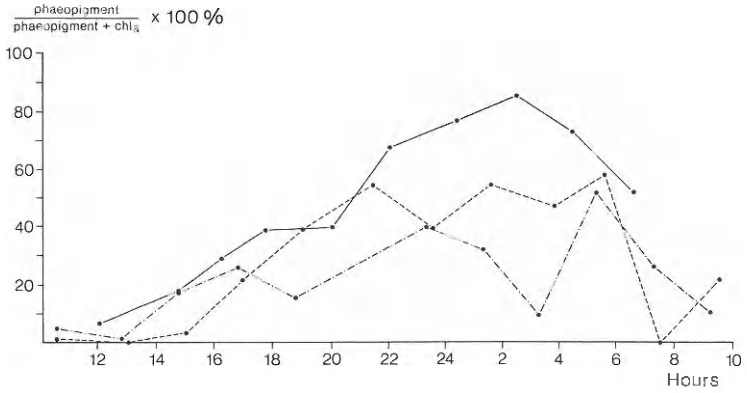

FIG. 4. Phaeopigment to total pigment ratio (in %) in guts of *Pseudocalanus* sp. during 17-18 February (●———●), 16-17 March (●– – – –●) and 7-8 April (●–·–·–●).

DISCUSSION

Diurnal variation in feeding rate

Diurnal variation in feeding rate, as observed for both *C. hamatus* and *Pseudocalanus* sp. in the present study (Fig. 3) seems to be a common phenomenon among planktonic copepods. Hayward (1980) compared the gut fullness of ten planktonic copepod species in the North Pacific Central Gyre, and found that nine species exhibited a circadian rhythm, with the highest indices of gut fullness during night. Mackas & Bohrer (1976) found evidence of diel periodicities in five out of six species studied in the Bedford Basin and on the Nova Scotian continental shelf. Dagg & Grill (1980) and Boyd *et al.* (1980) likewise found diurnal variation in feeding rate in various copepod species from the New York Bight and off the Peruvian coast, respectively. Other workers (e.g. Boucher & Samain 1974, Tande & Slagstad 1982) have found a pronounced diel variation in amylase activity in copepods, with the highest activity during night. Accordingly, the more complete degradation of chlorophyll to phaeopigments in the guts of *Pseudocalanus* sp. during night (Fig. 4) may reflect a higher digestion activity during periods of high feeding activity.

There was a significant seasonal difference in the feeding periodicity in both *C. hamatus* and *Pseudocalanus* sp. In March, for example, both species fed at a high rate during the 10-12 dark hours, and showed a vanishing feeding rate

during day. In April, on the other hand, when there was plenty of food available at the middle depth, both species fed at a moderate rate more or less continuously all the 24 hours. The significance of this difference is not clear. However, consistent with this observation, Boyd *et al.* (1980) found that the diel periodicity in feeding rate of three copepod species was very pronounced at a station with a low food concentration, whereas the copepods fed almost continuously at a station with a plentiful food supply. Boyd *et al.* (1980) interpreted this observation in the light of competition among copepod species in accordance with the theoretical consideration on niche separation by Schoener (1974) that temporal specialisation is unlikely to occur when food is relatively abundant, but becomes increasingly likely as food abundance decreases. These considerations apparently do not apply to the present case, partly because there is no separation in time between the species studied (although they might separate relative to other species), and more important, because the copepods deplete the resource (phytoplankton) only to a minor degree (see below), and thus probably do not compete for a common resource.

In spite of the difference in the diel amplitude of feeding rates, the daily rations remained more or less constant (except for May – see below) (Table 1). Runge (1980) studied the effects of starvation on feeding behaviour in *Calanus pacificus*, and found, in accordance with Mullin (1963), McAllister (1970) and present observations, that previously starved specimens fed at a considerably higher rate than continuously fed animals, and that a diel feeding rhythm with 8-10 h feeding would therefore yield the same daily ration as continuous feeding.

A circadian feeding rhythm in planktonic copepods is often considered a result of vertical migration (e.g. Gauld 1953), i.e., during the night copepods gather in the chlorophyll-rich surface layer, where food uptake takes place, and descend to deeper, chlorophyll-poor water during the day. The adaptative significance of this pattern has been discussed by Enright (1977) and others. However, in Øresund no vertical migration was detected, and the periodicity in gut content is therefore not due to continuous feeding in varying food concentrations, but is caused by a genuine periodicity in feeding activity.

Even though diel variation in feeding rate most often occurs with vertical migration, feeding periodicity seems to be a more general phenomenon than vertical migration, and diel variation in feeding rate independent of vertical migration has been documented for other planktonic copepods as well (Mackas & Bohrer 1976, Boyd *et al.* 1980, Dagg & Grill 1980, and Hayward 1980). The adaptative significance of this behaviour remains unclear.

The functional response

In laboratory studies of copepod feeding, where algae from monocultures have been used as food, feeding rate normally initially increases with algal concentration, reaching a plateau above which ingestion rate remains constant (e.g. Frost 1972, and Harris & Paffenhöfer 1976). Several attempts have been made to apply laboratory-derived feeding rates to natural situations (e.g. Hargrave & Green 1970, Mullin & Brooks 1976). However, results from studies with natural seston as food, or results from studies of *in situ* copepod feeding, are equivocal. Some authors find no or only a weak correlation between food concentration and feeding rate (e.g. Boyd *et al.* 1980, *Centropages typicus*), while others find the shape of the functional response similar to that found in the laboratory, i.e., with satiation feeding (e.g. Gamble 1978), and others again find a correlation with food concentration but without satiation (e.g. Poulet 1974, Mayzaud & Poulet 1978, Koeller *et al.* 1979, Dagg & Grill 1980, and Huntley 1981).

Our data indicate satiation feeding (Fig. 2), especially when feeding rate at the very high algal concentration on April 7 is considered. However, our data share a great scatter with the above mentioned data sets, indicating that food concentration is not the sole factor influencing feeding rate. For our data the seasonal variation in circadian rhythm discussed above interferes with the functional response in Fig. 2. To this comes that even though there is a significant correlation between ingestion rate and algal concentration, based on the weekly morning samples from 22 ‰S depth, the estimated daily rations are independent of the depth and algal concentration on a given date (Fig. 3, Table 1). This further obscures a clearcut conclusion regarding the nature of the functional response.

The shape of the functional response *in situ* has been widely discussed in the literature (see review by Conover & Huntley 1980). However, a major difficulty in this discussion is to define a proper measure of 'food concentration' in the heterogeneous particle assemblage available to the suspension feeding copepod: Should particle number, particle volume, particulate carbon, chlorophyll, or some other measure be preferred? This difficulty becomes apparent when considering the surprisingly low gut contents and algal ingestion rates found in our May experiments. Whereas large diatoms dominated until April, practically no algae were retained on a 20 μm mesh size plankton gauze in May. Probably small flagellates dominated the Øresund algal community in May (Edler 1977, Thomsen 1979), and the estimated low algal ingestion rate may thus be caused by this altered algal composition. The difficulty of defining the functional response *in situ* is but one reason that makes the application of laboratory-measured feeding rates to natural situations questionable.

Comparison of field and laboratory estimated feeding rates

The maximum *in situ* ingestion rates recorded in the present study are somewhat larger than maximum ingestion rates measured in the laboratory (Kiørboe *et al.* 1982), when compared on a chlorophyll basis. On March 16-17, for example, a maximum algal ingestion rate of 1.2 ng chl. $\cdot$ $ind^{-1} \cdot h^{-1}$ in *C. hamatus* (equal to 2.2 ng chl. $\cdot$ $(\mu g\ dw)^{-1} \cdot d^{-1}$) was recorded in surface water (2 °C) around midnight (dry wt of *C. hamatus*: 13 μg; Nicolajsen 1982). In the laboratory we found a maximum ingestion rate of 0.94 ng chl. $\cdot$ $(\mu g\ dw)^{-1} \cdot d^{-1}$ in *C. hamatus* fed the diatom *Ditylum brightwellii* (extrapolated to 2 °C from measurements between 5 and 15 °C, Kiørboe *et al.* 1982). For energetic considerations it is more convenient to compare ingestion rates on a carbon basis, however, thereby introducing the uncertainties of conversion factors as carbon : chlorophyll ratios are quite variable (e.g. Strickland 1965).

During the spring phytoplankton bloom in the Øresund, a carbon : chlorophyll-*a* ratio of 30 for the particulate matter has been measured in water samples where phytoplankton algae totally dominated (Nicolaisen & Christensen, unpubl.). Algal counts and volume measurements has yielded a C : chlorophyll-*a* ratio of 45 in March (S.M. Pedersen, unpubl.). Applying the former ratio to the field measurements and a ratio of 80 to the laboratory measurements (Kiørboe *et al.* 1982), the above ingestion rates correspond to 17 and 19 % body C $\cdot$ d^{-1} for the field and the laboratory measurements, respectively (Carbon content of *C. hamatus*: 5.2 μg, Nicolajsen (1982)).

Due to the pronounced circadian feeding rhythm, the daily algal rations measured in the field were, however, always considerably less than corresponding maximum rations in the laboratory (Table 2). It seems to be a common phenomenon, that copepods under more natural circumstances exhibit feeding rates less than the maximum rates on a pure algal diet found in the laboratory. Poulet (1974) thus found that *Pseudocalanus* sp. on a monthly basis ingested between 2.2 and 17.9 % body C $\cdot$ d^{-1} during the year, except for March, when an ingestion rate of 55 % body C $\cdot$ d^{-1} at a very high food concentration was recorded. From measurements of gut fullness and gut turnover Zagorodnyaya (1974, quoted in Corkett & MacLaren 1978) calculated a daily ration for ad. ♀ *Pseudocalanus* in the Black Sea between 5.7 (January) and 12.1 % wet wt $\cdot$ d^{-1} (March). Both data sets thus agree with ours. However, maximum ingestion rates of *Pseudocalanus minutus* recorded in the laboratory (at higher temperatures, however) are much higher, up to 140 % bodyC $\cdot$ d^{-1} (see review by Corkett & McLaren 1978). Dagg & Grill (1980) likewise found that the daily ration of *Centropages typicus* in the New York Bight was considerably less than maximal (similar estimates arrived at by gut content method, Coulter Counter measurements and egg production measurements). Further examples of such differences are given by Dagg & Grill (1980). The reason for this discrepancy

TABLE 2. *Pseudocalanus* sp. and *Centropages hamatus*. Daily algal rations (% body C · d^{-1}) at various depths and days in the Øresund during spring 1981, and maximum algal ration at ambient temperature measured in the laboratory. Carbon content of *Pseudocalanus* sp. 4.4 μg and of *C. hamatus* 5.2 μg (Nicolajsen 1982). –, no measurements.

Date	Depth, m	Temp., °C	Ration*, % body C · d^{-1}		Max. ration**, % body C · d^{-1}
			Pseudocalanus	*Centropages*	*Centropages*
Feb. 17-18	5	1.0	7.0-11.7	–	17.1
	9-13	1.1	7.2-12.0	–	17.3
	18-25	1.8	5.1- 8.5	–	18.7
Mar. 16-17	3- 5	1.9	6.5-10.8	7.0-11.7	19.0
	8- 9	2.3	6.2-10.3	6.2-10.3	19.9
	21-22	4.1	8.1-13.5	–	24.7
Apr. 7-8	3- 5	3.8	4.6- 7.7	6.7-11.2	23.8
	9-13	3.4	7.4-12.3	6.3-10.5	22.7
	21-22	4.6	8.0-13.3	–	26.2
May 26-27	5	11.8	–	3.4- 5.7	61.2
	7-10	7.0	0	0	34.7
	22	5.3	0.2- 0.3	–	28.2

*Calculated from Table 1 assuming a C : chl-*a* ratio between 30 (lower limit) and 50 (upper limit).

**Extrapolated to ambient temperature from maximum ingestion rates measured in the laboratory between 5-15 °C on the diatom *Ditylum brightwellii* (Kiørboe *et al.* 1982).

may be, that while natural particle suspensions are heterogeneous and variable with respect to size and quality, laboratory food suspensions most often are homogeneous and of high quality. Actually, maximum feeding rates of *Pseudocalanus* are quite variable, and depend to a high degree upon the kind of food offered (see review by Corkett & McLaren 1978).

The daily rations estimated in the present work are algal rations and are thus minimum estimates, since copepods may derive additional food from particulate carbon of non-algal origin. If the copepods eat algae and detritus in proportion to their occurrence, as argued by Poulet (1976), the daily rations may actually be substantially higher than shown in Table 2, since algae constitute between 10-70 % (averaged over the water column) of the particulate carbon in the Øresund during spring (Nicolaisen & Christensen, unpubl.). Our data suggest that this is not so. On March 16-17, for example, the chlorophyll concentration in the 22 ‰ S depth was 4.5 μg · l^{-1}, and on April 10 it was about 10 times higher (44 μg · l^{-1}). As the concentration of organic detritus between February and April is nearly constant (averaging 0.4 mg dw · l^{-1}, Nicolaisen & Christensen, unpubl. data), the algal : detritus ratio on March 16 is only one tenth of this

ratio on April 7. Consequently the algal ingestion rate of a non-selective feeder should change accordingly. However, for both species, the estimated morning ingestion rates are similar on the two dates (0.5 ng chl. · ind^{-1} · h^{-1}, Fig. 2). Accordingly, recent high speed cinematographic studies on copepod feeding have indeed shown copepods to be selective filter feeders (e.g. Koehl & Strickler 1981, and Paffenhöfer *et al.* 1982). On the other hand, reported respiration rates of *Pseudocalanus elongatus* and *C. hamatus* (Marshall & Orr 1966) corresponded to 2.4-7.1 % body C · d^{-1} and 4.1-8.7 % body C · d^{-1} (extrapolated to 2 °C by a $Q_{10} = 2$, Vidal (1980)), thus leaving only minor energy for defaecation, growth and reproduction at the daily algal rations estimated in Table 2.

Grazing impact of mesozooplankton on the phytoplankton community during spring phytoplankton bloom in the Øresund

The algal grazing rates estimated in the present study may form the basis of a crude estimate of copepod grazing impact on the phytoplankton community during the spring phytoplankton bloom in the Øresund. On March 17, for example, oblique plankton hauls showed a density of 400 *Pseudocalanus* sp. (C IV-VI) · m^{-3} and 140 *C. hamatus* (C IV-VI) · m^{-3}, together accounting for 61 % of the total zooplankton biomass (>200 μm) in the Øresund (Nicolajsen 1982). Together these two species consume about 6 ng chlorophyll-*a* · l^{-1} · d^{-1} (from Table 1). Assuming the other zooplankters to have a similar algal consumption, a total of about 10 ng chl. · l^{-1} · d^{-1} is consumed by the mesozooplankton (>200 μm). The grazing pressure thus amounts to about 1 % of the phytoplankton standing stock · d^{-1}. As the doubling time of the phytoplankton biomass is about 5-6 days at this time of the year (Nicolaisen & Christensen, unpubl.; cf. also the tenfold increase of phytoplankton biomass between March 17 and April 7), this corresponds to a grazing pressure of about 5-6 % of the net primary production.

On a carbon basis, the mesozooplankton algal consumption on March 17 equals 0.3-0.5 μg C · l^{-1} · d^{-1}, assuming a C : chl. ratio between 30 and 50. The primary production on March 9, averaged over the water column, was measured to 24 μg C · l^{-1} · d^{-1} (^{14}C measurements, G. Ærtebjerg Nielsen, pers. comm.). The total mesozooplankton algal grazing arrived at in this alternative way thus amounts to about 1.25-2.1 % of the primary production.

Using similar calculations, zooplankton densities from Nicolajsen (1982) and primary production averages from earlier years (Edler 1977, Gargas *et al.* 1978), crude estimates of the mesozooplankton grazing pressure in the Øresund between February and May can likewise be arrived at. It appears, that throughout this period, mesozooplankton algal grazing represents less than 1-5 % of the phytoplankton production.

This picture does not fit into the classical view, that the majority of the primary production in the sea is consumed by copepods, and that the phytoplankton community primarily is checked by copepod grazing (e.g. Steele 1974, and Cushing 1976). The present findings for the Øresund are, however, consistent with observations in the nearby Kiel Bight, that the majority of the spring phytoplankton bloom sediments to the bottom (e.g. Smetacek 1980, and Peinert *et al.* 1982). Similar observations from other shallow areas on phytoplankton sedimentation (e.g. Forsskåhl *et al.* 1982) and copepod grazing (e.g. Deason 1980, and Joiris *et al.* 1982) likewise question the central role of planktonic copepods in neritic food chains, especially when the spring phytoplankton bloom is considered. This apparently contrasts to open sea systems, where zooplankton grazing represents more than 40-100 % of the particulate primary production, also during the spring bloom (e.g. Williams & Lindley 1980, Joiris *et al.* 1982 and references herein), more or less in accordance with the classical view. Later in the production season, during summer and autumn, when temperatures rise and zooplankton biomass show a tenfold increase in the Øresund (Nicolajsen 1982), a significant share of the phytoplankton production may flow through the planktonic copepods. This is also indicated by a vanishing phytoplankton sedimentation rate during summer and autumn in the nearby Kiel Bight (Smetacek 1980, Peinert *et al.* 1982).

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