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DIURNAL CHANGES IN THE MATTER FLUX OF A SHALLOW-WATER ECOSYSTEM IN A BALTIC INLET

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ABSTRACT

In contrast to well investigated seasonal changes in the matter flux of aquatic ecosystems, our knowledge of diurnal changes is rather limited. Our preliminary investigations into the diurnal variation of the matter flux were carried out on an animal community (incl. rotifers, crustaceans, juv. fishes) of a shallow water in the Darss-Zingst estuary (southern Baltic), by determining the standing stocks and feeding rates. Grazing pressures on the pool of bacteria, phytoplankton, protozooplankton and detritus and on the zooplankton pool varied considerably in the course of a day. The percentage of the total ration consumed by individuals of a single species also showed remarkable diurnal variation. The diurnal changes in the direction of matter flux were caused mainly by variations in the standing stocks of producers and consumers due to migration and irregular changes in hydrographic conditions and by diurnal changes in specific rates of production and consumption. In view of the diurnal variations in the rates of production and reproduction by the phytoplankters and zooplankters respectively, the impact of predation on specific species should depend on the time of predation. Both migrational behaviour and diurnal changes in consumption rates could act as effective niche separation mechanisms in plankton communities.

INTRODUCTION

The structure and function of aquatic ecosystems are generally characterized by daily mean values for standing stocks and conversion rates. Nobody would ignore seasonal changes in ecosystem analysis, but diurnal variations are sometimes overlooked despite their rather similar amplitudes of fluctuation in abiotic and biotic factors. This probably reflects the fact that ecologists prefer working during the daytime. Elton (1927) already stimulated the discussion on day and night rhythms in ecosystems. Remmert (1969, 1976) demonstrated that completely different food chains could exist in one and the same biotope at different times of the day. Several investigators (e.g. Magnus 1964, Fischer & Rosin 1968) reported on daytime specific species interactions in aquatic ecosystems. For marine plankton McAllister (1970) stated that its production depends on diurnal patterns in the feeding activity of herbivorous zooplankton. In the course of the ecosystem analysis of the Barther Bodden it therefore seemed necessary to study the diurnal changes in the food web of the plankton. This report presents the results of preliminary studies on a littoral plankton community.

We are thankful for valuable comments by Prof. H. Remmert.

MATERIALS AND METHODS

The study area (0.5 m depth) is situated on the western shore of the Barther Bodden, a typical estuary of the southern Baltic (see Fig. 1). Our investigations were carried out during a 48-hour period from the 8th to the 10th of June 1982. Diurnal fluctuations in some environmental parameters are shown in Fig. 2. All parameters, including standing stocks and consumption rates of fishes, were determined every two hours. Zooplankton was collected by integrated sampling (cf. Arndt *et al.* 1981, Vietinghoff *et al.* 1984). Abundances and individual lengths were measured in subsamples (stamp pipette) under a microscope (51 ×, 160 ×). Bio-volumes were calculated according to Bottrell *et al.* (1976). Fishes were caught by 8 simultaneously working traps (each 1 m^2) in order to determine abundance and species composition. Length/weight relationships (Debus, unpubl.) were used to calculate individual wet weights. All wet weights were converted to mg C · $ind.^{-1}$ according to Heerkloss & Vietinghoff (1981). The absolute feeding rates were calculated by multiplying the species abundance and the specific feeding rate. Unfortunately, data on diurnal changes in specific feeding rates of zooplankters are rather rare in literature. Only Nauwerck

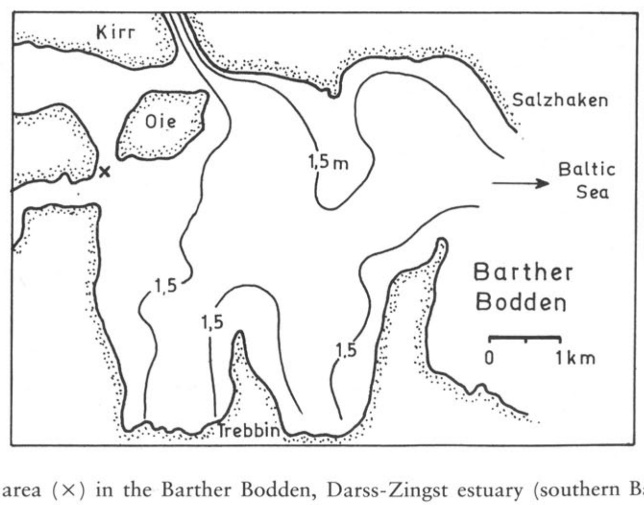

FIG. 1. Study area (×) in the Barther Bodden, Darss-Zingst estuary (southern Baltic, G.D.R.).

(1959) has reported on diurnal feeding rhythms of rotifers, for example. Our studies on natural populations of *Brachionus plicatilis* (O.F. Müller) and *Keratella cochlearis* (Gosse) revealed that both have their maximum feeding rates in the early afternoon (Arndt in prep., ^{14}C method). Mean values from these studies were used here (cf. Fig. 3A). The means yielded by several experiments were available for *Eurytemora* sp. (Fig. 3C) (cf. Heerkloss *et al.* 1981, ^{14}C method). Cladocerans seem to feed more intensively during the night (e.g. Haney & Hall 1975). We determined the feeding rates of *Chydorus sphaericus* (O.F. Müller) only in the morning. It was assumed that their feeding rate is twice as high during the night (Fig. 3B). The daily mean values given by Monakov & Sorokin (1959) were used for *Megacyclops viridis* (Jurine) since little is known regarding the diurnal feeding rhythms of cyclopoids. The feeding rhythms of juveniles of *Gasterosteus aculeatus* L. and *Rutilus rutilus* (L.) were also studied during the investigation period (the means for both days are given

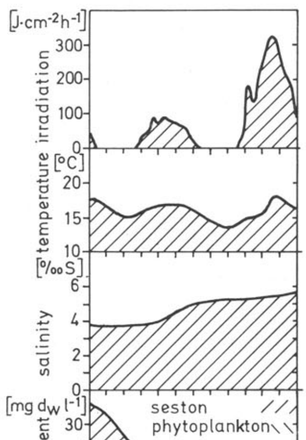

FIG. 2. Diurnal variations in some abiotic and biotic parameters during the investigation period (8.-10.6.1982, all times in Middle European Time).

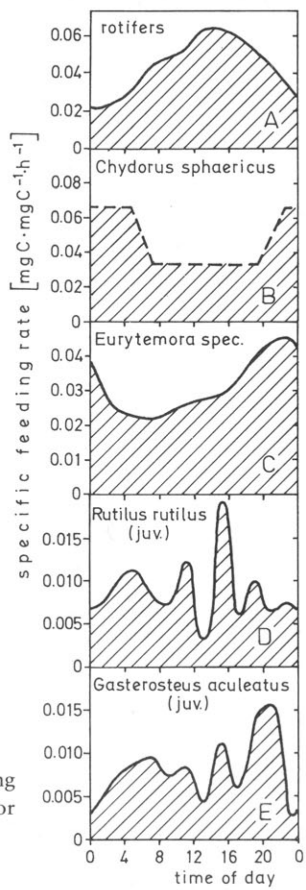

FIG. 3. Diurnal changes in specific feeding rates of zooplankters and juvenile fishes (for details, see text).

in Fig. 3D & E). Gut contents (n = 10-20) were analysed for dominant size classes, and the speed of digestion was measured as described by Boruzki *et al.* (1974). Mysids were not investigated in the course of this study. Mean values for June (Fig. 7) were taken from Jansen *et al.* (1983).

RESULTS AND DISCUSSION

The results for the diurnal variations in standing stocks and absolute feeding rates are summarized in Fig. 4 (A, B). The dominant rotifer species were *Brachionus quadridentatus* (Hermann), *B. calyciflorus* (Pallas), *Filinia longiseta* (Ehrenberg) and *Keratella* spp. Their abundances increased until the end of the experiment due to water currents from central parts of the estuary which carried high abundances of *B. quadridentatus*. *Chydorus* lived in closer contact with the substrate during the daytime and joined the plankton during the night. It was the most important consumer among the zooplankters. *Eurytemora* (mainly adults of *E. affinis* (Poppe) with most features of the *hirundoides* form) showed higher abundances during twilight. This species migrates both vertically

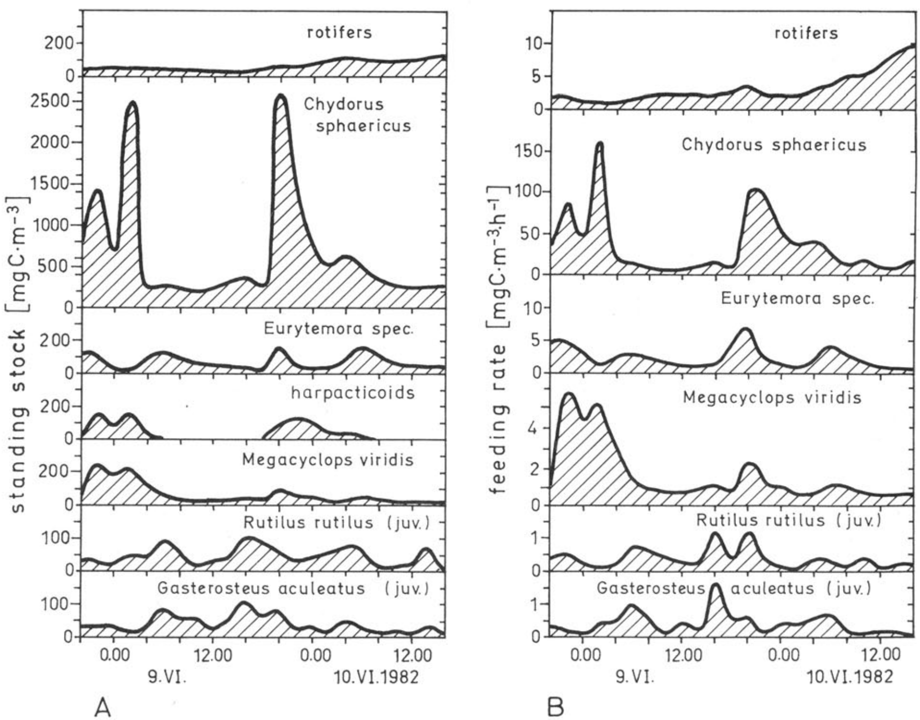

FIG. 4. Diurnal variations in standing stocks (A) and absolute feeding rates (B) of dominant zooplankters and fishes.

and horizontally (Arndt, unpubl.). Harpacticoids ascend from the sediment during the dark hours (cf. Arndt *et al.* 1982), but, since little is known of their feeding behaviour at night, they were excluded from further discussion. The typical littoral cyclopoid *Megacyclops viridis* (Jurine) (mainly cop. IV-VI) seemed also to live in closer contact with the substrate during the daytime. The older stages of this species are known to be mainly carnivorous. The fishes were represented in significant biomasses only by juveniles (L_t = 10-15 mm) of *Rutilus rutilus* and *Gasterosteus aculeatus*, respectively (cf. Bast *et al.* 1980). Diurnal variations in abundances were caused by different rates of immigration and emigration into and out of the investigated area. The distinct feeding maxima observed for both species and both days during the daytime confirm the studies published by several authors (e.g. Lebedewa & Grigorasch 1978, Worgan & FitzGerald 1981).

Like those of other authors (e.g. Mackas & Bohrer 1976, Huntley & Brooks 1982), our studies indicated that diurnal changes in feeding activity correspond to changes in migrational activity. We conclude that the effect of diurnal vertical

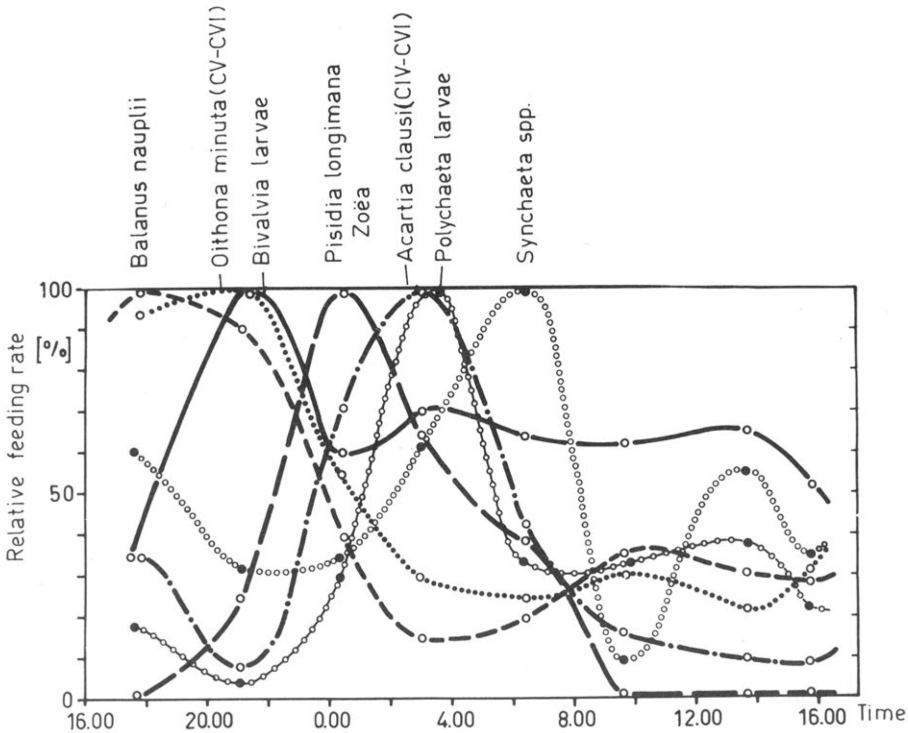

FIG. 5. Diurnal changes in consumption rates of different zooplankton populations in a coastal water of the Black Sea (0-10 m depth). The daily maximum of the feeding rate (ml · m^{-3} · h^{-1}) of each group corresponds to 100% (*in situ*-technique by means of ^{14}C-tracer algae, after Arndt, in press).

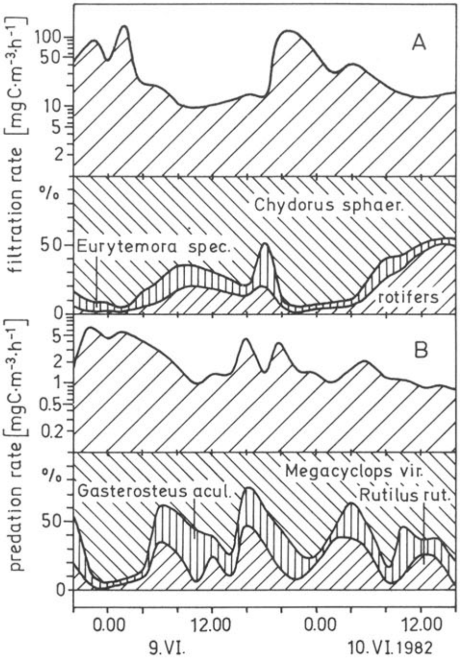

FIG. 6. Diurnal variations in filtration rate (A, incl. rotifers, *Ch. sphaericus, Eurytemora* sp.) and predation rate (B, incl. *M. viridis, G. aculeatus, R. rutilus*) (upper graphs) as well as in the percentage of the total ration consumed by single species (lower graphs).

migration as a niche separation mechanism in plankton (cf. Lane & McNaught 1970) is supported by diurnal changes in specific consumption rates. Similar results were obtained during comparative studies in the Black Sea (see Fig. 5).

Fig. 6 summarizes the consumption rates of filtrators and predators. It is evident that the grazing pressures on both the detritus-phytoplankton pool (incl. bacteria and protozooplankton) and the zooplankton pool changed considerably in the course of a day. The percentage of the total ration consumed by individuals of a single species also showed remarkable diurnal variations. Among filtrators *Chydorus* was the most effective filtrator during the night, while the importance of *Eurytemora* and the rotifers increased during the daytime. Of predators, the dominant night feeder was *Megacyclops*, whereas fishes fed most intensively during the hours of daylight. It should be considered that quantitative effects for the matter flux could be caused by seasonal changes in day lengths (in temperate and arctic regions) which influence the duration of feeding periods of consumers (Remmert, pers. comm.).

According to McAllister (1970), phytoplankton production depends on the diurnal feeding rhythms of herbivores. Since the herbivorous zooplankters found in our study area differ in terms of food selectivity (cf. Spittler 1976, Heerkloss 1979), the grazing impact on each phytoplankton species varies in the course of a day. Those phytoplankton species which are consumed out of their 'optimal time of being grazed' (night) would get some disadvantage for their population development. On the other hand it is known that brood release of zooplankters could differ in the course of a day (cf. Wimpenny 1938, Marshall & Orr 1955, Arndt unpubl.). Recent studies on rotifers and cladocerans (e.g. Ruttner-Kolisko 1978, Keen 1979) showed that diurnal changes in water temperatures influence the time and the amount of egg production (for a summary of this phenomenon see Hoffmann 1980). Predation during the time of highest egg ratios will have a more pronounced negative effect on zooplankton recruitment than predation at lowest egg ratios. Thus the impact of predation on specific zooplankters, too, should depend on the time of predation.

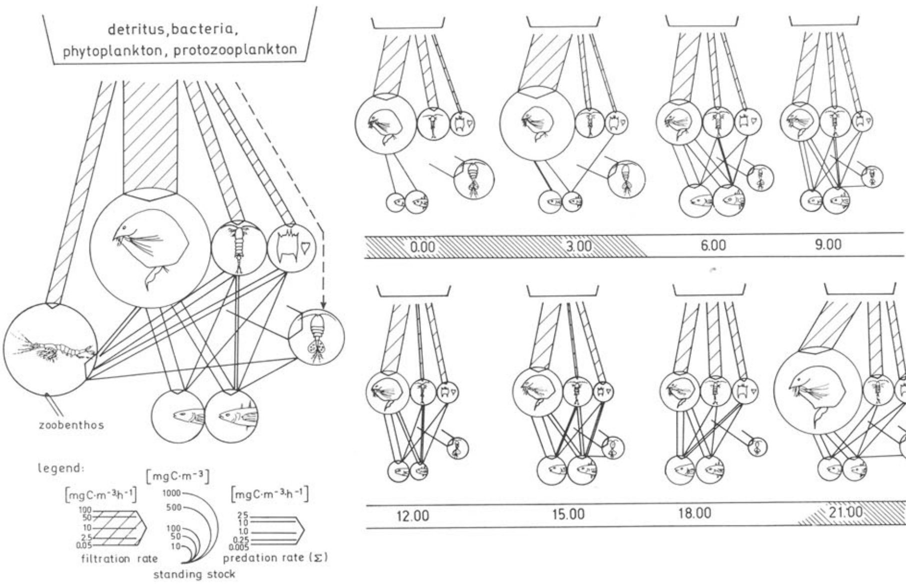

FIG. 7. Matter flux in a littoral plankton community of the Darss-Zingst estuary (June 9th, 1982). Daily means (left side, double scale) and diurnal changes (right side, mysids were not investigated) are shown.

The diurnal variations in the dominant paths of the matter flux through this littoral zooplankton community are demonstrated for June 9th in Fig. 7. Obviously the daily means (left side, *Neomysis* parameters for the study area from Jansen *et al.* 1983) give no impression of the real interactions between populations in the course of a day (right side).

Despite our assumptions and the possible inaccuracies in our determination of standing stocks and conversion rates, the remarkable diurnal changes in the matter flux of the investigated part of the ecosystem stress the importance of the daytime aspect for the analysis of the structure and function of aquatic ecosystems.

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