Grazing pressure of the calanoid copepod *Temora longicornis* on a *Phaeocystis* dominated spring bloom in a Dutch tidal inlet

F. C. Hansen[1], W. H. M. van Boekel[2]

[1]Netherlands Institute for Sea Research, PO Box 59, 1790 AB Den Burg, The Netherlands
[2]University of Groningen, Dept of Marine Biology, PO Box 14, 9750 AA Haren, The Netherlands

ABSTRACT: Between 30 March and 11 May 1990, total copepod abundance and the abundance, biomass and gut fluorescence of *Temora longicornis* were determined and related to the abundance and succession of phytoplankton development in a Dutch tidal inlet. Gut pigment values were highest in females and lowest in young copepodites, but weight-specific pigment concentrations were about similar. Pigment levels measured in the guts were relatively high at the beginning and end of the period of investigation when diatoms dominated the phytoplankton community, and low during the *Phaeocystis* dominated period, when ambient chlorophyll concentrations were highest. For the latter period, calculated ingestion rates in *T. longicornis* were low and estimated daily consumption amounted to less than 1 % of the phytoplankton standing stock, suggesting a negligible grazing impact on the development of the *Phaeocystis* bloom. In spite of the low grazing on phytoplankton, *T. longicornis* biomass increased by one order of magnitude. The discrepancy between low grazing pressure and copepod development is explained by assuming that *T. longicornis* switched to heterotrophic food: a bloom of ciliates present during the *Phaeocystis* dominated period.

INTRODUCTION

Copepod grazing has traditionally been regarded as having an important function in coupling phytoplankton to higher trophic levels, leading to fish production (Steele 1974). Increased nutrient inputs into North Sea coastal waters in the past 2 decades correlate not only with an increase in phytoplankton biomass but also with a shift in its community composition towards flagellates (Cadée 1986, Radach et al. 1990). In particular since 1973, blooms of the prymnesiophyte *Phaeocystis* sp. have increased (e.g. Cadée 1986), which has been reported to cause nuisances and possible economic drawbacks in fishery (e.g. Savage 1932) and tourism (Lancelot et al. 1987). Environmental problems are suspected from dimethylsulfide (DMS) release (Turner et al. 1988 and references cited therein) and mass production and sedimentation (Wassmann 1990) of organic matter, for which the impact on the benthic and pelagic food web structure is still unclear. Since 1988, *Phaeocystis* bloom dynamics have been studied by a group of European

scientists within a joint EEC project. A major question to be answered is the ultimate fate of *Phaeocystis* and in this context the possible role of copepods in controlling *Phaeocystis* blooms.

The literature concerning copepod grazing on *Phaeocystis* is contradictory. On the one hand, *Phaeocystis* is regarded as unsuitable food (e.g. Schnack 1983, Daro 1986, Verity & Smayda 1989). This holds for the colonies, because they are sticky and partly too large (up to ca 20 mm), as well as for the small flagellates (3 to 8 μm) which are at the lower end of the size spectrum of retainable algae for most herbivorous copepods. Possible negative effects on copepods by the release of antibacterial acrylic acid (Sieburth 1960) and DMS (Gibson et al. 1990) have not yet been studied in detail. On the other hand, *Phaeocystis* ingestion by copepods has been reported (e.g. Lebour 1922, Estep et al. 1990) and recent laboratory studies quantifying grazing (Huntley et al. 1987, Tande & Båmstedt 1987, Hansen et al. 1990) indicate that copepods are potential *Phaeocystis* consumers. In this respect, the calanoid copepod *Temora longicornis*

seems to be a promising candidate, because of its high abundance during spring in North Sea coastal waters (e.g. Fransz & van Arkel 1983 and references cited therein) and its ability to feed on *Phaeocystis* colonies (Weisse 1983) and single cells (F. Hansen unpubl. obs.).

There are strong indications that food quality and composition have a major impact on copepod grazing activity (e.g. Cowles et al. 1988, Estep et al. 1990, Klein Breteler et al. 1990, F. Hansen unpubl.). Differences in food quality and composition may also be responsible for contradictions in reports regarding copepod grazing on *Phaeocystis* in laboratory and field studies. Direct estimates of copepod grazing on a *Phaeocystis* bloom in the field are scarce and contradictory. This study measures *Temora longicornis* grazing activity in the course of a *Phaeocystis* dominated spring bloom in the field by means of the gut fluorescence method, in order to evaluate the importance of *T. longicornis* predation for *Phaeocystis* bloom dynamics.

MATERIAL AND METHODS

Samples were collected from the Marsdiep (Fig. 1), a eutrophicated and well-mixed tidal part of Dutch coastal waters. A detailed description of the hydrography of this area was given by Postma (1954). To follow phytoplankton and zooplankton development, quantitative surface water samples were taken frequently between 30 March and 11 May 1990, always at high tide. During this period, water temperature remained low until 24 April (8 to 10 °C), with a subsequent rise to 14 °C in mid-May.

Chlorophyll *a* (chl *a*) concentration in the samples was measured by applying the spectrophotometric method of Lorenzen (1967). Cell number and species composition of phytoplankton were determined with the Utermöhl sedimentation technique (Utermöhl 1958) in samples fixed with Lugol. Cell volumes of *Phaeocystis* and diatom species were determined by microscopical size measurements. Phytoplankton carbon was calculated by assuming that the chl *a* ratio *Phaeocystis*/diatoms equals the biovolume ratio *Phaeocystis*/diatoms in the samples and by applying a carbon/chl *a* ratio of 25 in diatoms (Riemann et al. 1982) and 29 in *Phaeocystis* (Lancelot-van Beveren 1980). The *Phaeocystis* colonies in the samples were all of the *globosa*-type (Jahnke & Baumann 1987).

To collect copepods, 60 l of water collected by bucket was poured into plastic bottles and gently filtered over a floating 300 µm gauze. Retained plankton were rinsed on pieces of 200 µm gauze and immediately deep-frozen by means of liquid nitrogen. Gauzes were
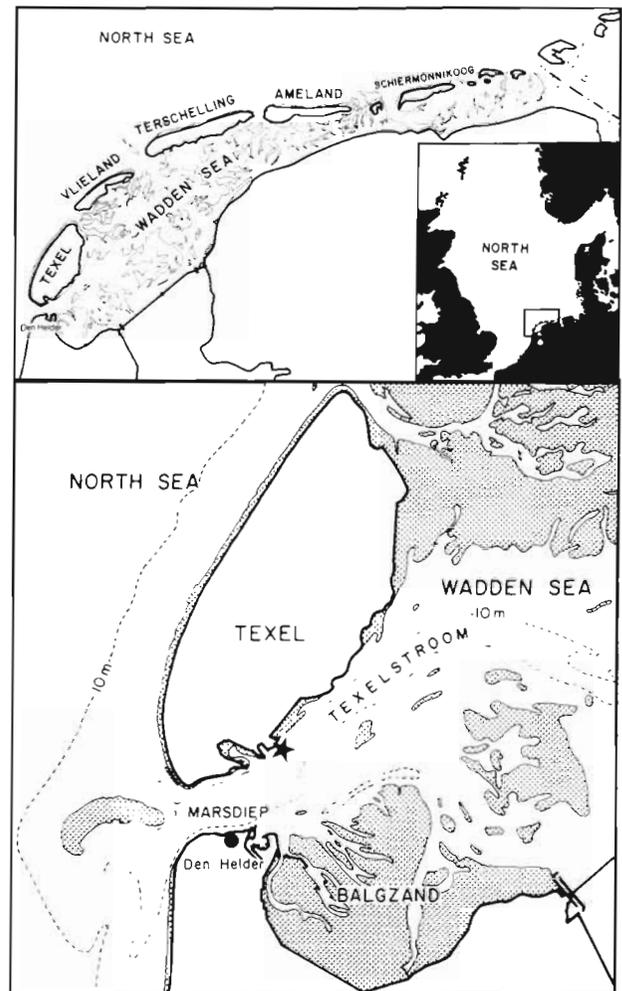

Fig. 1 Location of the Marsdiep area (asterisk indicates position of sampling site)

stored in the dark in Petri dishes at −24 °C for 2 to 4 mo. Copepods were collected from the gauzes and sorted for species under a dissecting microscope. *Temora longicornis* specimens were further sorted for sex and developmental stage, and their lengths measured. Young copepodite stages (stage ≤ C4) were distinguished from older copepodites (stage C5 plus C6), which were separated into males and females.

Temora longicornis gut fluorescence was determined as described by Baars & Oosterhuis (1984) with minor modifications. Copepods were homogenized using a Potter grinder. After 2 h of extraction in the dark at 5 °C, the solution was filtered through a GF/F filter mounted on a syringe. In the filtrate, chlorophyll *a* and phaeopigment concentrations were measured and gut fluorescence was taken as the sum of chlorophyll *a* plus phaeopigments, expressed as ng chl *a* equivalent per copepod. In preliminary experiments background fluorescence and changes in pigment concentration

due to storage and freezing were found to be negligible.

Gut pigment content (chl a plus derived phaeo-pigments) is expressed as ng chl a weight equivalent per copepod or per mg ash-free dry weight, calculated from size-weight relationships given by Klein Breteler & Gonzales (1988). *Temora longicornis* body carbon was taken as 40 % ash-free dry weight (Omori 1969). Copepod ingestion rates were calculated from gut fluorescence and temperature-dependent rates of gut clearance given by Dam & Peterson (1988).

RESULTS

Between 30 March and 9 April 1990, the phyto-plankton community in the Marsdiep was dominated by large diatoms (*Biddulphia sinensis, Thalassiosira* spp.). In the first half of April, both chl a and *Phaeo-cystis* cell concentration increased, with peaks on 13 and 15 April respectively (Fig. 2). At the peak of the *Phaeocystis* bloom, cell concentration exceeded 67×10^6 cells l^{-1} while the chlorophyll concentration amounted to 55 µg chl a l^{-1} Thereafter, *Phaeocystis* cell density and chlorophyll concentration declined sharply. Between 11 and 24 April, phytoplankton biomass was dominated by *Phaeocystis* (Fig. 3). In the second half of April small diatom species (*Plagio-gramma brockmanni, Asterionella* spp.) became increasingly important. *Cerataulina bergonii* domi-nated the phytoplankton community after 24 April. In the latter period, chlorophyll concentration decreased further down to 11 µg chl a l^{-1}.

Copepod abundance remained low until mid-April, reaching significantly higher concentrations in the latter part of the investigation period (Fig. 4). Gener-ally, *Temora longicornis* was the dominant copepod, comprising on average 80 % of the total copepod
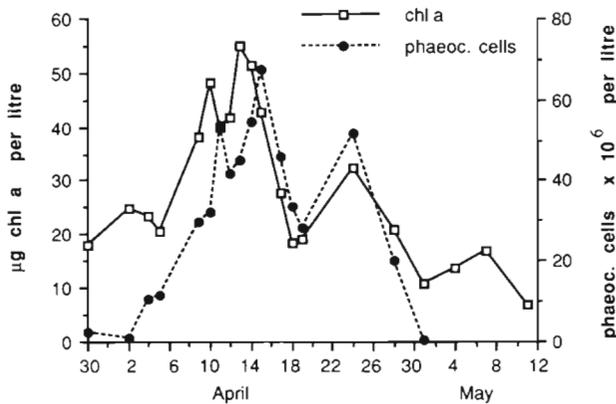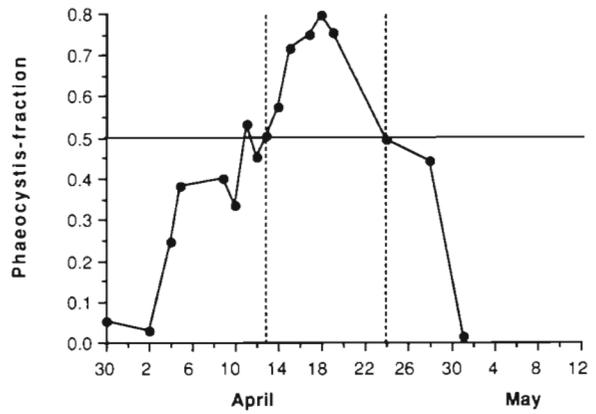

Fig. 3. *Phaeocystis* biovolume fraction of total phytoplankton biomass in Marsdiep. Vertical lines indicate period of *Phaeocystis* dominance

number. Other copepods mainly consisted of *Pseudo-calanus elongatus*, which appeared in higher concen-tration during May. An attempt was made to esti-mate *T. longicornis* production from biomass increase in the larger copepodites by the application of an exponential growth model (Fig. 5). The significant regressions for females (1) and males (2), ($r_1^2 = 0.80$; $r_2^2 = 0.74$; n_1, $n_2 = 9$; p_1, $p_2 < 0.01$), yielded minimum P/B ratios (including mortality, see 'Discussion') of 15 % d^{-1}, indicating good growth during the *Phaeo-cystis* dominated period.

Gut fluorescence of males and females (C5 + C6) and smaller copepodites did not resemble the course of the chlorophyll concentration in the water (Figs. 2 & 6), but appeared to be inversely correlated with *Phaeocystis* dominance (Fig. 3). During the *Phaeocystis* attributed chlorophyll increase, gut fluorescence declined, being lowest while *Phaeocystis* dominated the phyto-plankton community. Thereafter in May, while the phytoplankton community was mainly composed of

Fig. 2. Phytoplankton spring development in the Marsdiep from 30 March to 12 May 1990: chlorophyll a and *Phaeocystis* cell concentrations
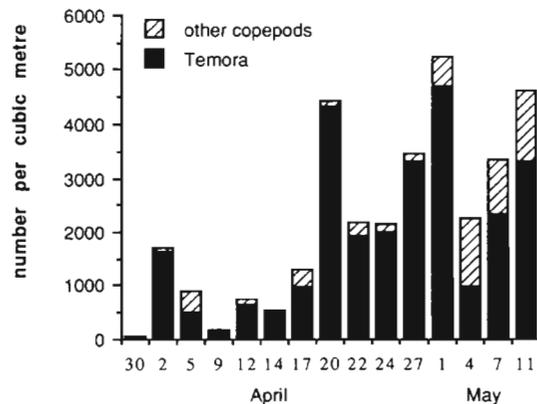

Fig. 4. Abundance of *Temora longicornis* and other copepod species in the Marsdiep in spring 1990 (mean concentrations of all stages concentrated on 300 µm gauze)
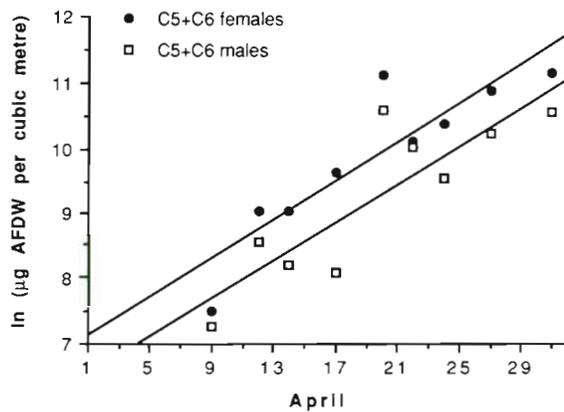
Fig. 5. Biomass of male and female C5 and adult *Temora longicornis* in the Marsdiep in spring 1990 (mean concentrations of all stages concentrated on 300 μm gauze). Exponential growth curves fitted according to: $B_t = B_0 \, e^{(P/B - m)t}$, where B_0, B_t: biomass at the beginning/end of studied period t (in days); P: production; m: mortality. (For results, see text)

several small diatom species, gut fluorescence showed an increase of a factor of about 4.

Generally females showed highest gut fluorescence, males lower, and copepodites the lowest gut fluorescence (Fig. 6). However, after correcting for body size differences, by expressing gut fluorescence per unit ash-free dry weight (AFDW), the gut fluorescences of the different sexes and stages were almost the same or rather higher in the smaller stages (Fig. 7). In the diatom dominated periods, calculated ingestion rates were much higher in April/May compared to March/April (Table 1), partly due to the higher gut evacuation rates in the latter period with higher water temperature.

Total daily phytoplankton ingestion by *Temora longicornis* was low, especially during the *Phaeocystis* dominated period. In this period, total ingestion
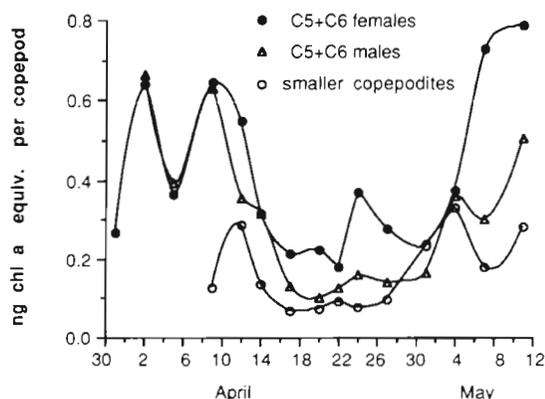

Fig. 6. *Temora longicornis*. Gut fluorescence of 3 age and sex classes in the Marsdiep during spring 1990 (mean concentrations of all stages concentrated on 300 μm gauze)
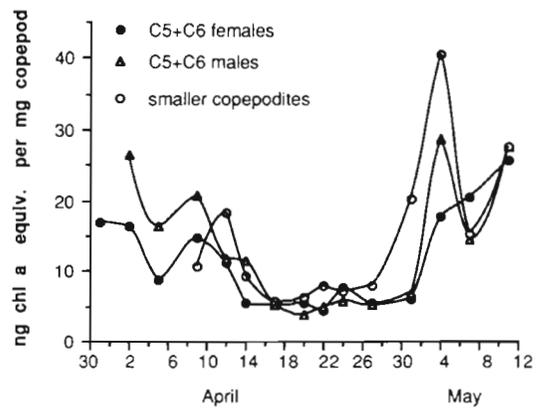

Fig. 7. *Temora longicornis*. Weight-specific gut fluorescence of 3 age and sex classes in the Marsdiep during spring 1990 (mean concentrations of all stages concentrated on 300 μm gauze)

ranged between 6 and 26 ng chl a l^{-1} d^{-1}. This is less than 1 % of the phytoplankton standing stock present. Thus it is concluded that grazing by *T. longicornis* did not have a significant impact on the dynamics of the spring *Phaeocystis* bloom. Considering the small biomass of the other copepods, this probably also holds for the whole copepod community.

DISCUSSION

The gut fluorescence method (Mackas & Bohrer 1976) allows the study of undisturbed grazing by copepods in the field and has therefore been widely implemented for the last 15 yr. The uncertainty in the determination of gut passage times suggests that one has to be cautious deriving absolute ingestion figures from gut fluorescence measurements (e.g. Penry & Frost 1990 and references cited therein). However, Kiørboe et al. (1982, 1985) and Peterson et al. (1990) have shown good agreement of this method with estimates obtained by the measurement of the decrease of chlorophyll and cells during incubation experiment as well as good correlation between ingestion measured with the gut fluorescence technique and egg production. Thus, for studying daily feeding rhythms or seasonal differences, as presented here, the gut fluorescence method may still be regarded as a useful tool.

Many authors have reported diel feeding rhythms in copepods (e.g. Mackas & Bohrer 1976, Stearns 1986, Tiselius 1988) although such rhythms may also be absent (Roman et al. 1988). Baars & Fransz (1984) and Dam (1986) found gut pigment content in *Temora longicornis* to be about twice as high at night as during the day. It has been proposed that light intensity is an important factor in controlling diel feeding rhythms

Table 1 *Temora longicornis* grazing pressure on the 1990 phytoplankton spring bloom before, during and after the *Phaeocystis* dominated period. Arithmetic means of weight-specific gut fluorescence (GF), gut passage time (GPT), specific daily ration (SDR), *T. longicornis* biomass (TB), total phytoplankton ingestion by *T. longicornis* (TPI), phytoplankton standing stock (PSS) and grazing pressure (GP) as ratio TPI/PSS for copepodite stages C5 + C6 females (f•), C5 + C6 males (m•) and younger copepodites (c•)

Date	Group	GF (ng chl *a* equiv. mg body C^{-1})	GPT (min)	SDR (mg C mg body C^{-1} d^{-1})	TB (mg C m^{-3})	TPI (mg C m^{-3} d^{-1})	PSS (mg C m^{-3})	GP (%)
29 Mar	f•	34.1	34.9	0.037	3.8	0.14		
to	m•	47.0	34.9	0.051	3.3	0.17		
12 Apr	c•	36.2	34.9	0.039	0.9	0.04		
	Sum				8.1	0.35	842	0.04
13 Apr	f•	14.0	33.1	0.017	11.7	0.20		
to	m•	15.5	33.1	0.019	6.4	0.12		
24 Apr	c•	18.1	33.1	0.022	2.6	0.06		
	Sum				20.7	0.38	969	0.04
25 Apr	f•	37.7	27.6	0.049	17.6	0.86		
to	m•	41.3	27.6	0.054	8.6	0.46		
11 May	c•	55.5	27.6	0.073	3.0	0.22		
	Sum				29.1	1.54	345	0.45

(e.g. Stearns 1986 and references cited therein). In the highly turbid Marsdiep area, copepods are exposed to low light levels during daytime as well. Hence, they might exhibit a much less pronounced daily feeding rhythm than copepods in other areas. Sampling took place at high tide, thus varying regularly between 07:00 and 19:00 h with 3 shifts from evening to morning sampling in the course of this study. However, neither an increase in gut fluorescence coinciding with these shifts was observed, nor could the observed variation of gut fluorescence be correlated to sampling time. Daro (1986) likewise reported that *T. longicornis* lost its feeding rhythm during a *Phaeocystis* bloom. Diel feeding rhythms were not investigated in this study and day-night differences in feeding could have led to an underestimation of daily ingestion and consumption rates calculated. However, this would not affect the major conclusions drawn in this paper.

The observed spring increase in *Temora longicornis* abundance is in accordance with previous studies in the Marsdiep area (Fransz & van Arkel 1983, Kuipers et al. 1990). The estimate for *T. longicornis* production in April (Fig. 5) was made under the assumption that biomass accumulation in the older stages reflected the average copepodite growth in the sampled waters. Fransz (1976) showed a similar spring development of *T. longicornis* in different areas along the Dutch coast. Assuming a daily mortality of about 10 % (e.g. Bakker & van Rijswijk 1987 and references cited therein), no advection, and a gross growth efficiency between 17 % (Harris & Paffenhöfer 1976) and 35 % (e.g. Berggren et al. 1988), the observed growth of *T. longicornis* would require an ingestion of 70 to 140 % of body weight daily. This value agrees well with rates obtained from growth experiments with *T. longicornis* cultures in the presence of excess food (Klein Breteler et al. 1990). During the *Phaeocystis* bloom, the calculated daily ration of *T. longicornis*, as based upon gut fluorescence measurements, amounted to only a small percentage of its body carbon, quite insufficient to cover its food demand. Even on the basis that *T. longicornis* fed solely on *Phaeocystis* colonies with a C/chl *a* ratio ranging between 55 and 245 (Lancelot & Billén 1990) and converted the mucus with the same gross growth efficiency (which is unlikely because it has a low nitrogen content), a considerable gap between autotrophic food intake and energy demand would still remain.

In order to explain the high growth rates, the hypothesis is put forward that *Temora longicornis* switched to a heterotrophic food source, at least during the *Phaeocystis* dominated period. We here consider 2 major possibilities for this food source: detritus, probably coated with bacteria, and microzooplankton. Unfortunately, there is very little information on the quality and quantity of detritus in the Marsdiep and to what extent detritus might be utilized by *T. longicornis*. However, during the *Phaeocystis* dominated period a bloom of ciliates was present exceeding copepod biomass (R. Bak unpubl.). Protozoa are judged to be high-quality food for zooplankton (see review by Stoecker & Capuzzo 1990), in contrast to *Phaeocystis* for which a biochemical investigation reports a low nutritional value (Claustre et al. 1990). If copepod grazing on *Phaeocystis* is affected by the availability and quality of alternative food sources, this might explain why most laboratory studies indicate that *Phaeocystis*, when offered alone or in mixture with

other phytoplankton, is appropriate food, whereas field studies indicate grazing to be depressed during *Phaeocystis* blooms (Daro 1986, van Rijswijk et al. 1989). Laboratory grazing studies on copepods have shown higher feeding rates on ciliates compared to phytoplankton (Stoecker & Sanders 1985, Williamson & Butler 1986, Stoecker & Egloff 1987), as well as positive selectivity for ciliates in mixtures with phytoplankton (Wiadnyana & Rassoulzadegan 1989).

Ciliates are thought to be the major predator on *Phaeocystis* single cells (Weisse & Scheffel-Möser 1990). If copepods are able to control ciliate abundance they may indirectly have a considerable impact on *Phaeocystis* bloom dynamics. Whether copepod grazing enhances or depresses *Phaeocystis* development will then depend on the availability and type of alternative food sources. We are continuing research on this topic and suggest that further grazing studies should concentrate more on heterotrophic microzooplankton and its possible function as a link between phytoplankton and larger zooplankton.

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