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Spatial and temporal patterns of lake outlet benthos

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With 6 figures and 1 table in the text

Introduction

Lake-outlet streams are known to have high abundances and biomass of invertebrates (MÜLLER 1955; CUSHING 1963; MACIOLEK & TUNZI 1968; CARLSSON et al. 1977; SHELDON & OSWOOD 1977; STATZNER 1978; OSWOOD 1979). Lake-outlet communities are typically dominated by a filter-feeding guild, which benefits from the large output of seston from the lake. The influence of the lake on the benthos decreases with the distance from the lake and SHELDON & OSWOOD (1977) have shown that the decrease in numbers of filter-feeders follows a power function.

In this study the spatial and temporal patterns of the benthic invertebrates along a South Swedish lake outlet were investigated and related to abiotic factors.

Material and methods

The study was performed in the River Klingavälsån, the outlet of the eutrophic Lake Sövdesjön (Fig. 1). The benthic macroinvertebrates were sampled 7 times, viz. Nov 1978, Feb, May, Jun, Aug 1979, Mar, Jul 1980. At each of the 9 stations (A-I, Fig. 1) 10 samples were taken in each of four transects along 10 m of the river with a core sampler (area: 24 cm², depth: 15 cm). The samples were preserved in 70% alcohol. Dry weight was determined after drying at 60 °C for 24 h (molluscan dry weights are without shells). All animals were classified into trophic categories (see MALMQVIST & BRÖNMARK 1984 for details). Sediment samples (50 per station) were taken with a smaller core

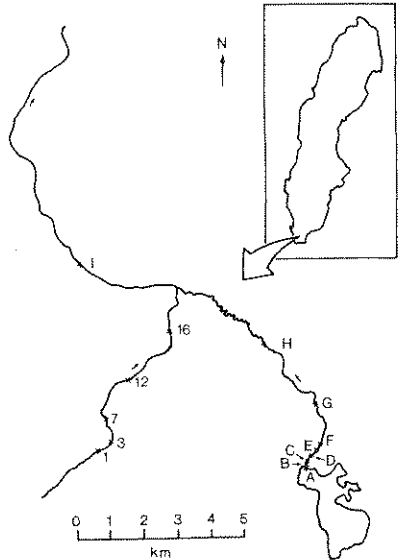


Fig. 1. Map of the investigation area.

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Patterns of lake outlet benthos

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Introduction

Abundances and biomass of invertebrates (MÜLLER, ARLSSON et al. 1977; SHELDON & OSWOOD 1977; Malmqvist et al. 1984) are typically dominated by a filter-feeding fauna near the lake. The influence of the lake on the distribution of invertebrates (SHELDON & OSWOOD 1977) have shown that a power function, $N_D = aD^{-b}$, where N_D is density, D the distance from the lake, respectively, and a and b are constants.

Methods

The outlet of the eutrophic Lake Sövedsjön was sampled 7 times, viz. Nov 1978, Feb, May, Jun, Aug, and Dec 1979. In each of four stations (Fig. 1) 10 samples were taken in each of four trophic categories (see MALMQVIST & OSWOOD 1984) (molluscan dry weight) were taken with a smaller core

sampler (area: 4.5 cm²) designed to take the top 3 cm of the sediment. Organic content was determined after combustion at 550 °C for 2 h. Water samples were taken and chlorophyll-*a* analysed (LORENZEN 1967). The chlorophyll-*a* values were scaled to percentages of the value of station B. The distribution patterns of selected species were fitted to a power function (SHELDON & OSWOOD 1977): $N_D = aD^{-b}$, where N_D is density, D the distance from the lake, respectively, and a and b are constants.

Results

The chlorophyll-*a* concentrations showed two temporal peaks, a spring peak in April–May and a second, higher one, in July (Fig. 2). In months with a chlorophyll-*a* concentration > 30 mg · m⁻³ there was a significant decrease with the distance from the lake (Fig. 3). Oxygen content was at a minimum before ice break-up with a saturation value of 47% at the lake outlet.

The abundance and biomass of the dominant trophic guilds in relation to the distance from the lake are presented in Fig. 4. The density and biomass of filter-feeders and scrapers and the biomass of predators decreased with the distance from the lake, while deposit-feeders showed a bimodal distribution peaking at stations A and G. Filter-feeders, mainly *Unio pictorum* and *Anodonta piscinalis* made up the bulk of the biomass throughout the year, but had a minimum, together with scrapers, in the summer (Fig. 5). The densities of selected guilds and species provided significant negative correlations with the distance from the lake (Table 1), except for *Gammarus pulex* which increased downstream.

The abundance of deposit-feeders showed no significant correlation with the organic content of the sediment ($P > 0.05$).

Net-spinning trichopterans showed a succession of species along the river (Fig. 6). *Holocentropus dubius* occurred in low numbers just at the lake outlet, gradually replaced by *Neureclipsis bimaculata*, *Hydropsyche angustipennis*, *H. pellucidula*, and *H. siltalai*, respectively.

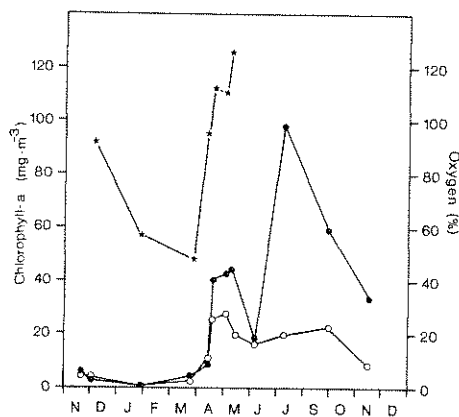


Fig. 2. Chlorophyll-*a* concentrations at stations A (solid dots) and E (open dots), and oxygen saturation at B (asterisks).

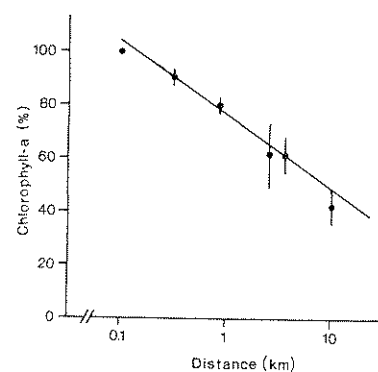


Fig. 3. Chlorophyll-*a* concentrations as a function of the distance from the lake. The concentration is given as percentages of this at station B. Vertical bars indicate S.D.

Map of the investigation area.

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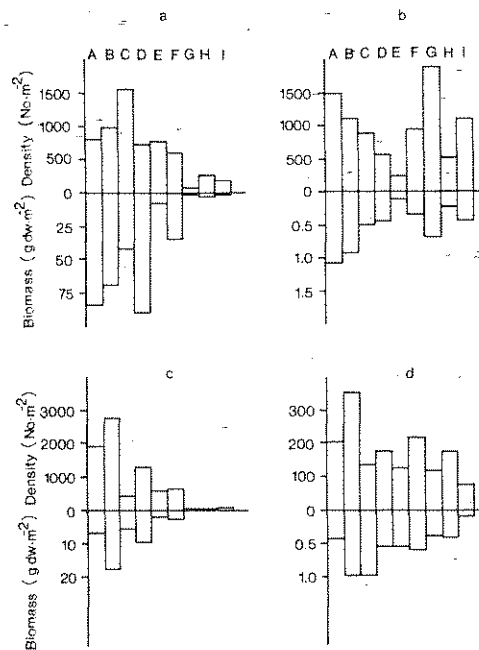


Fig. 4. Abundance and biomass of trophic guilds in relation to the distance from the lake: a) filter-feeders, b) deposit feeders, c) scrapers, d) predators.

Table 1. Correlation coefficients and the constant a in the power function $N_D = aD^{-b}$ for some selected species and trophic guilds as well as for the whole community. All coefficients have been calculated on number of individuals except for filter-feeders, which have been calculated also for biomass.

Species/Guild	r	a
All animals	-0.25	-1.38
Filter-feeders	-0.52	-0.53
Filter-feeders (biomass)	-0.82	-1.03
<i>Unio pictorum</i>	-0.84	-1.02
<i>Neureclipsis bimaculata</i>	-0.54	-0.88
<i>Bithynia tentaculata</i>	-0.81	-1.66
<i>Chironomus plumosus</i>	-0.78	-1.56
<i>Erpobdella octoculata</i>	-0.77	-0.89
<i>Gammarus pulex</i>	0.49	0.70

Discussion

The high density and biomass of invertebrates, especially filter-feeders, at the lake outlet of Sövedsjön and the subsequent decrease downstream are in accordance with the general idea of the functioning of a lake outlet (see e.g. MÜLLER 1955; MACIOLEK & TUNZI 1968; SHELDON & OSWOOD 1977). In these previous studies insect larvae were found to dominate the filter-feeding guild in contrast to the present investigation in which unionid mussels dominated.

The power function, which predicts the decrease of filter-feeders with the distance from the lake, gives a good fit to the distribution of *Unio pictorum*. As a consequence the fit of the biomass of filter-feeders as a guild is also good, since unionids by far dominate

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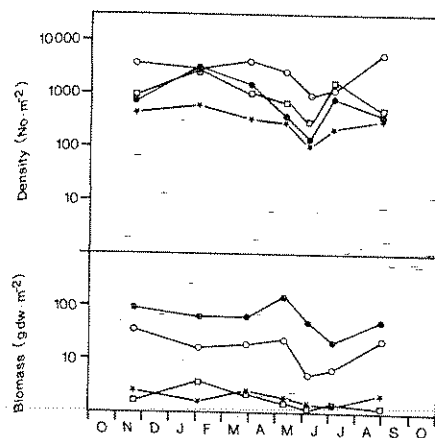


Fig. 5. Temporal patterns in density and biomass of the different trophic guilds: filter-feeders (solid dots), scrapers (open dots), deposit feeders (squares), and predators (asterisks) at station B. The data derive from sampling performed from Nov 1978 to Aug 1979 except for those from Mar and Jul which date from 1980.

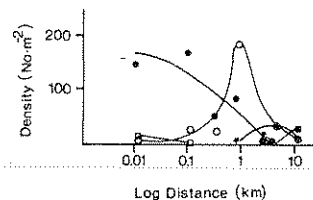


Fig. 6. The densities of different filter-feeding caddis larvae as a function of the distance from the lake. Solid dots: *Neureclipsis bimaculata*, open dots: *Hydropsyche angustipennis*, asterisks: *H. pellucidula*, solid squares: *H. siltalai*, open squares: *Holocentropus dubius*. Curves were fitted by eye.

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the total biomass. The abundance of filter-feeders, however, yields a lower correlation coefficient, possibly because their distribution is influenced also by biotic interactions (see below).

The distribution of *Bithynia tentaculata* and *Chironomus plumosus*, both facultative filter-feeders (TASHIRO & COLMAN 1982; McLACHLAN & CANTRELL 1976), provides a fairly good fit to the power function. This is also true for the predator *Erpobdella octoculata*, probably because of the decline in prey density (mainly chironomids) with distance. Increasing downstream, *G. pulex* constitutes a notable exception to the general pattern.

The declining number of filter-feeders downstream a lake has been assumed to be caused by decreasing seston concentrations. However, several authors have failed to demonstrate a negative correlation of seston with the distance from the lake (CARLSSON et al. 1977; SHELDON & OSWOOD 1977; OSWOOD 1979). These authors suggested that the main factor affecting the invertebrate distribution was the quality of the seston, not the quantity. In the River Klingavälsån the POC concentrations showed no significant decrease with distance in the first 600 m downstream the lake (t-test, $P > 0.05$, BRÖNMARK & MALMQVIST unpubl.). However, the chlorophyll-*a* concentrations, which could be regarded as an approximation of seston quality, declined with the distance (Fig. 3).

Not only the availability of food influences the distribution pattern of a species. BRÖNMARK & MALMQVIST (1982) suggested that biotic interactions partly influenced the distribution of unionids in the River Klingavälsån. Net-spinning caddis larvae showed a successional pattern in this lake outflow with *N. bimaculata* dominant near the lake, replaced further downstream by hydropsychid species. Net-spinning caddis larvae have been reported to be spatially separated along rivers, a pattern suggested to be caused by

differences in e.g. temperature and seston particle size distribution (HILDREW & EDINGTON 1979; GEORGIAN & WALLACE 1981; ROSS & WALLACE 1983).

The decrease in density and biomass during the summer probably has several explanations. The changes in unionid bivalves may reflect the seasonal migrations in connection with mating (HAUKIOJA & HAKALA 1974). Also other taxa show seasonal migration between microhabitats. This is the case of *B. tentaculata* and *N. bimaculata* (BRÖNMARK unpubl.) which are found in the benthos during the winter, but migrate to the vegetation during the spring and summer. In this study no sampling was performed in the vegetation. The flight periodicity of insects also influences the density and biomass of the lake outlet benthos.

In conclusion, the lake outlet is a very productive habitat with high concentrations and quality of food. The change in food quality, rather than quantity, downstream the lake influences the distribution patterns of benthic invertebrates. Moreover, in the very dense populations, biotic interactions, e.g. competition for space (cf. BRÖNMARK & MALMQVIST 1982), are likely to affect the distribution.

Acknowledgements

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