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Diurnal Variation in Feeding and Assimilation Rates of Planktonic Rotifers and its Possible Ecological Significance*

key words: diurnal feeding rhythm, planktonic rotifers

Abstract

Though rotifers play an important role in many pelagic ecosystems, there is a lack for studies on diurnal variations in feeding behaviour. Diurnal feeding rhythms of estuarine populations of Brachionus plicatilis and Keratella cruciformis f. eichwaldi and a pond population of K. cochlearis were investigated using ¹⁴C-Chlorella and ¹⁴C-labelled natural bacteria populations, respectively, as a tracer food during in situ experiments. A ⁵¹Cr/¹⁴C double tracer technique was used to determine assimilation efficiencies.

All species had about two times higher feeding rates during day than during dark hours. There was a tendency for higher values during the afternoon. No trend was found regarding diurnal changes in assimilation efficiency.

Diurnally segregated niches between microphagous daytime active rotifers and nighttime active crustacean populations in pelagic ecosystems are demonstrated and their ecological significance with special regard to changes in food quality and predation pressure is discussed.

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1. Introduction

For estimating the ecological importance of zooplankters in the matter flux of pelagic ecosystems determinations of feeding rates are a necessary prerequisite. Since the first observations of diurnal differences in feeding activity of zooplankters by

^{*} Dedicated to the memory of our engaged teacher in ecology Prof. Dr. Werner Schnese (10. 6. 1929—20. 9. 1985)

Marshall (1924) many crustacean populations have been investigated regarding their daily patterns of food consumption. In most cases nocturnal or evening maxima in feeding rates corresponded to higher migrational activity of crustaceans during the evening or nighttime (e.g. Gauld 1953, Mackas & Bohrer 1976). It has been shown that weight specific feeding rates during the night could be several times higher than during the day. Therefore, in some studies the diurnal feeding rhythms (DFR) were considered when calculating the daily mean of feeding rates of crustaceans (e.g. HEERKLOSS et al. 1984). The knowledge about the importance of rotifers for the matter flux of limnetic and estuarine ecosystems has much increased during the last decades (e.g. May et al. 1987). Several species have been intensively investigated regarding their feeding rates (for a review cf. Starkweather 1980). So far, DFR have poorly been investigated. Probably most authors assume that they do not exist because of the low migrational activity reported from retifers and the necessity of ciliary movement in order to prevent sedimentation. But, since the vertical distance of rotifer migration is very small (generally only 0.5-5 m), its significance has probably been underestimated in many studies. Those few studies which report on diurnal vertical migration of rotifers often showed a so-called "reverse" migration characterized by upward migration during daytime (e.g. Bayly 1986). The question arises whether or not there are also changes in feeding activity (corresponding to diurnal changes in migrational activity) analogous to crustacean zooplankton. However, our search in literature for reports on diurnal changes in feeding activity revealed only the study by NAUWERCK (1959), who stated that the rotifer plankton (pocled species) feeds more actively in the light than in the dark. But quantitative data are lacking up to know. The only further report we found was that by Bogdan & Gilbert (1982, p. 925), who cited in one sentence an unpublished work by Starkweather et al. indicating "no rhythmic diel variations in clearence rates of Keratella and Polyarthra . . . ".

For the investigation of diurnal feeding rhythms of rotifers we carried out experiments during mass occurrence in estuarine populations of *Brachionus plicatilis*, *Keratella cruciformis* f. *eichwaldi*, and in a limnetic population of *Keratella cochlearis*, respectively. In addition, the assimilation rate was investigated, since it is known that assimilation efficiency of zooplankters often varies with changes in feeding rate (e.g. Hayward and Gallup 1976, Pilarska 1977). Repeated observations about reversed vertical migrations give rise to the question whether or not there are daytime restricted niches within pelagic zooplankton communities (cf. Arnot in press).

2. Material and Methods

a) Feeding experiments on estuarine populations of Brachionus plicatilis and Keratella cruciformis f. eichwaldi

Experiments were carried out during mass occurrence of both species in the Warnow estuary at the Old Port of Rostock (G.D.R.). Investigations were performed in the course of a day at August 17/18, 1982, and August 23/24, 1982, in about 3–4 hours intervals. In situ water temperatures ranged between 14 and 19 °C; salinity was around 7 ‰ S. Prior to each experiment rotifers were caught by means of a plankton net (56 μm) equipped with a bottle containing biotope water in order to prevent damaging of organisms. After the catch the 0.51-bottles were stored for 15 minutes in situ for relaxing of rotifers. At the start of the experiment 10 ml of a ¹⁴C-labelled suspension of Chlorella vulgaris (mean diameter 3 μm) was added (final concentration 2×10⁶ cells/ml). Chlorella is known as a valuable food source for Brachionus plicatilis (e.g. Hirayama et al. 1979). After a feeding period of 15 minutes rotifers were concentrated with care on a 56 μm net and placed in the dark part of a horizontally working light trap. After two minutes rotifers which had migrated into the illuminated vessel containing unlabelled biotope water were filtered and resus-

pended in a new vessel containing filtered biotope water with a drop of chloroform. Again, 2 minutes later rotifers were fixed with formalin (2 %). The procedure of light trapping after the experiment served for a separation of active specimens and for cleaning of mouth parts from not incorporated radioactive food particles. Specimens removed from the experimental vessel directly after the addition of radioactive food were used as a control. For measurement of radioactivity of the food aliquots from the feeding vessels were filtered on membrane filters (SYNPOR 6; 0.45 µm pore size). About one day after each experiment 100 specimens of B. plicatilis or 150 specimens of K. c. eichwaldi, respectively, were placed on each of six glass fiber filters for determination of radioactivity. This long time of storage was necessary to reduce the variability between the experiments due to fixative induced loss of 15 (Holtby and Knoechel 1981). Thus, the absolute feeding rate may be underestimated but the relative changes should be recognizable. All membrane and glass fiber filters were dried for 24 h at 60 °C. GM-counting was used for measurement of radioactivity (VEB Meßelektronik Dresden). All parameters which are known to influence feeding rate of rotifers were held under natural conditions (temperature, light, physiological status of rotifers) or under constant conditions (food and rotifer concentration, all experimental manipulations) during the course of a day. Filtration rate (FR) was calculated according to Sorokin (1968) using an absorption coefficient for rotifers of 1.05 (SOROKIN pers. comm.) by the following formula

$$FR \left[\mu l \times ind^{-1} \times h^{-1}\right] = \frac{(R_{ZF} - R_{ZC}) \left[\text{cpm} \times ind^{-1}\right] \times 1.05}{R_{PH} \left[\text{cpm} \times \mu l^{-1}\right] \times t \left[h\right]} , \tag{1}$$

with R_{PH} as radioactivity of phytoplankton, R_{ZF} and R_{ZC} as radioactivity of feeding zooplankton and control, respectively, and t as experimental time. For a better comparison of DFR each filtration rate was calculated as a percentage of the daily mean value. Since food concentration was held constant during one set of experiments (control by haemocytometer counts), the relative changes in filtration rate can also serve as an estimate of the relative changes in feeding rate.

b) Feeding experiments on a limnetic population of Keratella cochlearis

A mass occurrence of *K. cochlearis* in the Schwanenteich, a small shallow man-made pond in the centre of Rostock (G.D.R.), was used to study diurnal variations in feeding activity. Plankton was dominated at this time by a dense bloom of *Aphanizomenon flos-aquae* and high concentrations of bacteria (Roloff *et al.* 1983, Jost pers. comm.).

Feeding rates were determined using biotope water which was filtered through a sieve (10 µm mesh size) and labelled in the dark with \(^{14}\text{C-glucose}\) for 48 h prior to the experiment. The labelled pico- and nanoplankton (<10 µm) should be a suitable food source for the microphagous K. co-chlearis (cf. Pourrior 1977). The experimental procedure was the same as for the experiments in brackish water (see above) with the following exceptions: Rotifers were added after a relaxing period of 15 minutes to the labelled biotope water. Following a feeding period of 15 minutes rotifers were filtered and set into unlabelled water for cleaning mouthparts without separation by means of light-trapping.

c) Determination of assimilation efficiency (AE)

To take into account that the ¹⁴C assimilated gets lost by respiration already during the time of experimental feeding the ⁵¹Cr/¹⁴C double labelling technique by Carlow and Fletcher (1972) was used instead of measuring ¹⁴C incorporation into the body tissue. AE was determined during most of the *K. cochlearis* feeding experiments. Some further studies were carried out on the same population during winter (1–5 °C) and on the estuarine population of *Brachionus plicatilis*. The following procedure has been applied: A laboratory culture of *Chlorella vulgaris* (diameter 3 µm) was labelled with ¹⁴C-NaHCO₃ and ⁵¹Cr-Na₂CrO₃, respectively, about 48 hours before each experiment. Directly before the experiment the ¹⁴C- and the ⁵¹Cr-culture were mixed at a known concentration and used as a tracer food for rotifers. Animals were caught and separated immediately before the experiment. After a relaxing period of 15 minutes the tracer food was added (about 1.0 × ×10⁶ cells/ml) and experimental vessels were exposed for 120 minutes under in situ conditions. After this time rotifers were filtered and placed in a vessel with filtered biotope water containing

yeast $(1.0 \times 10^7 \text{ cells/ml})$ and stored at in situ temperature for 60 minutes. After this period of fecal excretion rotifers were removed by filtration and fixed in formaldehyde. Aliquots of the yeast medium which contained the fecal products of the rotifers were concentrated on membrane filters for determination of ratios between both isotopes in feces (51Cr/14C). The fixed rotifer samples were used to estimate the abundance of rotifers during the experiments. The ratios bettween both isotopes in the food were determined from subsamples of water in the feeding vessels filtered on membrane filters. For determination of radioactivity a GM-counter was used for the β -nuclide (14C) whereas a NaJ-crystal scintillation counter was used for the γ -nuclide (51Cr). An overlapping of ¹⁴C-cpm (8-13 % of c.p.m. determined with GM-counter) was taken into account in the second case. Measurements of the efficiency of chromium assimilation (2-4% calculated from feedig and assimilation rates in separate experiments) were used to correct the 14C/51Cr ratio of the feces. It was assumed that rotifers did not select between algae labelled with the different isotopes. Factors known to influence assimilation efficiency of rotifers were held constant (food quality, food concentration, all experimental manipulations) or under natural conditions (temperature, light, physiological status of rotifers) in the course of experiments. Assimilation efficiencies were calculated using the following formula:

$$AE \left[\%\right] = 1 - \frac{(^{14}\text{C}/^{51}\text{Cr})_{\text{feees}}}{(^{14}\text{C}/^{51}\text{Cr})_{\text{food}}} \times 100.$$
 (2)

3. Results and Discussion

a) Diurnal variations in feeding rate

The results on relative changes in feeding rates are shown in Figs. 1–3. All experiments revealed significantly higher feeding rates during daytime compared to night-time (p < 0.01). For all of the three species mean feeding activity during daytime was

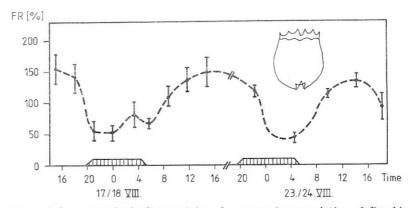


Figure 1. Diurnal changes in the feeding activity of an estuarine population of Brachionus plicatilis (100 % = daily mean value; shaded areas indicate the dark period; vertical bars represent 95 % confidence limit, n=5).

about two times higher than during the night (B. plicatilis 1.9; K. c. eichwaldi 2.7; K. cochlearis 1.7). Maximum and minimum values differed up to four times. Absolute daily mean values of filtration rates of the three species were as follows: B. plicatilis 1.63 µl/ind./h, K. c. eichwaldi 0.14 µl/ind./h, and K. cochlearis 0.43 µl/ind./h, respectively. These values are in the range of values reported from literature (Starkweather 1980). Relative feeding rate of the two species, B. plicatilis and K. cochlearis, which

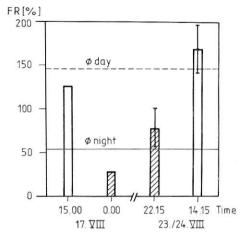


Figure 2. Differences between day and nighttime feeding activity of an estuarine population of Keratella cruciformis f. eichwaldi (shaded columns represent experiments during the dark period; continuous line = mean value for the dark period; broken line = mean value for the light period).

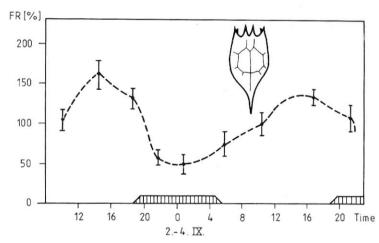


Figure 3. Diurnal changes in feeding activity of a pond population of Keratella cochlearis.

were investigated in more detail, increased slowly from sunrise till afternoon. At sunset a relatively abrupt decrease in feeding activity took place.

Since all parameters which are known to influence feeding behaviour were held at in situ conditions or constant in the course of experiments, the observed changes in feeding activity should represent a natural behaviour. Of course, this result has to be verified by experiments during different seasons with other populations and other species, respectively. Nauwerck (1959) from his experiment with a mixture of several rotifer species also reported a higher feeding activity during daytime.

b) Assimilation efficiency (AE)

One important question for interpretation of diurnal changes in feeding activity is whether the assimilated part of the ingested food varies in the course of a day. Though there are some data on assimilation efficiency of planktonic rotifers (e.g. DOOHAN 1973,

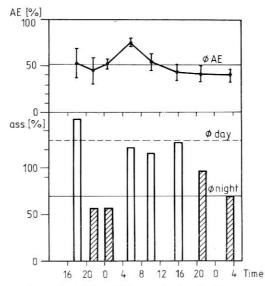


Figure 4. Diurnal changes in assimilation efficiency during feeding experiments with a pond population of *Keratella cochlearis* (upper panel) and diurnal changes in corresponding assimilation rates (lower panel).

PILARSKA 1977), no data on possible diurnal variations seem to exist. Therefore, we investigated AE in the course of feeding experiments on Keratella cochlearis. Except for the experiment in the early morning all experiments revealed similar values not significantly differing from the daily mean of 50.3 % (see Fig. 4 upper part). The maximum in early morning may have physiological reasons (corresponding to the onset of higher feeding activities during daytime), but this is only a speculation since comparable experiments are lacking. Additional experiments on K. cochlearis during winter showed mean AE values of 40.1° ₀. AE values for B. plicatilis in August were 22.9 %. In the course of these experiments no diurnal trend in assimilation efficiency was found. The values of AE for both species were in the range of values reported in literature. Direct comparisons with data from literature are difficult since the food quality and food concentration should have the most important influence on AE. Similar experiments on rotifers' AE in our laboratory using only ¹⁴C as a tracer resulted always in lower values than with the double tracer technique (Heerkloss & ARNDT unpubl.). Determinations of ¹⁴CO₂-excretion (precipitation method according to Sorokin 1968) showed that this may be largely due to respiration losses during feeding (ARNDT unpubl.).

Diurnal changes in the amount of assimilated food (relative feeding rates multiplied by the corresponding AE-values) indicated that the assimilated food is twice as high during daytime compared to the night (see Fig. 4, lower panel).

c) Influence of external factors

One important external factor which can influence feeding activity of rotifers in surface waters may be water temperature. It is well known that increasing temperatures within certain limits lead to increasing feeding rates. During our experiments diurnal changes in temperature (see Fig. 5) correspond to changes in feeding rate. But

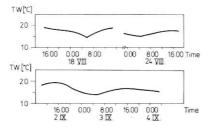


Figure 5. Diurnal changes in water temperature during in situ experiments with estuarine populations of *Brachionus plicatilis* and *Keratella cruciformis* f. *eichwaldi* (upper panel) and a pond population of *K. cochlearis* (lower panel).

since water temperature varied generally less than 5 °C, the more than twofold increase in feeding rate (even in the morning) cannot be explained by temperature variations alone. Light is known as an important stimulus of timing in vertical migration of planktonic crustaceans (e.g. Angel 1986). Little is known about the influence of light on behaviour of planktonic rotifers (e.g. Argal 1965, Preissler 1980). Our experiments on phototaxis of *Brachionus plicatilis* (Arndt unpubl.) showed positive phototaxis during the whole day. So the light could serve as a stimulus for higher activity of rotifers at the surface during daytime. Much more studies are necessary to clarify diurnal changes in rotifer activity. Possibly biotic interactions could have favoured a genetical fixation of ecologically advantageous feeding time (see below).

d) Ecological significance of daytime feeding in rotifers

Many studies regarding diurnal vertical migration of planktonic rotifers showed reverse migration (e.g. Pennak 1944, Burris 1980). It is very probable that, in the same way as in other zooplankters, migrational activity is linked with feeding activity. So one can conclude from the mostly daytime activity that daytime feeding is a more general behaviour. Our conclusion is supported by our own observations in the shallow eutrophic waters of the Darß-Zingst estuary, where rotifers showed highest abundances in the surface waters during daytime (1.2 times higher than during the night, p < 0.01; Arnot et al. 1984 b) corresponding to our results about feeding activity.

Several different theories concerning the adaptive significance of diurnal activity patterns of zooplankters have been discussed in literature (for review see BAYLY 1986, ANGEL 1986). We agree with the opinion of BAYLY (1986) that the diurnal pattern of activity "should be treated as having multiple causation and different major adaptive functions in different situations". In literature, most attention was given to the following factors (cf. Kerfoot 1986):

- 1. energetic and demographic advantage by daily migration into cooler water layers;
- coupling of cool-water metabolic advantage with migration timed to crop the daily peak of primary production;
- 3. light-dependent vertical migration to avoid visual predators;
- 4. avoidance of short-wave irradiation during day.

Those factors or explanations should be favoured in discussion which have the most striking effect on natality and mortality of the population under consideration.

Regarding natality of planktonic rotifer populations migrational activity as a matter of breeding concentration or searching for new habitats is of no meaning. And also the energy bonus by migrating into deeper cooler waters seems to be of no importance

for rotifers, which are inefficient migrators (cf. Epp & Lewis 1984). According to the hypothesis introduced by Enright (1977) it is advantageous for zooplankters to feed at the time of maximum assimilate content of algae in the evening. Unfortunately, this has seldom been tested experimentally (cf. Lampert et al. 1988). Our own experiments revealed that copepods (Eurytemora affinis) which were only allowed to feed during those hours of the day in which the content of fresh assimilates in algae is highest (afternoon) have higher (two-fold!) reproductive rates than copepods which were allowed to feed in early morning. This was mainly caused by higher assimilation efficiency of fresh assimilates (Arnot 1985, Arnot unpubl.). Probably this is the case in rotifers too. The tendency of higher feeding activity in the afternoon supports this interpretation.

Regarding mortality the well-founded predation hypothesis (ZARET 1980) can explain a large part of diurnal activity patterns in crustacean zooplankton. But rotifer loss rates induced by visually feeding predators are much lower than those of planktonic crustaceans. In eutrophic estuarine waters we found that only 8 per cent of annual mean rotifer production is consumed by visually feeding planktivores, whereas 27 per cent of copepod and 47 per cent of cladoceran production are lost via predation (ARNDT 1986). Loss rates smaller than 10 per cent should not limit rotifer production (cf. Hillbricht-Ilkowska & Pourriot 1970). But tactile predators such as cyclopoids and other aquatic arthropods, which are themselves influenced by visually feeding predators, have their maximum of feeding activity mostly during night. Recent results (e.g. Burns & Gilbert 1986) have shown that herbivorous planktonic crustaceans not only compete with rotifers for food but are also able to disturb and kill rotifers during their feeding process. Thus rotifer populations should have relatively lower or equal risk to be predated and disturbed when active during daytime compared to nighttime activity. Therefore, many rotifer populations can use the afternoon peak in phytoplankton assimilates without suffering from especially high predation pressure during that time.

It seems that the behaviour of rotifers supports the hypothesis that herbivores show reverse activity where primary carnivores are active during the night to avoid visually feeding secondary carnivores. This phenomenon has been observed by Ohman et al. (1983) for a zooplankton community in marine coastal waters. Since rotifers have to spend much energy for migration (EPP & Lewis 1984), they should not be able to perform strong downward migration as it is known for some planktonic crustaceans. Possibly passive sinking during night when light stimulus is lacking or a more random and probably reduced movement takes place leads to a slightly deeper population mean depth in most cases. Whether or not this behaviour can serve as a predator defense has to be studied in future. But from the knowledge regarding prev localization by tactile predators (e.g. Kerfoot et al. 1980) it is arguable that reduced activity of rotifers during night even when staying at or near the depth of daytime activity can work as an effective mechanism. This would be similar to the "dead-man" response described for small cladocerans (cf. Kerfoot et al. 1980). The body shape of nearly all planktonic rotifers which have no special appendages for escape or defense would support low sinking rates at the time of reduced activity to ensure low metabolic needs for later upward migration.

From the above discussion one can conclude that there should be time segregated niches of microphagous planktonic rotifers and crustaceans. Two examples from our own studies support this conclusion:

1.) During one set of experiments on feeding of *Brachionus plicatilis* in the Unterwarnow estuary (Rostock, G.D.R) feeding activity of the co-occurring calanoid copepod *Eurytemora affinis* was determined by the same procedure as for rotifers. Figure 6 shows that the time of feeding activity of both of the dominant microphagous species during that time is clearly segregated in the course of the day. Evening and night time

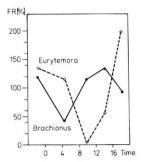


Figure 6. Comparison of diurnal changes in feeding activity of co-occurring populations of the rotifer *Brachionus plicatilis* and the calanoid copepod *Eurytemora affinis* in the Warnow estuary (100 % = daily mean value of the filtration rate of each species).

feeding activity seems to be a general phenomenon in *E. affinis* (cf. Heerkloss *et al.* 1984, Arnot 1985). Planktivorous predators at this time were investigated only qualitatively. Juvenile roach and stickleback were dominant planktivorous predators during the light period and *Megacyclops viridis* during the dark period. Gut content analysis of fishes at this time revealed preferential consumption of *Eurytemora* adults. Laboratory feeding experiments on *M. viridis* showed that this is a voracious predator on *B. plicatilis* (Arnot 1985).

Table 1. Diurnal changes in the percentage of food consumption by different groups of herbivorous and planktivorous pelagic animals in an estuarine shallow-water ecosystem of the southern Baltic (after values from Arndt et al. 1984 a and Arndt unpubl.)

functional groups	\mathbf{Day}	Night
Herbivores		
rotifers	25 %	$5^{-0}/_{0}$
calanoids and	75 %	95 %
cladocerans	, ,	
Planktivores		
mysids and fishes	$60^{-0}/_{0}$	$35^{-0}/_{0}$
cyclopoids	40 %	$65^{-0}/_{0}$

2.) Table 1 summarizes our results from ecosystem analysis in a shallow estuarine water south of the Darß-Zingst peninsula (for details see Arndt et al. 1984 a) indicating the same trend for higher activity of rotifers during day (accompanied by relatively lower grazing pressure) and relatively higher activity of microphagous crustaceans during night (also accompanied by relatively lower grazing pressure).

Figure 7 shows an attempt to generalize our observations and those from other authors about the relative diurnal changes in the composition of zooplankton communities in most other pelagic ecosystems. Nevertheless, even if rotifer populations show no diurnally varying feeding activity there seems to be no doubt, that during the dark the relative importance of planktonic crustaceans within the grazer community is—as a rule—much greater than that of rotifers. According to Fig. 7 one can distinguish between a food chain or a part of the food web which is more important during day-time and another food chain or another part of the food web which is more important during the night. This is similar to the observations that had been published on terres-

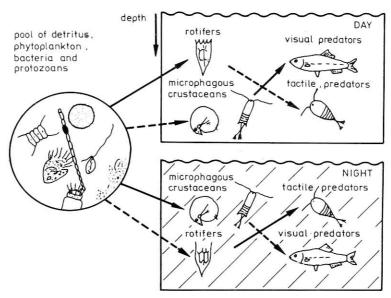


Figure 7. Hypothesis of day and night time segregated niches within microphagous metazooplankton in pelagic ecosystems (arrows with continuous lines indicate interactions of relatively higher importance).

trial ecosystems (REMMERT 1969, 1976). But it seems that overlapping in diurnal activity patterns in pelagic ecosystems is much more pronounced.

Time segregated feeding of different zooplankton groups should also have some influence on diurnal interactions between zooplankters and their food particles. Mc Allister (1970) showed in a model that phytoplankters which are grazed during the photosynthetically inactive dark hours have higher production rates than phytoplankters which are continuously grazed. Thus feeding of rotifers during daytime on the smaller but more productive nanoplankton fraction vs. crustacean night feeding on the larger nanoplankton can work as a balancing mechanism between smaller and larger nanoplankton.

4. Conclusion

Our experiments on diurnal feeding activity of three species of rotifers all showed about two times higher feeding rates during day than during night. Though further studies are required, our results indicate the importance of diurnal variations in determinations of rotifer feeding activities and calculations of daily feeding rates, respectively. Furthermore, the analysis of pelagic food webs points to the existence of daytime restricted niches within the pelagic community. The relatively higher feeding activity of rotifers during the day and crustaceans during the night can be well explained by the diurnal changes in food quality and predation pressure. Perhaps our results, though only preliminary, can stimulate more research regarding rotifer activity to get more insight into diurnal interactions within the pelagic zone.

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