Vol. 13: 37–46, 1983 | MARINE ECOLOGY – PROGRESS SERIES
Mar. Ecol. Prog. Ser. | Published July 28

Natural ingestion rates of the copepods *Neocalanus plumchrus* and *N. cristatus* calculated from gut contents*

M. J. Dagg and K. D. Wyman**

Louisiana Universities Marine Consortium, Star Route Box 541, Chauvin, Louisiana 70344, USA

ABSTRACT: Gut contents of copepodid stage V *Neocalanus plumchrus* and *N. cristatus* from 5 depth strata were measured with a gut fluorescence method, every 3 to 7 h, during five 24 h stations in the Bering Sea. Levels of gut fullness were generally higher during the phytoplankton bloom in May than post-bloom in June. However, within each 24 h period, levels of gut fullness varied with depth and time, and were not related to ambient chlorophyll concentrations. This probably indicates that individuals of both species were vertically mobile. Gut evacuation rate, used to convent gut-content data to feeding rates, was exponential and temperature dependent. Short-term feeding rates varied within each 24 h period and sometimes were much higher than rates measured by more traditional methods which involve 12 to 24 h incubations.

INTRODUCTION

While much effort has been made to determine accurately the abundance and distribution of zooplankton on fine temporal and spatial scales (e.g. Haury et al., 1978; Longhurst and Williams, 1979; Mackas and Boyd, 1979), the physiological behavior of plankton on similar scales has remained insufficiently studied. For example, diel vertical migrations, in which copepods swim through tens or hundreds of meters in a few hours, are commonly noted in sampling studies but little is known about the natural feeding behavior associated with these migrations. Furthermore, food is heterogeneously distributed on fine scales in the ocean, and the feeding behavior of copepods swimming through these patches is likely important to the animals' daily nutrition. Yet, with few exceptions (e.g. McAllister, 1970; Corner et al., 1972; Roman and Rublee, 1980; Runge, 1980), the measurement of feeding rates has involved 12 to 24 h incubations. The objectives of this paper, therefore, were to measure feeding of marine copepods over short time intervals in the natural environment, and to determine the variation in feeding rate associated with depth, time of day, and season.

METHODS AND MATERIALS

Microscopic examination of gut contents can provide information on the feeding activity and natural diet of copepods (Marshall, 1924) on scales determined by the sampling regime; selected species and stages can be collected many times during the day and from many depths and locations. Recently, a modification of this approach has been used to provide information on the feeding activity of copepods over short time intervals and small spatial scales. With this method, phytoplankton pigments in the guts of freshly collected copepods are measured via whole animal fluorescence, and used to indicate the amount of phytoplankton ingested in the short period prior to collection (Mackas and Bohrer, 1976; Boyd et al., 1980; Dagg and Grill, 1980). This is possible because, although most of the ingested chlorophyll is quickly degraded to phaeopigments, the phaeopigments remain unchanged and are eventually defecated (Shuman and Lorenzen, 1975).

At 3 stations on the outer continental shelf and over the continental slope in the Bering Sea (Fig. 1) zoo-

* This work is part of a multi-disciplinary study titled 'Processes and Resources of the Bering Sea Shelf' or PROBES; it was supported by the Division of Polar Programs, National Science Foundation, under Grant No. DPP76-23340

** Present address: Oceanographic Science Division, Brookhaven National Laboratory, Upton, New York 11973, USA

0171-8630/83/0013/0037/$ 02.00

plankton were sampled with a 0.5 m closing net towed vertically through 5 depth strata: 120 to 80 m, 80 to 60 m, 60 to 40 m, 40 to 20 m, and 20 to 0 m. Collections were made 4 or 5 times during each 24 h station. Stations were occupied once in mid-May, at the peak of the spring bloom, and once in mid-June, after the spring bloom. After each net tow, *Neocalanus plumchrus* V and *N. cristatus* V were immediately sorted; between 3 and 5 individuals were used for each analysis of gut fluorescence, and replicates from each net tow were analyzed whenever possible. All data on copepod fluorescence were corrected for the small amount of analytical interference that is due to the copepod's tissues: starved *N. plumchrus* gave values equivalent to 0.24 ng chlorophyll copepod^{-1} (n = 18, sd = 0.21) and 0.31 ng phaeopigment copepod^{-1} (n = 18, sd = 0.24); starved *N. cristatus* gave values equivalent to 0.37 ng chlorophyll copepod^{-1} (n = 7, sd = 0.20) and 0.34 ng phaeopigment copepod^{-1} (n = 7, sd = 0.14).

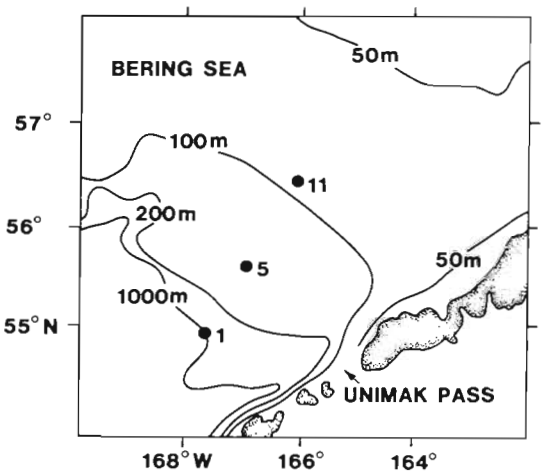

Fig. 1. Station locations

Ambient concentrations of chlorophyll *a* were determined from samples taken by Niskin bottles immediately before or after each series of vertical net tows.

For each gut-content analysis, copepods were rinsed onto a 333 µm mesh sieve with filtered seawater, then washed onto a 24 mm glass-fiber filter. At this point, the degree of gut fullness was sometimes estimated by briefly examining the copepods under a dissecting microscope, and sometimes the sample was frozen for up to 6 h. Simple experiments showed that neither of these procedures had any noticeable effects on the resultant levels of gut fluorescence. The sample was homogenized in 10 ml of 90 % aqueous acetone and the fluorescence of the filtrate was measured before and after acidification with 10 % HCl using a Turner Designs Model 10 fluorometer. The chlorophyll and phaeopigment content of each copepod was calculated using equations for *in vitro* fluorometry (Strickland and Parsons, 1968) modified slightly to:

$$\text{ng chlorophyll copepod}^{-1} = \frac{K(f_o - f_a)}{n} \quad (1)$$

and

$$\text{ng phaeopigment copepod}^{-1} = \frac{K(Rf_a - f_o)}{n} \quad (2)$$

where K = machine calibration constant; f_o and f_a = fluorescence readings before and after acidification; n = number of copepods; R = acidification ratio.

Although each measure of gut contents represents the amount of chlorophyll recently ingested, the actual chlorophyll content of the copepod gut is small; phaeopigments (phaeophorbide and phaeophytin) usually make up >85 % of the total pigments measured and only a small amount of chlorophyll is not digestively degraded (Shuman and Lorenzen, 1975; Hallegraeff, 1981; our observations). While Shuman and Lorenzen (1975) and Jeffrey (1974) concluded that the degraded chlorophyll was completely converted to phaeophorbide, Hallegraeff (1981) found only 20 to 50 % converted to phaeophorbide, the rest to phaeophytin. However, Hallegraeff's analyses included fecal pellets that were up to 3 d old and their pigment content may have changed during this period. Analysis of some recently fed copepods by high pressure liquid chromatography indicated all the phaeopigment in the copepod guts was phaeophorbide (Falkowski, pers. comm.). To convert the phaeophorbide content of a copepod gut back to the amount of chlorophyll it represents, a factor of 1.51 must be applied because the molecular weight of phaeophorbide is 66.3 % that of chlorophyll. The resultant weight of chlorophyll, added to the weight of undegraded chlorophyll in the gut, is the amount of chlorophyll originally ingested that is represented by the gut-content analysis.

The rates of gut evacuation for *Neocalanus plumchrus* and *N. cristatus* were determined on shipboard. For these experiments copepods that had been previously fed natural or concentrated surface water were placed, 3 to 5 per bottle, in 1-l containers of filtered seawater. Bottles were attached to a slowly rotating wheel in a dark incubator kept at sea-surface temperature. The decline rate of gut contents was determined by periodically analyzing the copepods from one bottle over an 8 to 12 h period. All data are corrected for the small amounts of interference from the copepod tissues.

RESULTS

Natural levels of gut fluorescence

In mid-May, during the spring bloom, chlorophyll concentrations in the surface waters at both Station 1 and 5 were usually >8.0 µg l^{-1}, whereas during the post-bloom period in mid-June, concentrations were always <1.0 µg l^{-1} and usually <0.55 µg l^{-1} (Figs. 2 and 3). Phaeopigment concentrations in surface waters

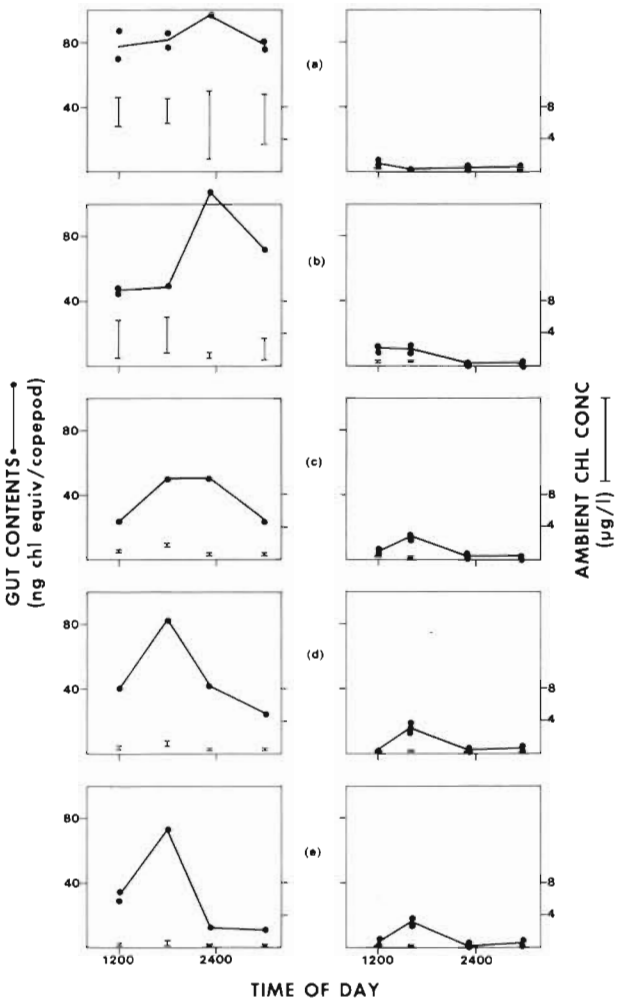

Fig. 2. *Neocalanus plumchrus*. Gut contents from Station 1: (a) 20 to 0 m, (b) 40 to 20 m, (c) 60 to 40 m, (d) 80 to 60 m, (e) 120 to 80 m, during May (left) and June (right). Range of chlorophyll concentrations encountered in each depth stratum is represented by vertical lines

were about 10% of the chlorophyll concentrations observed during both periods. In a very general way, the levels of gut fullness in *Neocalanus plumchrus* and *N. cristatus* (Fig. 4) reflected these temporal differences; in both copepods high levels were commonly found in May, but never in June. Apart from this general seasonal difference, however, there was little

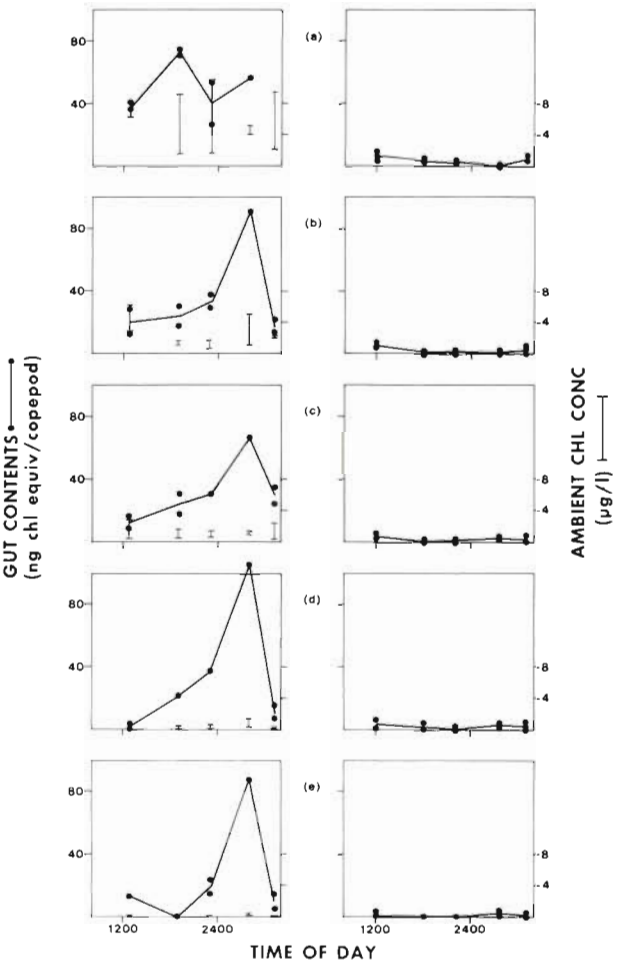

Fig. 3. *Neocalanus plumchrus*. Gut contents from Station 5. Depths and months as in Fig. 2

apparent relationship between gut fullness and the chlorophyll concentration of the ambient seawater. For example, during May, the maximum level of gut contents in *N. plumchrus* from surface and bottom samples was approximately the same even though chlorophyll concentrations were much higher in surface waters (Figs. 2 and 3). Similarly, the levels of gut fullness in *N. cristatus* did not closely correspond with the chlorophyll concentration in the water from which the copepods were collected (Fig. 4). The lack of correlation between gut content and ambient chlorophyll concentration for *N. plumchrus* and *N. cristatus* is clearly seen when all data for each copepod are plotted together (Fig. 5); no relationship is evident for either copepod.

There appeared to be some temporal pattern in the gut fullness of *Neocalanus plumchrus* at Station 5 in May (Fig. 3); levels were highest during the early morning, dark, sampling period in all four subsurface samples. This pattern was not observed at Station 1 (Fig. 2) but, since the early morning sampling period

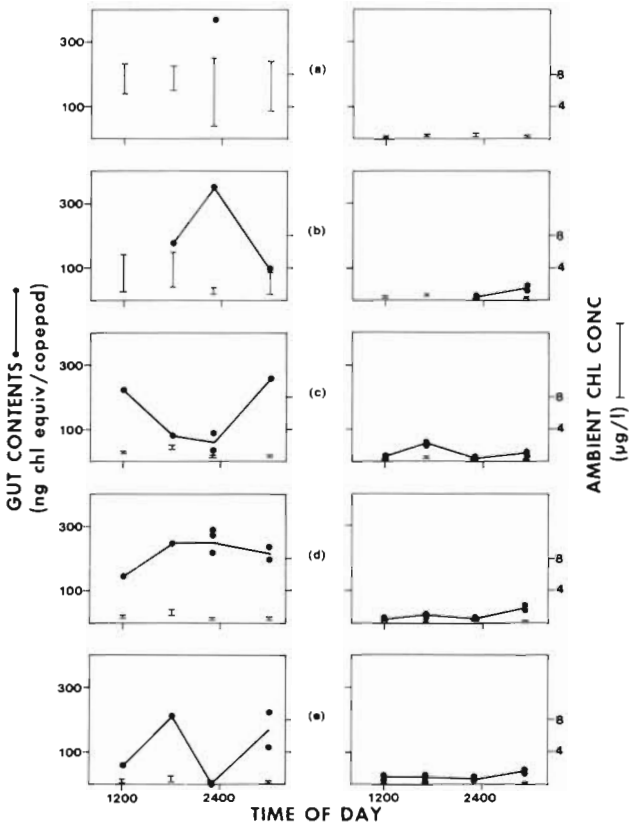

Fig. 4. *Neocalanus cristatus*. Gut contents from Station 1. Depths and months as in Fig. 2

was missed, could have existed. No other patterns of temporal synchrony were evident except possibly a late afternoon increase in *N. plumchrus* at Station 1 in June (Fig. 2).

The level of gut fullness did not appear to be associated with depth in either copepod, except that *Neocalanus plumchrus* routinely had high values in surface waters during May (Figs. 2 and 3).

Neocalanus cristatus is much larger than *N. plumchrus*. Dry weights of individuals from May averaged 5631 µg (n=3) and 567 µg (n=8), respectively. Not surprisingly, maximum levels of gut fullness in *N. cristatus* were higher than those observed in the smaller *N. plumchrus*. In May, the highest level of gut contents observed in *N. cristatus* was 3.4 times the highest level observed in *N. plumchrus*; in June, the ratio was 3.8. Maximum levels of gut fullness in both copepods were lower in June; the maximum level in *N. cristatus* was 18 % that of the May maximum, whereas for *N. plumchrus* the value was 16 %.

Gastric evacuation rate

When *Neocalanus plumchrus* (Fig. 6) and *N. cristatus* (Fig. 7) with high levels of gut fluorescence were placed in filtered seawater, their gut contents declined rapidly in such a manner that only a small amount of material remained after 2 or 3 h. Studies of gastric evacuation in fish (reviews by Elliott and Persson, 1978; Jobling, 1981) and copepods (Gauld, 1957; Mackas and Bohrer, 1976; Dagg and Grill, 1980) indicate that the evacuation rate of food from the gut is exponential. Under these conditions, the evacuation rate of fluorescent pigments from a copepod gut is described by:

$$S_t = S_o e^{-Rt} \quad (3)$$

where S_o = initial level of gut contents; S_t = level at time t; R = instantaneous evacuation rate with units of 1/t. Specific equations for *N. plumchrus* and *N. cristatus* are given in the figure captions. The instantaneous evacuation rate, R, of *N. plumchrus* increased with temperature (Fig. 8).

Field application

Gut content represents the amount of phytoplankton ingested over some recent time period of unknown duration. Dividing gut content (ng copepod^{-1}) by the ambient chlorophyll concentration (ng ml^{-1}) yields an estimate of the volume of water processed by the copepod (ml copepod^{-1}) during this unknown time period. This calculation is likely to underestimate the volume of water actually processed because it assumes chlorophyll containing particles are removed with complete efficiency. Also, if the grazers migrate at all, the chlorophyll concentration surrounding the copepod while it was feeding may not be the same as the one surrounding it when it was captured. If it is assumed that all feeding occurred at the maximum chlorophyll concentration encountered in the water column, conservative estimates of the volume of water processed can be calculated.

Gut evacuation rate can be used to convert each measure of gut contents to an ingestion rate. Because evacuation is exponential, a constant fraction of the gut contents is defecated per time unit. For example, if the instantaneous evacuation rate, R, is 0.02 min^{-1}, then 2 % of the gut contents is egested min^{-1}. This is true regardless of the level of gut fullness. If it is assumed that ingestion and egestion are in equilibrium, then ingestion must also be 2 % of the gut contents min^{-1} in this example. Thus, in general, application of the gut evacuation rate, R, to the gut contents results in an estimate of the short-term ingestion rate. This concept has been thoroughly examined and successfully applied to many fish species (e.g. Elliott and Persson, 1978; Jobling, 1981). Ingestion rate min^{-1} is calculated from:

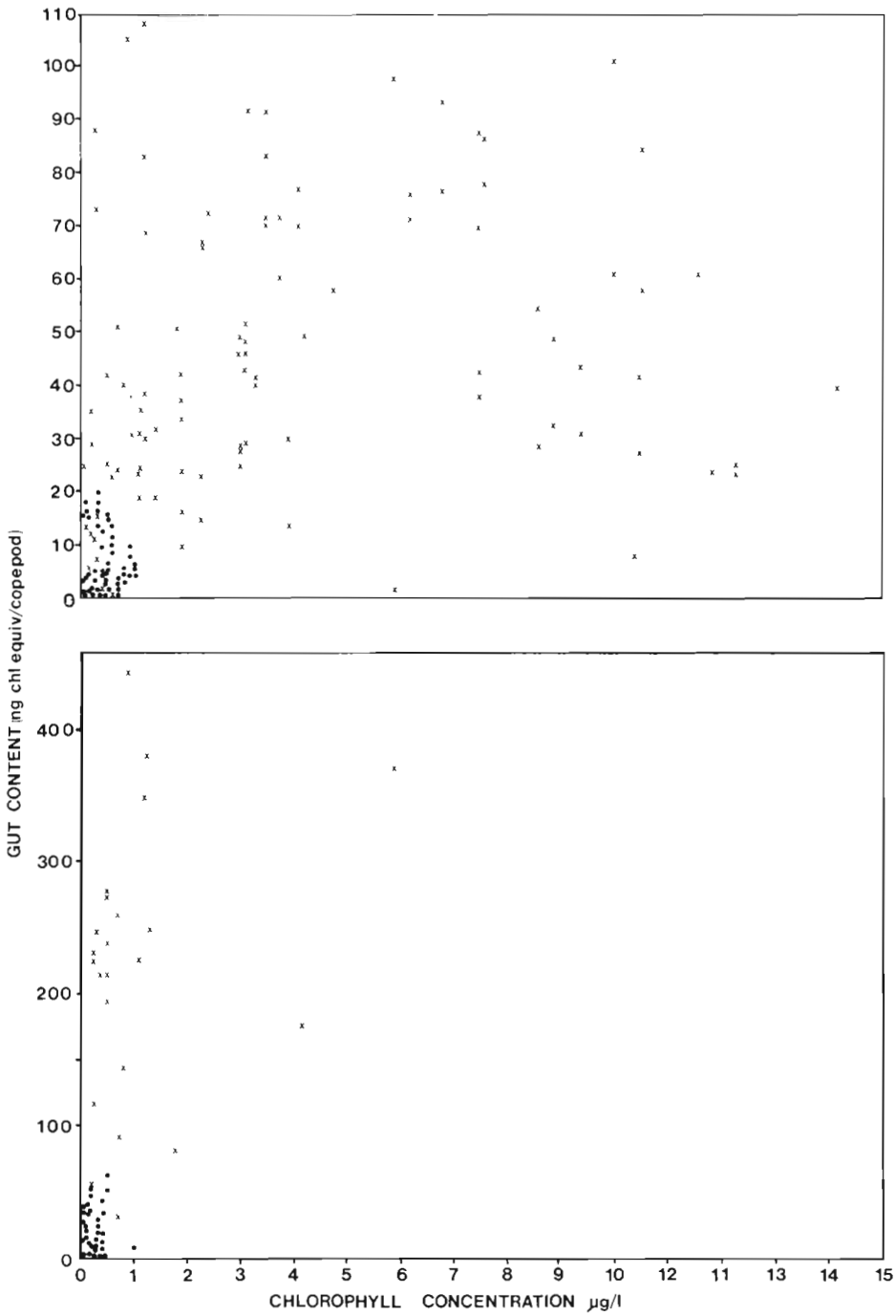

Fig. 5. *Neocalanus plumchrus* (top) and *N. cristatus* (bottom). Gut contents plotted against average chlorophyll concentration observed in the depth stratum from which the copepod was captured. Data from Station 11 included. Solid circles: June data; crosses: May data

$$I \text{ (ng chlor min}^{-1}) = S R \quad (4)$$

where S = level of gut contents (ng chlor); R = instantaneous evacuation rate (min^{-1}). By extrapolation over 60 min this equation can be used to estimate hourly ingestion rates.

Before Equation (4) is specifically applied to gut content data from Station 1, the instantaneous evacuation rate must be temperature corrected, wherever possible (Fig. 8). Surface temperature during mid-May at Station 1 was 5.5 °C and in mid-June was 7.4 °C; for *Neocalanus plumchrus* the instantaneous evacuation rates were calculated accordingly (Fig. 8) but this was not possible for *N. cristatus* because R was only measured at one temperature.

Ingestion rates of *Neocalanus plumchrus* during May were greater than 100 ng chlor h^{-1} somewhere in the water column during each sampling period but were much lower in June when the maximum observed value was 34 ng chlor h^{-1} (Table 1). A similar pattern was seen in *N. cristatus* with rates as high as

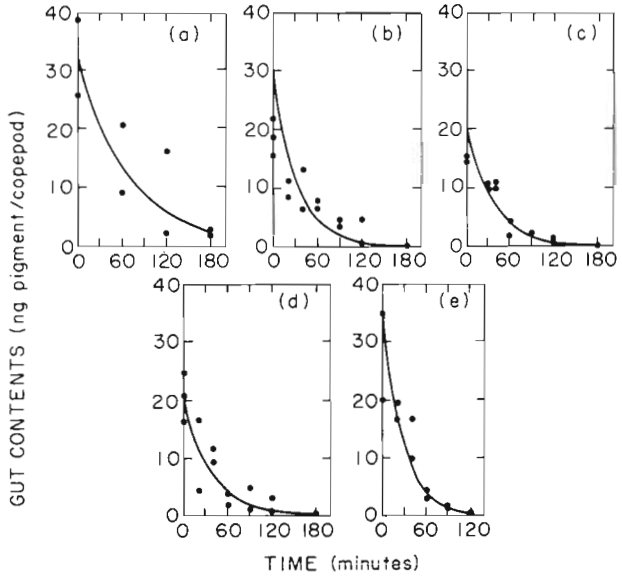

Fig. 6. *Neocalanus plumchrus*: Rate of gut evacuation at 5 temperatures: (a) 4.0 °C, $S_t = 32.0\,e^{-0.0146(t)}$, $r^2 = 0.74$; (b) 7.4 °C, $S_t = 29.7\,e^{-0.0316(t)}$, $r^2 = 0.76$; (c) 7.1 °C, $S_t = 20.8\,e^{-0.0278(t)}$, $r^2 = 0.92$; (d) 7.7 °C, $S_t = 19.7\,e^{-0.0272(t)}$, $r^2 = 0.82$; (e) 9.2 °C, $S_t = 37.5\,e^{-0.0388(t)}$, $r^2 = 0.95$

406 ng chlor h^{-1} in May but only 71 ng chlor h^{-1} in June (Table 1). Applying a carbon to chlorophyll ratio of 45 to these chlorophyll values (Iverson, pers. comm.) results in maximum ingestion rates of 6.1 µg C h^{-1} for *N. plumchrus* and of 18.3 µg C h^{-1} for *N. cristatus* in May, and 1.5 and 2.3 µg C h^{-1} in June.

Clearance rates are conservatively calculated from ingestion rates by assuming ingestion occurred at the maximum chlorophyll concentration observed in the water column (Table 1). In May, clearance rates were as high as 13.5 ml h^{-1} for *Neocalanus plumchrus* and

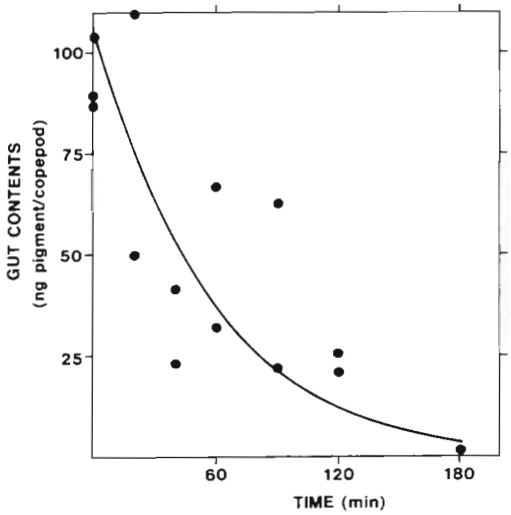

Fig. 7. *Neocalanus cristatus*. Rate of gut evacuation at 8.5 °C: $S_t = 108.7e^{-0.0183(t)}$, $r^2 = 0.70$

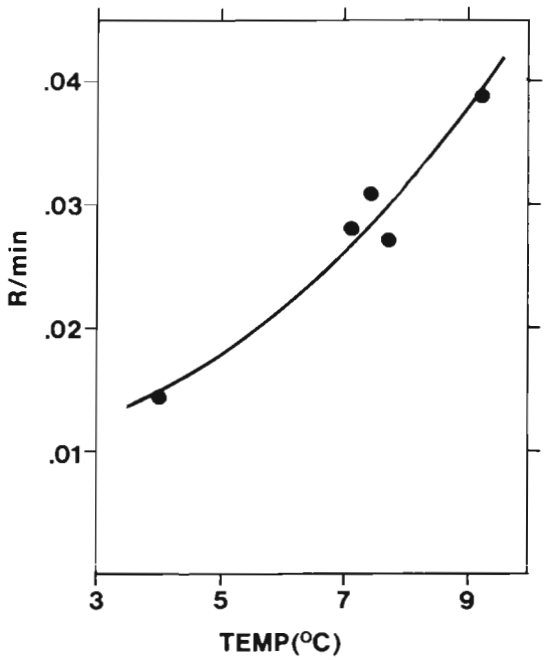

Fig. 8. *Neocalanus plumchrus*. Relationship between instantaneous evacuation rate and temperature

40.5 ml h^{-1} for *N. cristatus*. In June, when ambient chlorophyll concentrations were much lower than in May, the highest clearance rates were 55.6 ml h^{-1} for *N. plumchrus* and 123.5 ml h^{-1} for *N. cristatus* (Table 1).

DISCUSSION

Natural levels of gut fluorescence

The level of gut fullness observed in *Neocalanus plumchrus* and *N. cristatus* varied widely. In May, when phytoplankton concentrations were high in the surface waters at both stations, both copepods commonly, but not always, had high levels of gut contents, regardless of the depth from which they were collected. However, in June, when phytoplankton concentrations were low throughout the water column at both stations, high levels of gut fluorescence were never observed; in both copepods the maximum levels of gut fullness in June were < 20 % of the maximum levels observed in May. A similar pattern was seen in *Centropages typicus* females from the New York Bight; when maximum chlorophyll concentration in the water column was high, about 5 µg l^{-1}, the gut contents of *C. typicus* females varied widely, between 0.1 and 4.5 ng pigment copepod^{-1} (Dagg and Grill, 1980), but on another occasion when chlorophyll concentrations were low throughout the water column, individual females never contained more than 0.8 ng pigment

Table 1. Feeding information for (a) *Neocalanus plumchrus* V and (b) *N. cristatus* V at Station I in May (M) and June (J). Gut contents are the lowest and highest values observed in the water column during each sampling interval. Calculations of the volumes of water processed and clearance rates assume all feeding occurred at the maximum chlorophyll concentration

	Month	Time	Chl max (ng ml^{-1})	Gut contents (ng chl cop^{-1})	Volume processed (ml)	Ingestion rate (ng chl cop^{-1} h^{-1})	Clearance rate (ml cop^{-1} h^{-1})
(a)	M	1200	9.35	24– 88	2.5– 9.4	30–110	3.1– 11.7
	M	1800	9.08	49– 87	5.4– 9.5	61–108	6.7– 11.7
	M	2300	10.06	12–108	1.2– 10.7	15–135	1.5– 13.5
	M	0600	9.63	11– 93	1.1– 9.6	14–115	1.4– 12.0
	J	1200	0.49	3– 13	5.9– 25.5	5– 22	10.4– 44.9
	J	1630	0.61	1– 19	1.5– 31.6	2– 34	2.6– 55.6
	J	2300	0.70	1– 3	0.7– 4.0	1– 5	1.7– 7.0
	J	0530	0.48	1– 5	2.3– 9.8	2– 8	4.1– 17.2
(b)	M	1200	9.35	57–226	6.1– 24.1	62–248	6.7– 26.6
	M	1800	9.08	82–245	9.1– 27.0	91–269	10.0– 29.7
	M	2300	10.06	0–370	0.0– 36.8	0–406	0.0– 40.4
	M	0600	9.63	95–260	9.8– 27.0	104–285	10.8– 29.7
	J	1200	0.49	16– 27	33.3– 54.9	18– 29	36.6– 60.3
	J	1630	0.61	21– 65	34.3–106.1	23– 71	37.7–116.5
	J	2300	0.70	8– 29	11.1– 41.1	9– 32	12.3– 45.1
	J	0530	0.48	18– 54	37.5–112.5	20– 59	41.2–123.5

(Dagg, unpubl.). These studies suggest that copepods can feed at high rates as long as high phytoplankton concentrations are available somewhere in the water column but when concentrations are low throughout and no layer or patch of food is accessible to the copepods, feeding rates will be low. However, access to high food concentrations does not guarantee that grazers will have full guts. During May, gut fullness of *N. plumchrus* and *N. cristatus* ranged widely within a 24 h period and within a water column. It seems most likely that this variation is due to portions of the population feeding in regions of high chlorophyll concentration and then migrating to depth with their gut contents relatively intact. This phenomenon has been suggested previously. In a study of the chaetognath *Sagitta elegans*, Pearre (1973) suggested that although the surface waters of Bedford Basin never contained a large population, individuals fed primarily in the upper layers and then returned quickly to depth. The patterns of gut fullness seen in *N. plumchrus* and *N. cristatus* in May conform to Pearre's concept. Furthermore, the overall lack of correlation between gut fullness and the chlorophyll concentration at the specific depth from which copepods were collected appears to support the supposition that copepods with high levels of gut fullness had fed in a region of high food concentration and then migrated to a region of low food concentration.

For *Neocalanus plumchrus* and *N. cristatus* to migrate to depth with their gut contents relatively intact would require a rapid downward swimming because gut contents decrease rapidly when feeding ceases (Figs. 6 and 7). Sustained swimming speeds between 1.3 and 2.5 cm s^{-1} have been reported for species of the marine calanoid genera *Calanus*, *Euchaeta*, and *Metridia* (Hardy and Bainbridge, 1954; Enright, 1977) but considerably higher speeds might be required of *Neocalanus*. For example, descent through half the water column, 60 m, in 10 min would require a sustained speed of 10 cm s^{-1}. This suggests that, during May, copepods found in the deep layer (80 to 120 m) with high levels of gut contents did not obtain this material in the surface layer (0 to 20 m) but more probably from the 20 to 40 m layer, where chlorophyll concentrations were still quite high. In this regard it is interesting to note that *N. cristatus* was rarely abundant in the upper 20 m. Also, if patches of high food concentration existed at mid-depths, between the uniformly high food concentrations at the surface and the low concentrations near the bottom, the feeding migrations could be over an even shorter distance.

Lower temperatures at depth would not greatly decrease the gut evacuation rate because water at 100 m was only 1.3 to 1.9 °C cooler than surface water.

Other factors, however, may contribute to some of the observed variation in gut fullness. One such factor is a variation in the feeding behavior of the copepods. For example, copepods may feed more actively when hungry (Runge, 1980), and sometimes feed more actively at night than during daylight (Haney and Hall, 1975; Mackas and Bohrer, 1976; Dagg and Grill, 1980). Boyd et al. (1980) have even suggested that copepods commonly feed at high rates for short periods which are followed by periods of no feeding at all. Field studies such as this one and that of Boyd et al. (1980)

cannot be used to demonstrate definitively discontinuous feeding behavior because variations in gut contents can also be due to continuous feeding in a patchy food environment. Nevertheless, some of the variation in gut fullness observed in this study could be due to variations in filtering activity; at Station 5 in May there was a pronounced peak in the gut fullness of *Neocalanus plumchrus* from all 4 subsurface samples during the dark, early morning, period and an increase in feeding activity may have occurred during this period.

It is unlikely that all the observed variability in gut fullness of *Neocalanus plumchrus* and *N. cristatus* is due to variations in feeding behavior because the clearance rates required to obtain the observed high levels of gut fullness in deep waters where chlorophyll concentrations were low would be extremely high. For *N. plumchrus* in May rates 15 to 20 times greater than in surface water would be required. If such high rates (150 to 340 ml h^{-1}) were possible, then high levels of gut fullness might also be expected in June because chlorophyll concentrations were similar in June to concentrations in deep water in May. This was not observed.

A further alternative is that the gut evacuation experiments done on shipboard were not completely representative of the process *in situ*. If a copepod migrated to the surface, filled its gut, then descended to depth while delaying the onset of defecation, descent could be at a slower swimming speed. There is no evidence for this explanation, however.

Gut evacuation rate

If a copepod gut was like a conveyor belt, the time required for a marker to pass from one end to the other would equal the feeding duration represented by the gut contents. For example, if it took 30 min for a food particle to travel from mouth to anus, then the amount of food in the gut would be the amount ingested during the previous 30 min. Furthermore, when the copepods were placed in filtered seawater so that ingestion ceased, the rate of gut evacuation would be linear, and a constant amount of fecal material would be egested per unit time until the gut was emptied. However, a copepod gut is not like a conveyor belt. The anatomical structure is more like a reservoir than a tube, and, as illustrated by *Calanus finmarchicus* (Marshall and Orr, 1955), the gut has a blind diverticulum forward of the esophagal opening. Gut contents are continuously churned and mixed by movements of the gut wall (Gauld, 1957) and a marker does not maintain its integrity during passage (Dagg, unpubl.). Also studies of gastric evacuation in fish (reviews by Elliott and Persson, 1978; Jobling, 1981) and copepods (Gauld, 1957; Mackas and Bohrer, 1976; Dagg and Grill, 1980; this paper) indicate that the evacuation rate of food from the gut is not linear but exponential. This means that a constant proportion of gut contents is evacuated per unit time. When ingestion ceases, the amount of material egested per unit time will decrease, as was seen in *Neocalanus plumchrus* and *N. cristatus* in this study. If ingestion were continuous, both the amount of material egested and the proportion of gut contents egested per unit time would be constant.

Temperature affected the instantaneous evacuation rate of *Neocalanus plumchrus*; as temperature increased, R increased. This was also observed in the copepod *Centropages typicus* (Dagg, unpubl.) and in the trout *Salmo trutta* (Elliott, 1972). The relationship between R and temperature for *N. plumchrus* (Fig. 8) indicates a Q_{10} of ~ 5.4. This seems unreasonably high and suggests that more data are required to evaluate accurately this relationship. Although food remains in the gut for a shorter time at higher temperatures, the amount of nutrition extracted from the food is likely independent of the evacuation rate because assimilation efficiency is generally considered independent of temperature (Conover, 1966; Dagg, 1976).

Field application

When laboratory derived relationships between food concentration and ingestion rate are used to estimate feeding rates in the ocean, it is often concluded that natural food concentrations are insufficient for copepods to feed at maximum rates, or even to meet metabolic requirements (e.g. Mullin and Brooks, 1976; Dagg and Grill, 1980; Dagg et al., 1980). Apart from the consideration that the food concentration available to a grazer in the ocean is difficult to specify, there is a lack of information on the short-term feeding behavior of copepods, and on the role of grazer/patch interactions in the copepod's daily nutrition. If measurements of gut contents can be converted to short-term ingestion rates, a clearer understanding of copepod nutrition *in situ* may result. The approach used in this study is attractive because it easily provides data from different depths and times of day, and because the feeding being measured has occurred under natural conditions prior to the animal's capture.

Provided certain assumptions are valid, the gut evacuation rate can be used to convert each measure of gut contents to an ingestion rate. Because evacuation rate is exponential, a constant fraction of the gut contents is defecated per time unit. This is true regardless

of the level of gut fullness. The major assumption is that ingestion and egestion are in equilibrium and therefore that ingestion is also a constant fraction of the gut contents per time unit. If true, a short-term ingestion rate can be calculated from the gut contents, and from the independently measured gut evacuation rate.

The assumption that the egestion rate can be directly related to the ingestion rate is certainly valid when considered over fairly long time intervals; during 120 h long grazing experiments, Shuman and Lorenzen (1975) showed that every molecule of chlorophyll that disappeared from experimental vessels was converted to a molecule of phaeophorbide. However, over shorter periods ingestion and egestion rates may not always be in equilibrium. If copepods feed intermittently or in bouts of a few hours, as suggested by Boyd et al. (1980), the time course of the egestion process could be completely unrelated to that of ingestion. The products from a few hours of feeding could be egested in a few minutes, or the products of a few minutes of ingestion could require hours to digest and defecate. However, preliminary evidence from laboratory experiments (Dagg, unpubl.) does not support this concept and it seems that, although filtering activity varies with factors such as food concentration, hunger and time of day, it rarely ceases entirely.

Ingestion rates calculated for *Neocalanus plumchrus* and *N. cristatus* with this method ranged widely because levels of gut fullness ranged widely. Generally, however, maximum rates measured with more traditional bottle methods, which involve lengthy incubations, are lower than the maximum rates calculated in this study. For example, maximum ingestion rates of *N. plumchrus* and *N. cristatus*, calculated from experimental incubations of 16 to 22 h duration, were 1.9 μg C h^{-1} and 3.3 μg C h^{-1} (Dagg et al., 1982), and, in another study, maximum rates were 0.3 μg C h^{-1} and 2.4 μg C h^{-1} (Taguchi and Ishii, 1972). By comparison, maximum values for *N. plumchrus* and *N. cristatus* at Station 1 in this study were 6.1 μg C h^{-1} and 18.3 μg C h^{-1}. We believe that our maximum hourly rates are realistic but that they represent feeding activity that is occurring over only a rather small portion of each 24 h period for a given individual. Individuals do not maintain these high ingestion rates over 24 h periods because they migrate to regions of the water column which have lower food concentrations. Furthermore, ingestion rates in bottle experiments may be lower because the clearance rates of these two copepods are depressed relative to *in situ* clearance rates.

Clearance rates of *Neocalanus plumchrus* and *N. cristatus* which were determined by more traditional bottle incubations are lower than hourly rates calculated in this study. We observed rates at Station 1 as high as 13.5 ml h^{-1} for *N. plumchrus* and 40.4 ml h^{-1} for *N. cristatus* in May when phytoplankton concentrations were high, and as high as 55.6 ml h^{-1} and 123.5 ml h^{-1} in June when phytoplankton concentrations were low. In comparison, maximum rates of 2.6 ml h^{-1} and 14.2 ml h^{-1} were measured by Taguchi and Ishii (1972) for *N. plumchrus* and *N. cristatus*, respectively. Frost et al. (1983) measured rates up to 20 ml h^{-1} for both species at Station P in the subarctic Pacific. The reason for the differences between our clearance rates and those measured in these other studies is not obvious. One possibility is that our high rates represent short bursts of activity and that such bursts would be masked in a bottle experiment because the lengthy incubation would provide an average value only. However, as stated earlier, the majority of the variation in gut fullness cannot reasonably be attributed to such discontinuous clearance rates. The general good agreement between replicates further suggests that clearance rates are not discontinuous; intermittent activity would lead to a wide range in replicate measures of gut fullness unless such behavior was synchronized within each depth stratum. We believe our clearance rates represent the potential of these copepods in their natural environment, and that rates measured in bottle experiments are underestimates of *in situ* rates for these 2 copepods.

SUMMARY

(1) The level of gut fullness in *Neocalanus plumchrus* and *N. cristatus* varied with season, depth, and time of day.

(2) Lack of correlation between gut fullness and ambient chlorophyll concentration suggests that the copepods are migratory and that individuals often feed in waters not associated with the depth of capture.

(3) By assuming ingestion and egestion are in equilibrium over short time periods, the measurements of gut contents can be converted to short-term feeding rates. This requires an independent measure of the gut evacuation rate.

(4) Gut evacuation rate is exponential; this means that a constant proportion of gut contents is egested per time unit regardless of the level of gut fullness. This rate is temperature dependent.

(5) Short-term ingestion rates vary widely a 24 h period, and maximum values are considerably higher than average hourly rates determined from bottle experiments involving 16 to 24 h incubations.

Acknowledgements. We are indebted to J. Vidal and D. Ninivaggi for shipboard assistance. Discussions with A. Durbin, E. Durbin, and C. D. Wirick were particularly helpful.

LITERATURE CITED

Boyd, C. M., Smith, S. L., Cowles, T. J. (1980). Grazing patterns of copepods in the upwelling system off Peru. Limnol. Oceanogr. 25: 583–596

Conover, R. J. (1966). Factors affecting the assimilation of organic matter of zooplankton and the question of superfluous feeding. Limnol. Oceanogr. 11: 346–354

Corner, E. D. S., Head, R. N., Kilvington, C. C. (1972). On the nutrition and metabolism of zooplankton. VIII. The grazing of *Biddulphia* cells by *Calanus helgolandicus*. J. mar. biol. Ass. U.K. 52: 847–861

Dagg, M. J. (1976). Complete carbon and nitrogen budgets for the carnivorous amphipod, *Calliopius laeviusculus* (Krøyer). Int. Revue ges. Hydrobiol. 61: 297–357

Dagg, M., Cowles, T., Whitledge, T., Smith, S., Howe, S., Judkins, D. (1980). Grazing and excretion by zooplankton in the Peru upwelling system during April 1977. Deep Sea Res. 27: 43–59

Dagg, M. J., Grill, D. W. (1980). Natural feeding rates of *Centropages typicus* females in the New York Bight. Limnol. Oceanogr. 25: 597–609

Dagg, M. J., Vidal, J., Whitledge, T. E., Iverson, R. L., Goering, J. J. (1982). The feeding, respiration and excretion of zooplankton in the Bering Sea during a spring bloom. Deep Sea Res. 29: 45–63

Elliott, J. M. (1972). Rates of gastric evacuation in brown trout, *Salmo trutta* L. Freshwater Biol. 2: 1–18

Elliott, J. M., Persson, L. (1978). The estimation of daily rates of food consumption for fish. J. Anim. Ecol. 47: 977–991

Enright, J. T. (1977). Copepods in a hurry: sustained high-speed upward migration. Limnol. Oceanogr. 22: 118–125

Frost, B. W., Landry, M. R., Hassett, R. P. (1983). Feeding behavior of large calanoid copepods *Neocalanus cristatus* and *N. plumchrus* from the subarctic Pacific Ocean. Deep Sea Res. 30: 1–13

Gauld, D. T. (1957). A peritrophic membrane in calanoid copepods. Nature, Lond. 179: 325–326

Hallegraeff, G. M. (1981). Seasonal study of phytoplankton pigments and species at a coastal station off Sidney: importance of diatoms and nanoplankton. Mar. Biol. 61: 107–118

Haney, J. F., Hall, D. J. (1975). Diel vertical migration and filter-feeding activities of *Daphnia*. Arch. Hydrobiol. 75: 413–441

Hardy, A. C., Bainbridge, R. (1954). Experimental observations on the vertical migrations of plankton animals. J. mar. biol. Ass. U.K. 33: 409–448

Haury, L. R., McGowan, J. A., Wiebe, P. H. (1978). Patterns and processes in the time-space scales of plankton distributions, In: J. H. Steele (ed.) Spatial pattern in plankton communities. Plenum Press, New York, p. 277–327

Jeffrey, S. W. (1974). Profiles of photosynthetic pigments in the ocean using thin-layer chromatography. Mar. Biol. 26: 101–110

Jobling, M. (1981). Mathematical models of gastric emptying and the estimation of daily rates of food consumption for fish. J. Fish. Biol. 19: 245–257

Longhurst, A., Williams, R. (1979). Materials for plankton modelling: vertical distribution of Atlantic zooplankton in summer. J. Plankton Res. 1: 1–28

Mackas, D., Bohrer, R. (1976). Fluorescence analysis of zooplankton gut contents and an investigation of diel feeding patterns. J. exp. mar. Biol. Ecol. 25: 77–85

Mackas, D. L., Boyd, C. M. (1979). Spectral analysis of zooplankton spatial heterogeneity. Science, N. Y. 204: 62–64

Marshall, S. (1924). The food of *Calanus finmarchicus* during 1923. J. mar. biol. Ass. U.K. 13: 473–479

Marshall, S. M., Orr, A. P. (1955). The biology of a marine copepod. Oliver and Boyd, Edingburgh

McAllister, C. D. (1970). Zooplankton rations, phytoplankton mortality, and the estimation of marine production. In: J. H. Steele (ed.) Marine food chains. University of California Press, p. 419–457

Mullin, M. M., Brooks, E. R. (1976). Some consequences of distributional heterogeneity of phytoplankton and zooplankton. Limnol. Oceanogr. 21: 784–796

Pearre, S., Jr. (1973). Vertical migration and feeding in *Sagitta elegans* Verill. Ecology 54: 300–314

Roman, M. R., Rublee, P. A. (1980). Containment effects in copepod grazing experiments: a plea to end the black box approach. Limnol. Oceanogr. 25: 982–990

Runge, J. A. (1980). Effects of hunger and season on the feeding behavior of *Calanus pacificus*. Limnol. Oceanogr. 25: 134–145

Shuman, F. R., Lorenzen, C. J. (1975). Quantitative degradation of chlorophyll by a marine herbivore. Limnol. Oceanogr. 20: 580–586

Strickland, J. D. H., Parsons, T. R. (1968). A practical handbook of sea water analysis. Bull. Fish. Res. Bd Can. 167: 185–206

Taguchi, S., Ishii, H. (1972). Shipboard experiments on respiration, excretion and grazing of *Calanus cristatus* and *C. plumchrus* (Copepoda) in the northern North Pacific. In: A. Y. Takenouti (ed.) Biological oceanography of the northern North Pacific. Idemitsu Shoten, p. 419–431

This manuscript was presented by Professor G.-A. Paffenhöfer; it was accepted for printing on April 12, 1983