The drift of zooplankton and microzoobenthos in the river Strandaelva, western Norway*

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Abstract

The drift of zooplankton (rotifers, cladocerans, cyclopoid copepods) and microscopical zoobenthos (mainly bdelloid rotifers and small chironomid larvae) was investigated by filtering samples of river water. The number of drifting benthic rotifers varied between 1 000 and 6 000 ind. m^{-3} in the lake inlet, and between 30 and 500 ind. m^{-3} in the lake outlet, without any seasonal trend. The number of drifting insect larvae was approx. equal in the lake inlet and outlet, with a maximum in summer (250–300 ind. m^{-3}) and minimum in winter (*ca.* 10 ind. m^{-3}). Increasing water flow resulted in an increasing number of drifting zoobenthos. Downstream from the lake, the number of drifting benthic rotifers was increasing from approx. 300 ind. m^{-3} in the outlet to 6 500 ind. m^{-3} 3.4 km downstream, while the number of insect larvae was *ca.* 100 ind. m^{-3} in the outlet and leveled off at approx. 300 ind. m^{-3} after 200 m. The number of drifting zooplankton in the lake outlet varied between 20 and 2 000 ind. m^{-3} for crustaceans, and between 300 and 20 000 ind. m^{-3} for rotifers, both with a maximum in late summer/autumn and a minimum in winter. The number of drifting zooplankton decreased by some 45% in the first 200 m from the lake outlet, but some zooplankton was still found in the drift 3.4 km downstream. The largest species was removed first from the drift. The diurnal variation in the number of drifting zooplankton in lake outlets appear to be related to the vertical migration in the lake, i.e. the largest number drifting when most animals are in the upper water layers.

Introduction

Running water is always transporting organic matter, both in a dissolved and in a particulate form. Part of the particulate organic matter is made up of animals, either of terrestrial, planktonic, or benthic origin. Several authors have analysed the drift of macroinvertebrates in rivers (review in Hynes 1970). Relatively few authors, however, have examined the drift of zooplankton and microscopical zoobenthos, although it has long been realized that this is an important source of food for filter-feeding invertebrates and small fish in the rivers (i.e. Illies 1956; Nilsson 1957; Clifford 1972; Lillehammer 1973).

The microdrift consists of zooplankton and microscopical zoobenthos (lees than 2 mm in size). In rapidly running rivers, the drifting zooplankton must be considered allochthonous, originating in lakes or other bodies of stagnant water in the catchment area (Brehm 1911). This means that it is possible to know the exact point of origin of the zooplankton in a drift sample. In contrast to this, the place of origin of the zoobenthos in the drift can be anywhere on the river bed or on the bottom of lakes upstream from the point of sampling. This difference might be used when analysing the factors affecting the number of animals in the microdrift samples.

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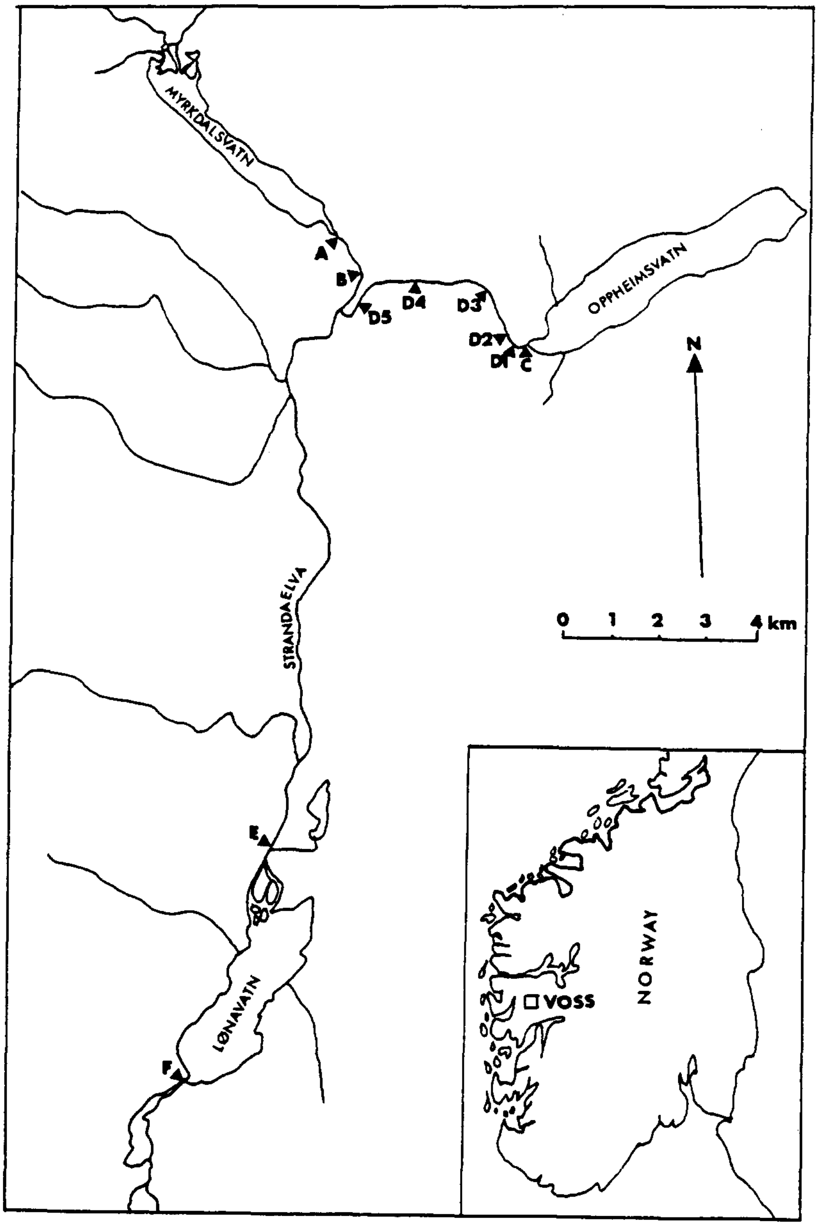

Fig. 1. The river Strandaelva, Voss, Western Norway, with sampling stations (A–F) indicated.

The aim of the present paper is to discuss the transport of zooplankton and microscopical zoobenthos in the river Strandaelva, Voss, western Norway, and the factors affecting this microdrift.

Sampling area

The river Strandaelva (Fig. 1) is part of the Voss River system, western Norway, which has been described in some detail by Matzow *et al.* (1976) and Faafeng *et al.* (1978). The present investigation was carried out in the part of Strandaelva situated between the lakes Myrkdalsvatn (alt. 230 m a.s.l.), Oppheimsvatn (alt. 337 m a.s.l.) and Lønavatn (alt. 77.5 m a.s.l.). This part of the river is usually narrow, with a fast current. The following sampling localities have been used during this investigation:

St. A: lies at the outlet of the lake Myrkdalsvatn, which is a deep, oligotrophic lake with short renewal time (Hauge 1957). At st. A the river is approx. 10 m wide, with a current speed above 1 m s^{-1}. The river bed consists of gravel and stones, mostly covered by *Fontinalis. St. B:* 650 m downstream from st. A. The river is somewhat wider and shallower than at st. A, but otherwise similar. *St. C:* lies at the outlet of the lake Oppheimsvatn. This lake is more nutrient rich than Myrkdalsvatn, mainly due to a longer renewal time and more agricultural land in the surroundings. At st. C the river is approx. 10 m wide with a current speed of *ca.* 0.7 m s^{-1}. The substratum consists of gravel and some stones, with some scattered tufts of *Fontinalis. St. D1:* is situated approx. 200 m downstream from st. C. The river is very similar to st. C, except for a somewhat higher current speed, and some large blocks in the substratum. The stations D2, D3, D4 and D5 are situated 600 m, 1 100 m, 2 100 m, and 3 400 m downstream from st. C, respectively. On this stretch the river is quite homogeneous, and similar to the appearance described for st. D1. *St. E:* is situated approx. 250 m upstream from the lake Lønavatn. The river is about 30 m wide, and the surface current speed is 0.5–0.7 m s^{-1}. The substratum is made up from gravel and some scattered stones. Approx. 50% of the river bed is covered by *Fontinalis. St. F:* lies at the outlet of lake Lønavatn, which is an oligotrophic and shallow lake with rapid water renewal (Matzow *et al.* 1976; Jonsson 1977). At st. F the river is approx. 25 m wide, and the current speed usually exceeds 0.7 m s^{-1}. The river bed is completely covered by *Fontinalis, Potamogeton* and *Callitriche.*

Methods and materials

Drift samples were taken by filtering five parallell samples of 25 l stream water through filters with mesh size 20 μm. The organisms collected were killed with boiling water, and fixed and kept on 4% formaldehyde until counting. The samples were examined and counted under a stereoscopic microscope and, in cases of doubt, the animals were identified under a compound microscope.

The sampling was done in the river Strandaelva from August 1973 through October 1974. Samples were taken at least once a month on stations E and F, more seldom on the other localities. A further description of material and methods is given in Matzow *et al.* (1976) and Sandlund (1977).

Results and discussion

The composition of the microdrift

The animals of the microdrift were mainly of planktonic and benthic origin, although a few terrestrial groups were also caught in the samples, e.g. Collembola and some winged insects.

The dominant benthic groups in the microdrift were rotifers and insect larvae. The rotifers were mainly of the order Bdelloidea, although individuals of the order Monogononta also appeared in significant numbers (e.g. *Lecane, Cephalodella*). The insect larvae were mainly small instars of the chironomid subfamilies Diamesinae and Orthocladinae.

The zooplankton in the microdrift were dominated by rotifers, the most important genera being *Polyarthra, Keratella, Kellicottia, Synchaeta* and *Conochilus.* Of the crustacean zooplankton, the cladocerans *Bosmina longispina, Daphnia longispina* and *Ceriodaphnia quadrangula* and nauplii and copepodids of cyclopoid copepods were common in the drift samples. A detailed account of the composition of the microdrift in Strandaelva is given in Matzow *et al.* (1976) and Sandlund (1977). The zooplankton fauna of the three lakes supplying organisms to the microdrift in Strandaelva is described by Nilssen (1975, 1976) and Synnes (1982).

Zoobenthos in the microdrift

As shown in Fig. 2, the number of benthic rotifers in the drift into and out of the lake Lønavatn varies considerably from one month to the next, but no seasonal trend can be found. However, the number of drifting insect larvae (mainly small chironomids) shows a clear maximum in the summer at both localities (Fig. 3). The reason for this is probably that the number of newly hatched chironomid larvae is at its maximum in the summer. It can be noted that while there is no marked difference between the average number of insect larvae drifting into and out of the lake (Fig. 3), the number of drifting benthic rotifers is approximately one order

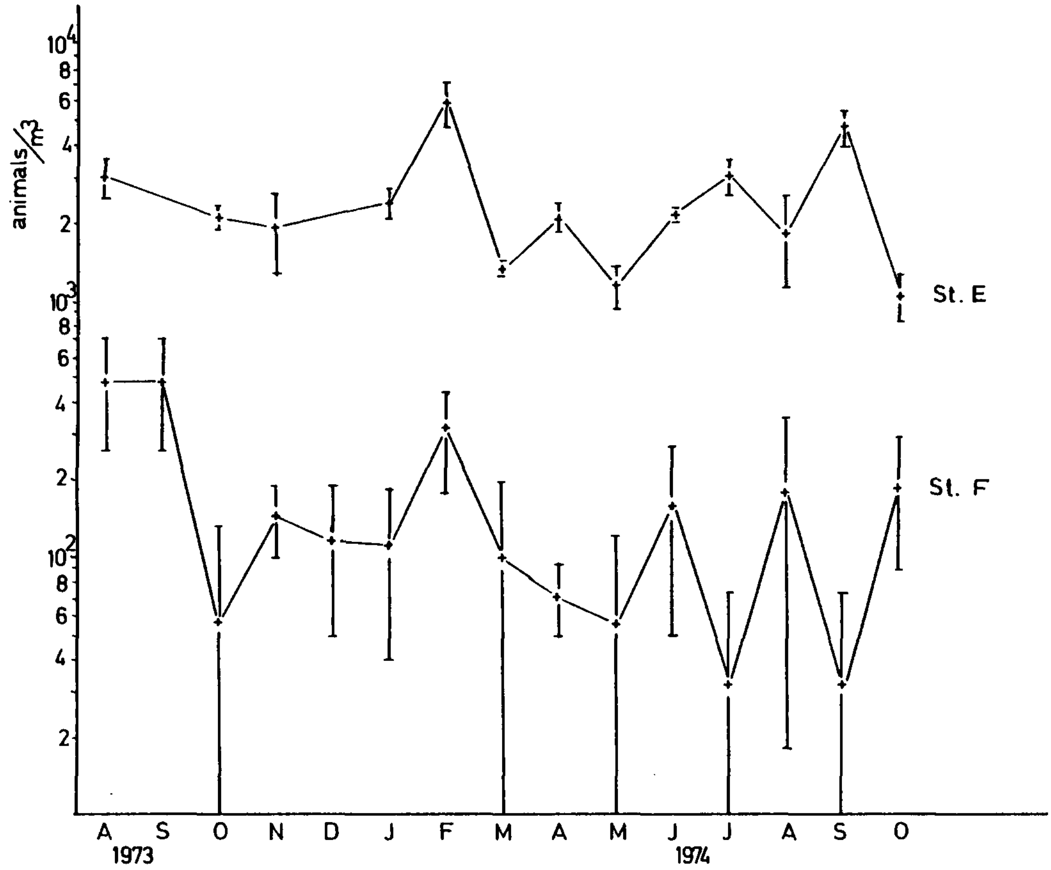

Fig. 2. The concentration of benthic rotifers in the drift in the inlet (st. E) and the outlet (st. F) of the lake Lønavatn, between August 1973 and October 1974. Vertical lines indicate 95% confidence limits.

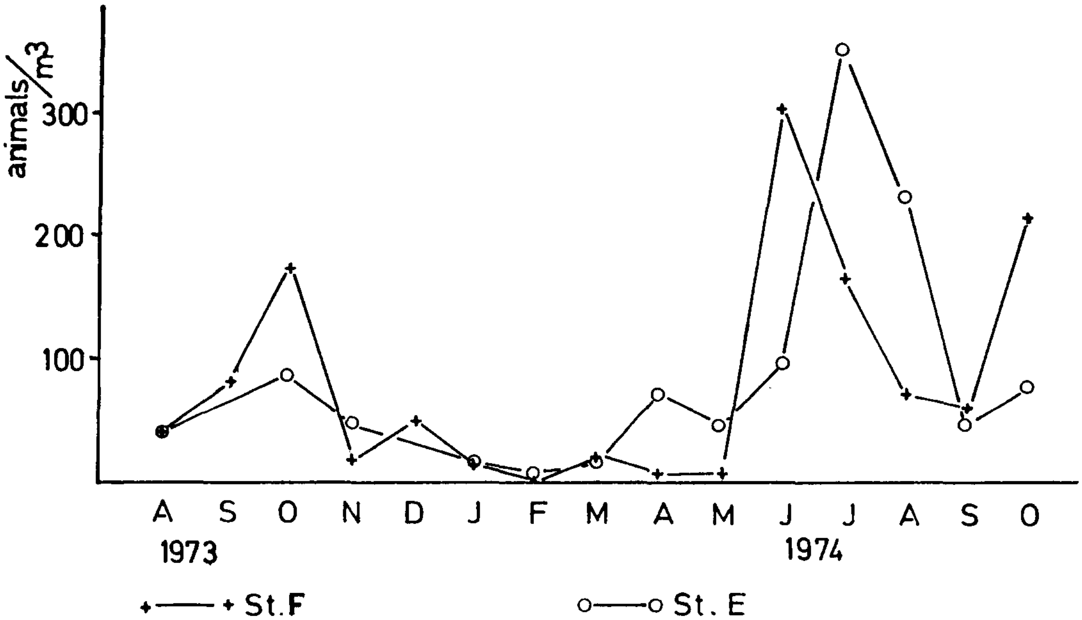

Fig. 3. The concentration of insect larvae in the drift into (st. E) and out of (st. F) Lønavatn, between August 1973 and October 1974.

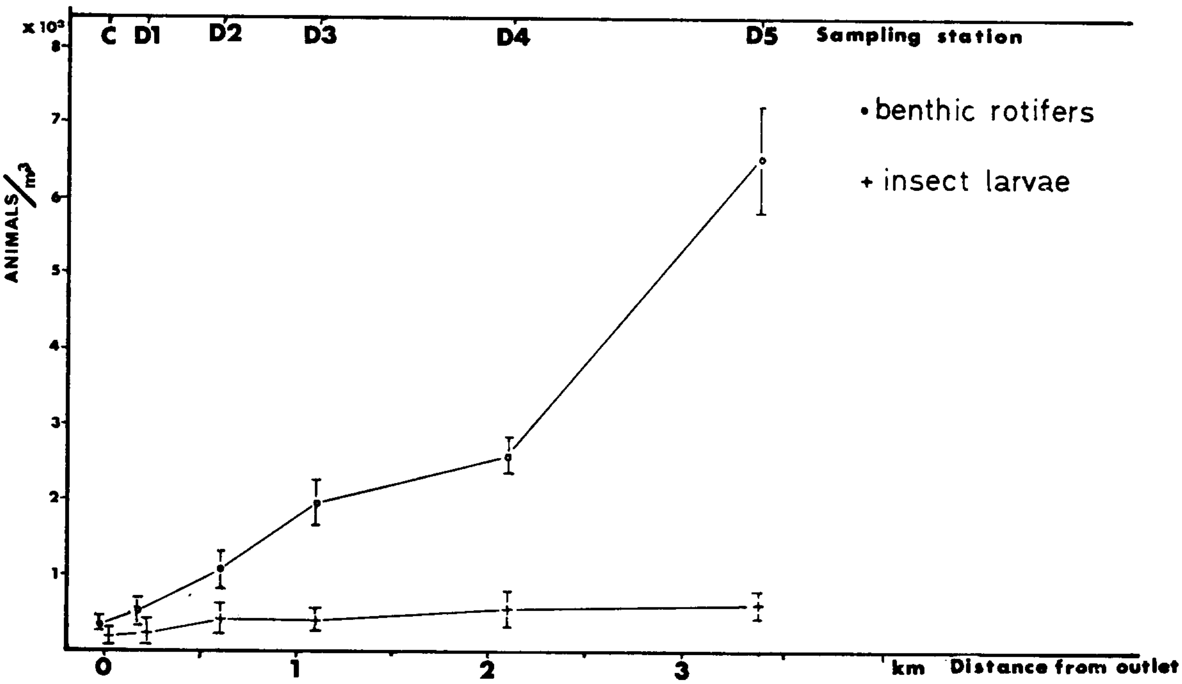

Fig. 4. The concentration of microzoobenthos downstream from the lake Oppheimsvatn. Vertical lines indicate 95% confidence limits.

of magnitude higher in the lake inlet than in the outlet (Fig. 2).

On two occasions samples were taken to detect any diurnal variation in the number of zoobenthos in the microdrift. For neither the benthic rotifers nor the insect larvae could any such variation be found (Sandlund 1977). In his investigation on the macrodrift in Strandaelva, Steine (1972) found a pronounced diurnal variation in the drift of e.g. larger Chironomidae and Ephemeroptera.

Figure 4 shows that the number of drifting zoobenthos increases with the distance downstream from the lake Oppheimsvatn. The number of benthic rotifers rises quite steadily from approx. 300 individuals m^{-3} in the lake outlet to approx. 6 500 ind. m^{-3} 3.4 km downstream. The number of drifting insect larvae in the lake outlet was approx. 100 ind. m^{-3}, and stabilized itself at twice that number approx. 1 km downstream. As this part of the river is quite homogeneous with respect to substratum, vegetation, and current speed, these results indicate that the benthic rotifers are transported for a much longer distance than are the insect larvae before settling or getting caught on the river bed again. This is also supported by the results in Figs. 2 and 3.

In order to consider the effects of variations in water discharge upon the number of drifting zoobenthos, samples were taken in the inlet and outlet of the lake Lønavatn during a short-term spate caused by heavy rainfall in July 1974. During the spate, the discharge into the lake varied between 35 and 105 $m^3\ s^{-1}$ (Fig. 5). The lake basin had a reducing effect on the spate, and the discharge out of the lake in the same period of eight days varied from 45 to 95 $m^3\ s^{-1}$ (Fig. 6).

Figure 5 shows that in the lake inlet, the number of both benthic rotifers and insect larvae increased with increasing water flow and decreased with decreasing water flow. In the lake outlet, the number of drifting benthic rotifers shows the same relationship to the changing water flow (Fig. 6), whereas the number of insect larvae in the drift decreases throughout the eight day sampling period. Due to the relatively long interval between the first and second sampling (3 days), there might have been an undetected increase in the number of drifting insect larvae during the first and second day of the spate. The difference between the drift pattern of insect larvae in the inlet and outlet of the lake might be connected with the distance that the animals are

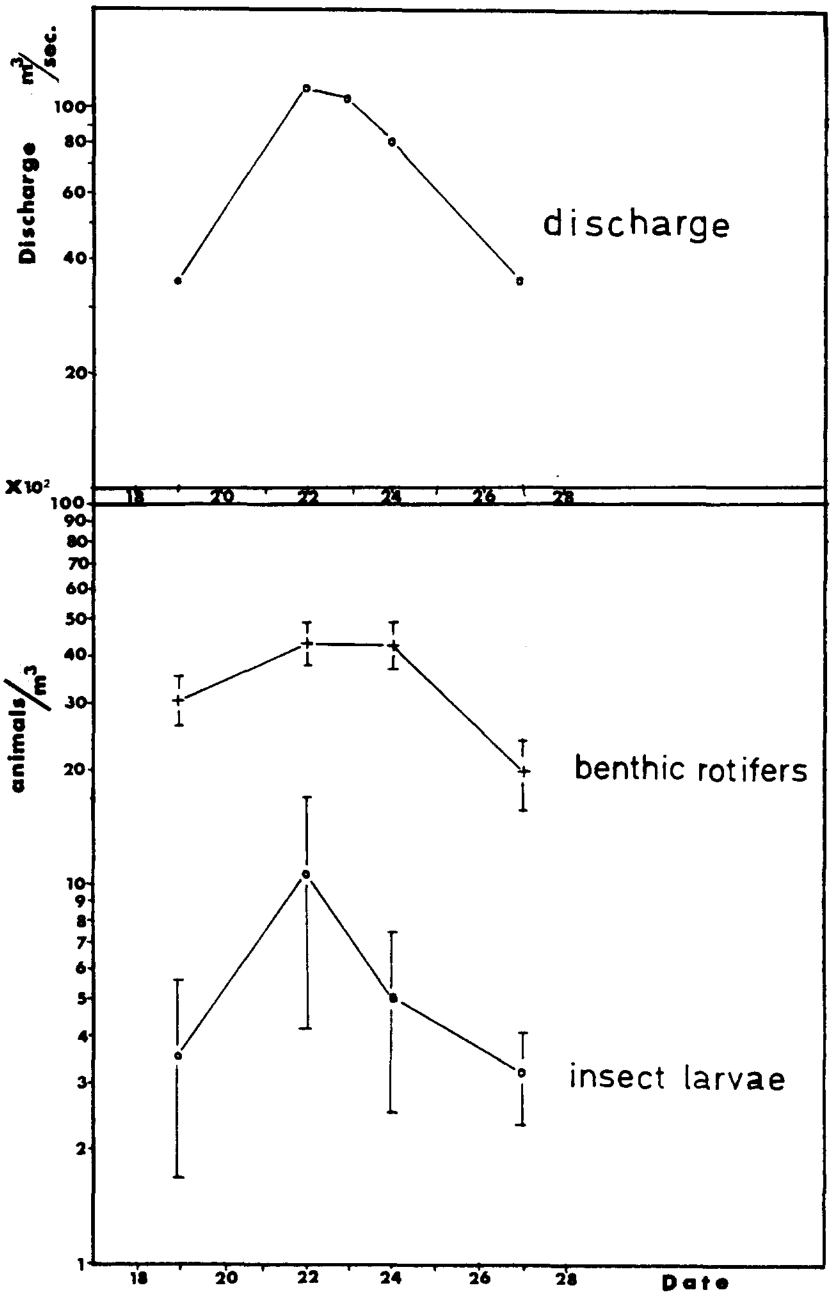

Fig. 5. The water discharge and the concentration of microzoobenthos drifting into Lønavatn (st. E), 19–27 July 1974. Vertical lines indicate 95% confidence limits.

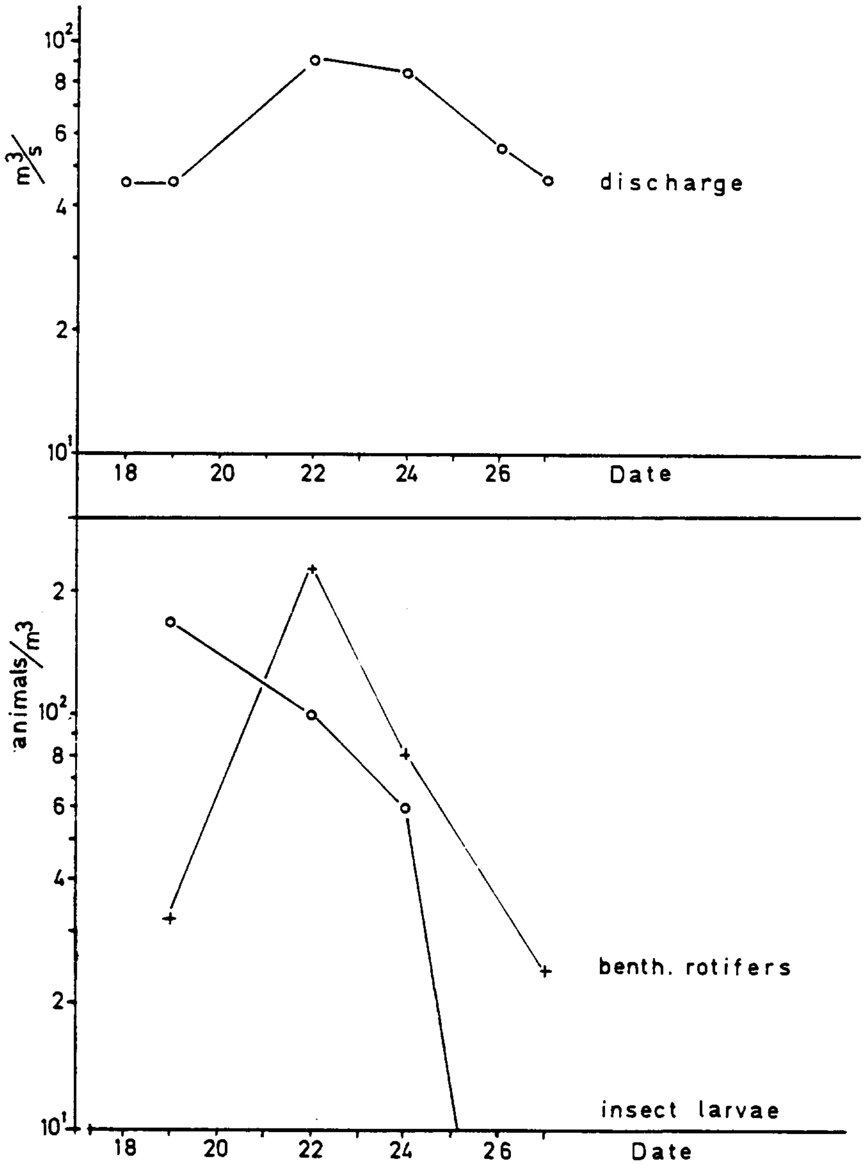

Fig. 6. The water discharge and the concentration of microzoobenthos drifting out of Lønavatn (st. F), 19–27 July 1974.

transported. This distance increases with increasing water flow (Chandler 1937). In the lake inlet, drifting animals are therefore supplied from further upstream when the water flow increases. In the outlet this will not be the case, as drifting animals entering a lake rarely get through the lake (Dendy 1944).

Zooplankton in the drift

Drift samples taken in the outlet of the lake Lønavatn during a short-term spate caused by heavy rainfall in July 1974 show that the concentration of plankton rotifers in the drift increased with increasing water flow (Fig. 7), whereas the concentration of crustacean zooplankton remained fairly constant. The different groups of crustaceans did, however, behave in different ways (Fig. 8). The number of *Bosmina* in the drift decreased, whereas the number of cyclopoid copepodids increased, and the number of nauplii remained nearly constant. An increase in the concentration of animals in the drift with increasing discharge is probably due to

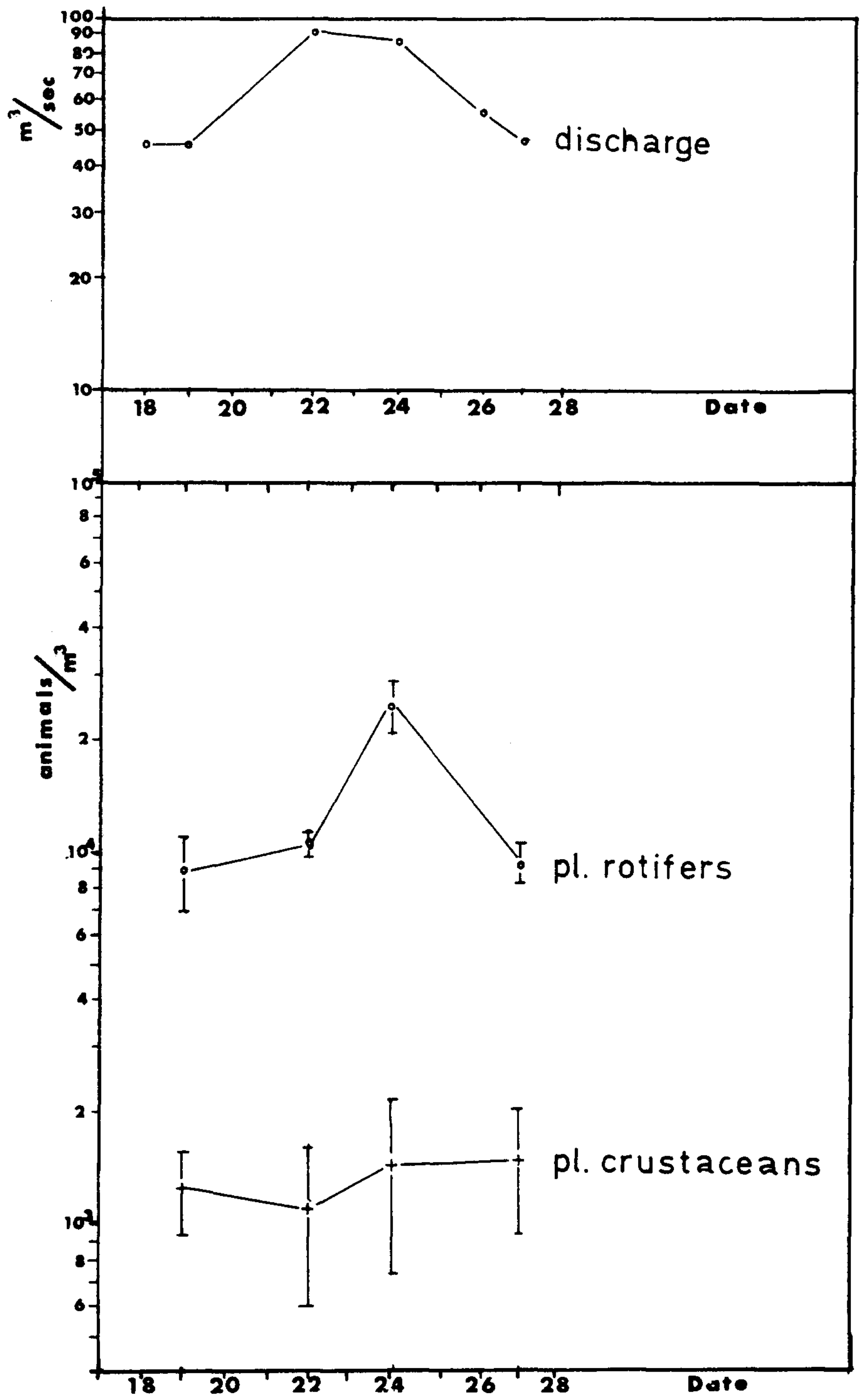

Fig. 7. The water discharge and the concentration of planktonic rotifers and crustaceans in the drift out of Lønavatn (st. F), 19–27 July 1974. Vertical lines indicate 95% confidence limits.

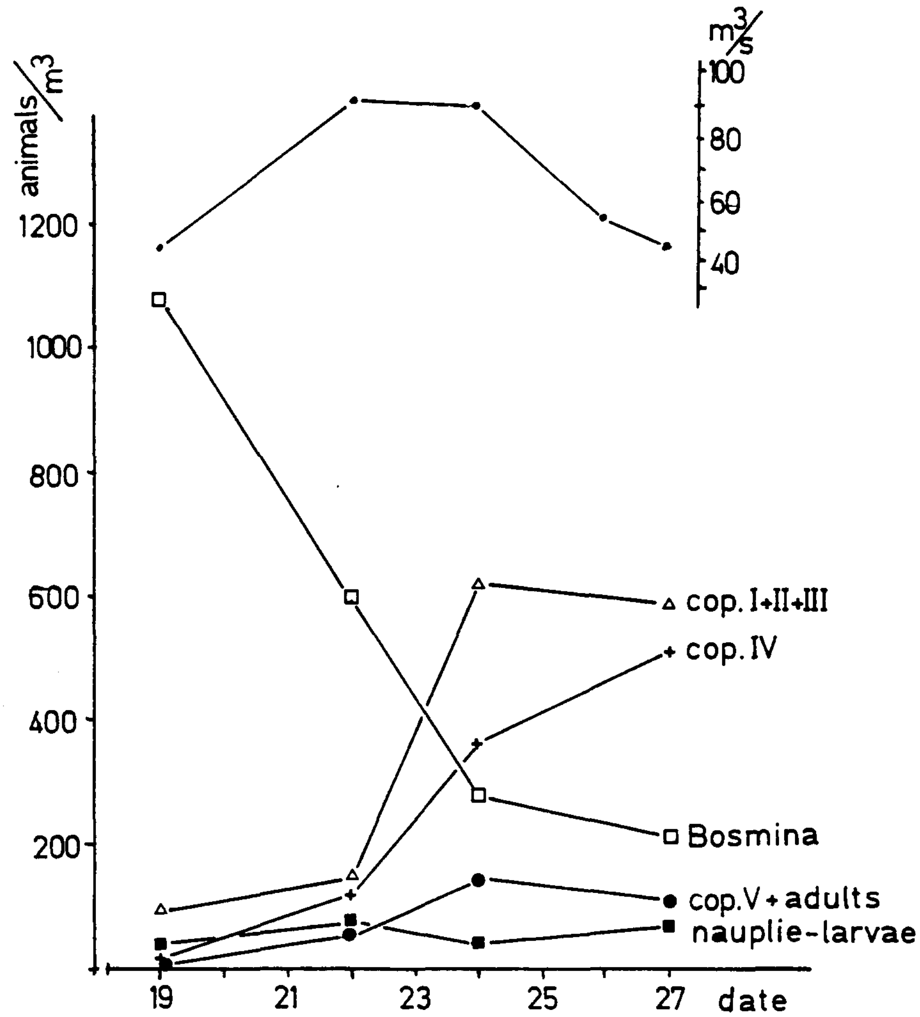

Fig. 8. The water discharge and the concentration of different crustaceans in the drift out of Lønavatn (st. F), 19–27 July 1974.

the increasing current speed in the lake close to the outlet. This causes a larger proportion of the zooplankton close to the lake outlet to be overpowered by the current and be swept out of the lake. *Bosmina* has been shown to move down to the bottom or closer to the shore at certain times of the year (e.g. Larsson 1978). Such behaviour connected with increased throughflow may explain why the concentration of this genus decreases with increasing water flow.

The variation in the number of zooplankton in the drift out of Lønavatn from August 1973 to October 1974 is shown in Fig. 9. Both crustaceans and rotifers appeared in largest number in late summer and autumn. This coincides with the maximum density of zooplankton in the lake (Nilssen 1975). The number of drifting rotifers was also high in December/January and March/April. On both occasions the water level was high or rising, due to rain and melting snow, respectively.

The number of zooplankton in the drift downstream from Oppheimsvatn decreased with increasing distance from the lake (Fig. 10). In approx. 200 m, from st. C to st. D1, about 45% of the zooplankton disappeared from the drift. However, there was still some zooplankton in the drift at st. D5 approx. 3 400 m from the lake. The same tendency appeared in samples taken at other times of the year (Table 1). The rate of loss from the drift varied somewhat between the different zooplankton spe-

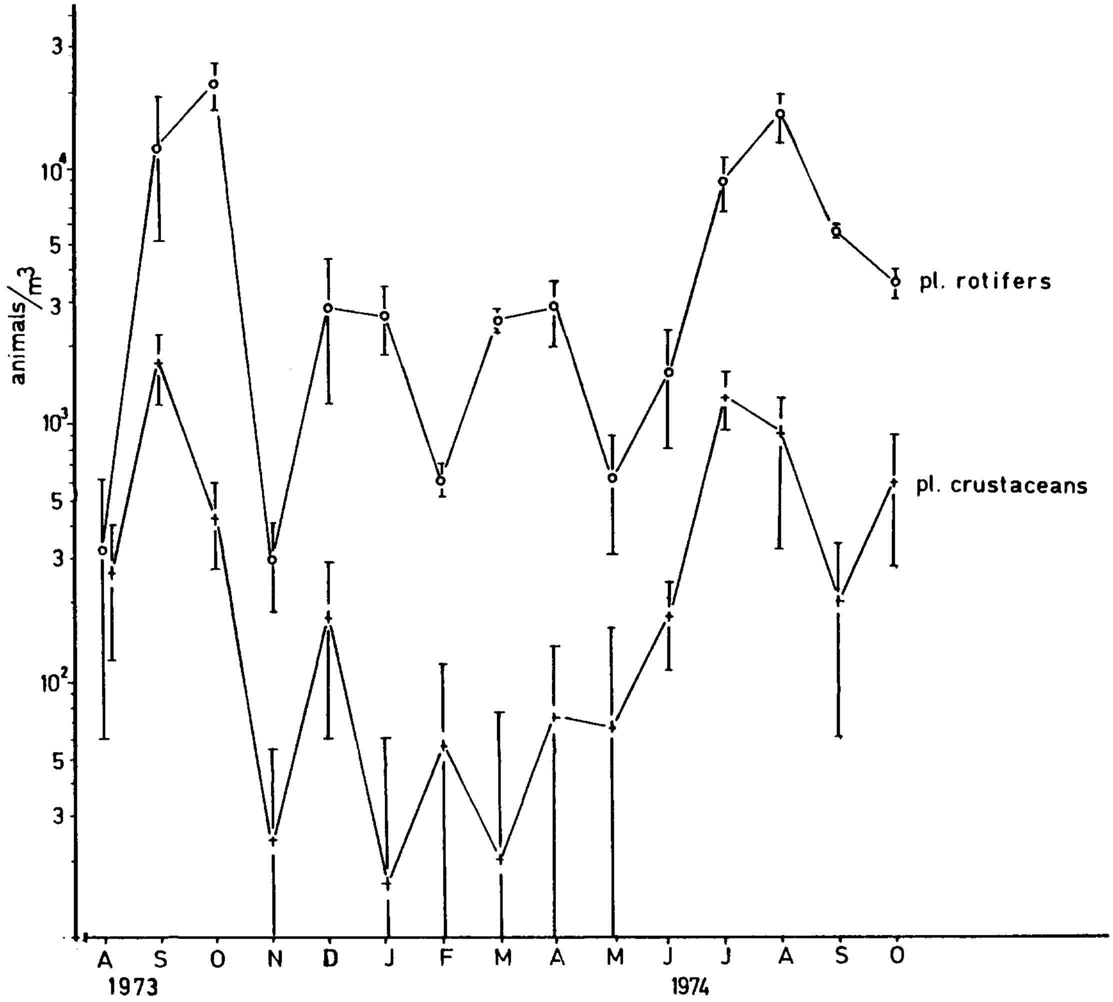

Fig. 9. The concentration of zooplankton in the drift out of Lønavatn (st. F) between August 1973 and October 1974. Vertical lines indicate 95% confidence limits.

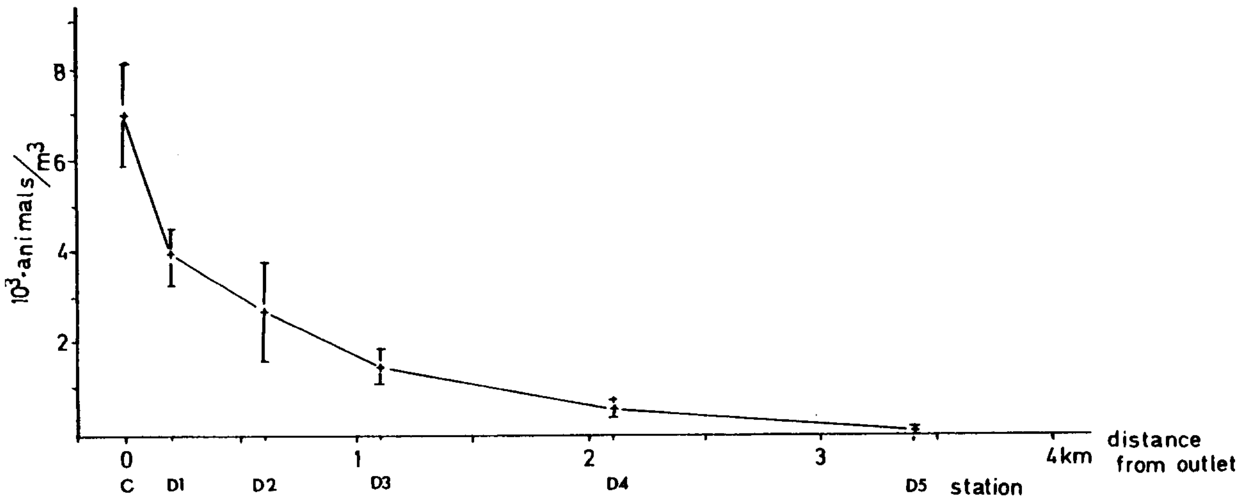

Fig. 10. The concentration of zooplankton in the drift at different stations downstream from the lake Oppheimsvatn, 17 June 1974. Vertical lines indicate 95% confidence limits.

Table 1. Percentage reduction of drifting zooplankton per 100 m downstream from the lakes Myrkdalsvatn (A–B) and Opheimsvatn (C–D3). The values are the average of four different samplings, and the numbers in parentheses give the 95% confidence limits.

Species	% reduction	
SMALL (<200 μm)	A–B	C–D3
Keratella hiemalis	3.4(± 4.9)	
K. cochlearis		4.2(±3.5)
Polyarthra spp.	9.7(± 6.0)	
MEDIUM (200–500 μm)		
Kellicottia longispina	4.3(± 3.5)	6.2(±4.1)
Cyclopoid nauplii	6.9(± 9.2)	7.2(±3.8)
LARGE (>500 μm)		
Cyclops spp. (ad., cop IV, V)	7.0(± 1.3)	7.3(±4.1)
Bosmina longispina	5.8(± 3.5)	7.4(±5.1)
Ceriodaphnia quadrangula	9.0(±10.8)	
Daphnia longispina		9.4(±3.8)

cies. The largest species (*Ceriodaphnia quadrangula* and *Daphnia longispina*) were first removed. Among the rotifers, *Kellicottia longispina*, with its long spines, and *Polyarthra*, with its appendages, were removed at the highest rate.

The diurnal variation in the number of some of the zooplankton groups in the drift out of Lønavatn is shown in Figs. 11–13. The variation in the number of *Synchaeta* indicates a maximum in the night or morning, and a minimum in the evening (Fig. 11). In September 1973 samples were taken in the lake to establish the pattern of vertical migration of the zooplankton (Nilssen 1975). This indicates that the maximum number of *Synchaeta* in the drift coincides with the highest concentration of this genus in the upper water layer in the lake. The corresponding results for the other important genus of planktonic rotifers, *Polyarthra*, is shown in Fig. 12. In September 1973 there was no clear pattern in the number of drifting *Polyarthra*, and almost no vertical migration could be detected in the lake. In August 1974, however, there was a clear tendency towards a variation in the number of drifting animals, with a maximum in the night or early morning and a minimum in the evening. This is largely the same pattern as demonstrated for *Synchaeta* (Fig. 11).

Figure 13 shows the number of drifting individuals of cyclopoid copepods out of Lønavatn. There are some differences between the nauplii and the copepodid stages, but the overall pattern is a minimum in the evening and a maximum in the night or morning. Nilssen (1975, pers. comm.) found a pronounced vertical migration in the cyclopoid copepods in Lønavatn, with a maximum number of animals in the upper water layer in the night.

The drift of *Bosmina longispina* in the outlet of Lønavatn showed no diurnal variation (Sandlund 1977). According to Nilssen (1975, pers. comm.), this species has no vertical migration in the lake, but a pronounced tendency to 'clump', which might produce large, unsystematic variations in the drift.

General discussion

The process of drifting might be divided into three parts: first the animal enters the drift, then it is transported for some distance, and finally it settles on the river bed, i.e. is removed from the drift.

The factors that cause the animals to enter the drift vary greatly between the zooplankton and the microzoobenthos, e.g. the behaviour of the animals have an impact on this. The microdrift consists of animals with virtually no ability to swim in a swift current, and therefore the process of drifting and settling on the river bed are mainly governed by environmental factors and the size and shape of the animals. This is valid for both the zooplankton and the zoobenthos of the microdrift.

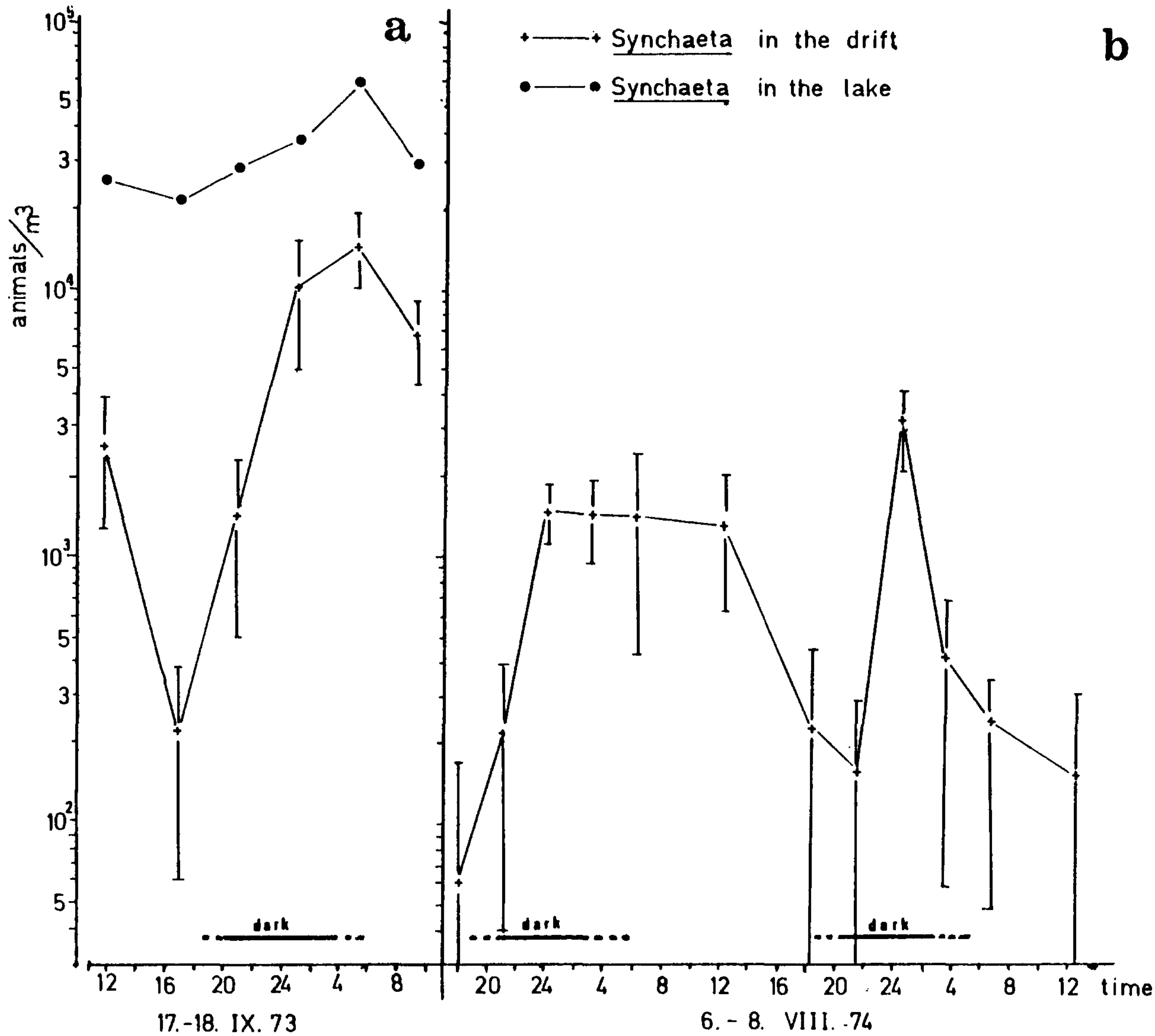

Fig. 11. The concentration of *Synchaeta* in the drift at st. F and in the upper 1 m layer in Lønavatn, 17–18 September 1973 (a), and in the drift at st. F, 6–8 August 1974 (b). Vertical lines indicate 95% confidence limits.

Entering the drift

The number of benthic animals entering the drift depends mainly on three factors: 1) the number of animals per unit area of river bed, 2) the erosive effect of the water current, and 3) the behaviour of the animals.

The influence of the density of animals on the number of animals drifting has been demonstrated for macroinvertebrates (e.g. Waters 1965). In my results the maximum of drifting small chironomids in summer supports this.

The erosive effect of the water current increases with increasing current speed. Consequently, with increasing water flow more animals are swept with the current and found drifting (e.g. Logan 1963; Maitland 1966). The increase in the number of drifting animals with the rising water level during a short-term spate in Strandaelva points to the same conclusion, even if the increased current speed also

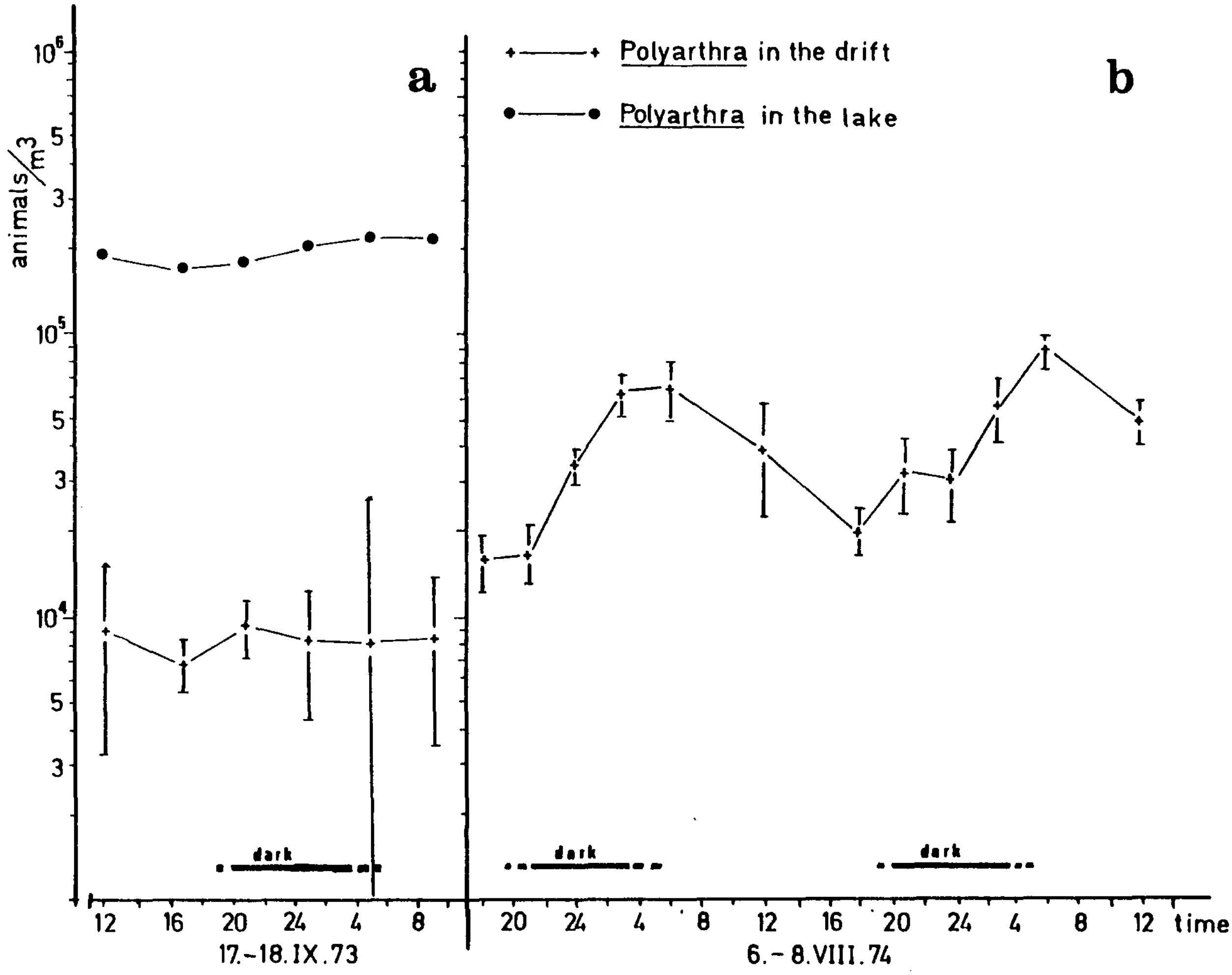

Fig. 12. The same as Fig. 12 for *Polyarthra.*

makes the animals stay in the drift for a longer distance (McLay 1970).

A diurnal variation in the drifting of macroinvertebrates in streams indicates that the behaviour of the animals influences their liability to be swept away by the water (e.g. Tanaka 1960; Elliott 1965). Little is known of the diurnal activity of benthic rotifers, but my results indicate that other factors are of greater importance for the number of animals found in the drift samples.

In swift streams like Strandaelva, virtually all the zooplankton in the drift originate in the lakes of the watercourse. Usually only the upper water layers of the lake enter the river at the outlet (Ruttner 1956). My results also indicate that the number of zooplankton in the upper layers of the water masses greatly influence the number of zooplankton drifting out of the lake. This is valid both for the diurnal and seasonal variations in the zooplankton. Some of the zooplankton groups, especially the crustaceans, will have some ability to swim against the current away from the outlet, and thus avoid being swept out of the lake (Ruttner 1963). Increasing water flow will increase the current speed in the lake outlet, and more animals are swept out of the lake, at least in the first stages of a spate. The observations from Strandaelva on rotifers and some of the copepods support this, whereas *Bosmina* appears to be able to avoid the increasing flowthrough. The part of the zooplankton population that is swept out of the lake will not be able to contribute with their genes to the next generation. Behaviour and

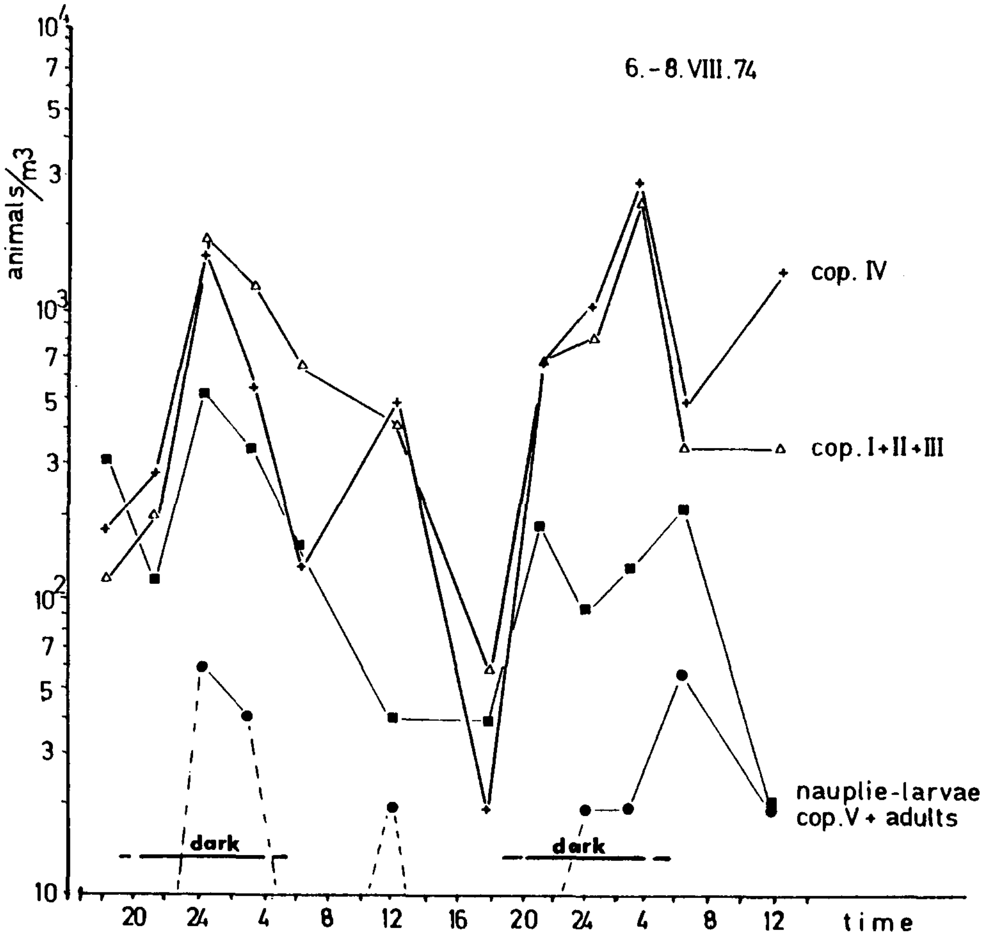

Fig. 13. The concentration of the different stages of cyclopoid copepods in the drift at st. F, 6–8 August 1974.

life history traits will therefore be selected to avoid this fate (e.g. Ravera & Tonolli 1956).

Once in the drift both zooplankton and microzoobenthos might be considered passive organic particles, as their ability to swim in a swift current appears negligible. The animals will therefore continue to drift until they are caught in the vegetation, in the deadwaters between the stones of the bottom, by predators, or are physically damaged by the turbulent water. The macrophyte vegetation in the river will be of utmost importance in removing animals from the drift (Chandler 1937; Madalinski 1961; Kubicek 1968). In Strandaelva, the dominant element of the vegetation is *Fontinalis.* Below the lake outlets, zooplankton stuck in the tufts of *Fontinalis* were easily found, and Asplund & Karlström (1975) also demonstrated the ability of Fontinalis to act as a particle trap. In the process of passive filtering, the size and shape of the drifting animals also influences the results. The present investigation shows that the largest animals were removed at the highest rate. In addition, small animals with long spines, e.g. *Kellicottia longispina,* are also easily caught in the vegetation and consequently disappear quickly from the drift. McLay (1970) also maintained that the size and form of the drifting animals influence their distance travelled.

The filter feeding macroinvertebrates (mainly Trichoptera) certainly remove a large amount of drifting microfauna along with other organic particles. Their dependence on food from lakes is demonstrated by the fact that biomass and density of filter feeders are usually significantly higher close to the lake outlet than elsewhere in the streams (e.g.

Briggs 1948; Illies 1956; Ulfstrand 1968). Fish also usually eat some drifting zooplankton. This is the case in Strandaelva with brown trout (Haraldstad 1981; Schei 1981), and in accordance with other investigations (e.g. Lillehammer 1973).

The distance travelled by the animals in the drift is related to the current speed and the water discharge. A swift current is usually very turbulent, and some investigators believe physical destruction by turbulence is important in removing animals from the drift (Marco 1974). However, during the present investigation, no fragments of drifting animals were found in the drift samples, so this factor is not believed to be of any great importance in Strandaelva.

The filtering capacity of the bottom vegetation is a function of water volume versus moss area (Asplund & Karlstöm 1975). Increasing water flow thus reduces the filtering capacity. In addition more animals enter the drift at rising water levels. Thus there are more animals drifting at any one point in the river when the discharge is increasing than at stable water levels.

Summary

The microdrift (i.e. the drift of zooplankton and microscopical zoobenthos) in the river Strandaelva, Voss, western Norway, was investigated from August 1973 to October 1974.

The microzoobenthos in the drift consisted mainly of benthic rotifers (mostly of the order Bdelloidea), and small instars of chironomid larvae. The composition of the drifting zooplankton reflected the zooplankton in the lakes of the river system, being dominated by the rotifers *Kellicottia longispina, Polyarthra, Keratella,* and *Synchaeta,* the cladocerans *Bosmina longispina, Daphnia longispina,* and *Ceriodaphnia quadrangula,* and nauplii, copepodids and adults of cyclopoid copepods.

There was a maximum concentration of drifting insect larvae in summer, whereas the benthic rotifers in the drift exhibited no seasonal trend. This was observed both in the inlet and outlet of the lakes in the river system. The number of insect larvae drifting in to and out from the lake was approximately equal, whereas the number of benthic rotifers entering the lake was about one order of magnitude higher than the number leaving the lake.

Samples taken at several localities in the outlet and downstream from the lake Oppheimsvatn showed that the concentration of drifting benthic rotifers increased for at least 3.4 km downstream from the lake outlet, whereas the number of insect larvae leveled off after approx. 500 m. Both this and the differences between lake inlet and outlet indicate that the drifting benthic rotifers are transported for a much longer distance than the drifting insect larvae.

Samples taken during a short-term spate demonstrated that in the inlet to the lake Lønavatn, the concentration of both benthic rotifers and insect larvae in the drift increased with increasing water flow and decreased with decreasing water flow. In the outlet of the lake, the benthic rotifers showed the same pattern, whereas the concentration of drifting insect lavae decreased throughout the period.

In the lake outlet, the concentration of drifting rotifer zooplankton was also positively correlated with water discharge. The concentration of total drifting planktonic crustaceans remained fairly constant throughout the spate, although some groups decreased (e.g. *Bosmina*), and others increased (e.g. cyclopoids).

The seasonal variation in the number of zooplankton drifting out of the lake largely reflected the density of zooplankton in the lake, reaching maxima in late summer and autumn. Heavy rain or melting snow causing spates might also produce maxima in the number of drifting zooplankton at other times of the year.

The number of drifting zooplankton decreased rapidly downstream from the lake outlet; the filtering effect of the bottom vegetation *(Fontinalis)* was probably the single most important factor removing animals from the drift. The form and size of the zooplankton organisms greatly influenced the distance travelled in the drift, as the largest species disappeared first.

The diurnal variation in the concentration of drifting zooplankton in the lake outlet reflected the vertical migration of the zooplankton in the lake. Maximum number of drifting animals occurred when most zooplankton was in the upper water layers in the lake. Thus, the diurnal variation in the drift differed between the species, depending on the degree of vertical migration.

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References

Asplund, C. & Karlström, U., 1975. Filtering capacity and colonization in artificial water 'mosses'. Report from the Rickleå field station No. 71: 1-7. (In Swedish with English summary.)

Brehm, V., 1911. Beobachtungen über die Entstehung des Potamoplanktons. Int. Revue. ges. Hydrobiol. 4: 311-314.

Briggs, J. C., 1948. The quantitative effects of a dam upon the bottom fauna of a small California stream. Trans. Am. Fish. Soc. 78: 70-81.

Chandler, D. C., 1937. Fate of typical lake plankton in streams. Ecol. Monogr. 7: 445-479.

Clifford, H. F., 1972. Drift of invertebrates in an intermittent stream draining marshy terrain of west-central Alberta. Can. J. Zool. 50: 985-991.

Dendy, J. S., 1944. The fate of stream drift when carried into lakes. Ecol. Monogr. 14: 333-357.

Elliott, J. M., 1965. Daily fluctuations of drift invertebrates in a Dartmoor stream. Nature, Lond. 205: 1127-1129.

Faafeng, B., Brettum, P., Kristoffersen, T., Lindstrøm, E.-A., Matzow, D., Nilssen, J. P. & Tjomsland, T., 1978. En undersøkelse av Vossevassdraget 1977. NIVA-rapport 0-76088, 167 pp. (In Norwegian.)

Haraldstad, O., 1981. Aurens habitat og ernæring i Myrkdalsvatnet, Voss. Unpubl. thesis, Univ. of Oslo. (In Norwegian.)

Hauge, H. V., 1957. Vangsvatn and some other lakes near Voss. A limnological study in Western Norway. Folia limnol. scand. 9: 1-189.

Hynes, H. B. N., 1970. The Ecology of Running Waters. Liverpool Univ. Press, Liverpool. 555 pp.

Illies, J., 1956. Seeausfluss-biozönosen lappländischer Waldbäche. Ent. Tidskr. 77: 138-153.

Jonsson, B., 1977. Demographic strategy in a brown trout population. Zool. Scr. 6: 255-263.

Kubicek, F., 1968. Die organische Drift des Svratka-Flusses in Abschnitt zwischen zwei Talsperren. Hydrobiologia 31: 402-416.

Larsson, P., 1978. The life cycle dynamics and production of zooplankton in Øvre Heimdalsvatn. Holarct. Ecol. 1: 162-218.

Lillehammer, A., 1973. An investigation of the food of one- to four-month old fry (Salmo salar) in the river Suldalslågen, West Norway. Norw. J. Zool. 21: 17-24.

Logan, S. W., 1963. Winter observations on bottom organisms and trout in Badger Creek, Montana. Trans. Am. Fish. Soc. 92: 140-145.

Madalinski, K., 1961. Moss dwelling rotifers of Tatra streams. Polsk. Archwm Hydrobiol. 9: 243-263.

Maitland, P. S., 1966. Studies on Loch Lomond. II. The Fauna of the River Endrick. Blackie, Glasgow. 194 pp.

Marco, V., 1974. Comportamento del plancton lacustre in ambiente lotico. Boll. Pesca Piscic. Idrobiol. 29: 81-95.

Matzow, D., Huru, H., Jonsson, B., Kvammen, P. I., Nilssen, J. P., Sandlund, O. T. & Østli, T., 1976. Investigations of freshwater biology in Lønavatn lake and Strandaelva river. Rep. Voss Project. Zool. Inst., Univ. Oslo 1: 1-235. (In Norwegian with English summary.)

McLay, C., 1970. A theory concerning the distance travelled by animals entering the drift of a stream. J. Fish. Res. Bd Can. 27: 359-370.

Nilssen, J. P., 1975. Ferskvannsbiologiske undersøkelser i Lønavatn, Voss. IIb. Cyclops abyssorum Sars, 1863 - en studie av dens taksonomi og økologi. Unpubl. thesis, Univ. of Oslo. (In Norwegian.)

Nilssen, J. P., 1976. Community analysis and altitudinal distribution of limnetic Entomostraca from different areas in Southern Norway. Polsk. Archwm Hydrobiol. 23: 105-122.

Nilsson, N.-A., 1957. On the feeding habits of trout in a stream of Northern Sweden. Rep. Inst. Freshwat. Res. Drottningholm 53: 51-77.

Ravera, O. & Tonolli, V., 1956. Body size and number of eggs in diaptomids, as related to water renewal in mountain lakes. Limnol. Oceanogr. 1: 118-122.

Ruttner, F., 1956. Einige Beobachtungen über das Verhalten des Planktons in Seeabflussen. Öst. Bot. Z. 103: 98-109.

Sandlund, O. T., 1977. Transport av zooplankton og mikroskopiske bunndyr i Strandaelva, Voss. Unpubl. thesis, Univ. of Oslo. (In Norwegian.)

Schei, T., 1981. Habitatutnyttelse hos allopatrisk auve i Oppheimgvatnet, Voss. Unpubl. thesis, Univ. of Oslo. (In Norwegian.)

Steine, I., 1972. The number and size of drifting nymphs of Ephemeroptera, Chironomidae, and Simuliidae by day and night in River Stranda, western Norway. Norsk ent. Tidskr. 19: 127-131.

Synnes, K., 1982. En sammenligning av zooplankton samfunnene i Myrkdalsvatn og Oppheimsvatnpå Voss. Unpubl. thesis, Univ. of Oslo. (In Norwegian.)

Tanaka, H., 1960. On the daily change of benthic animals especially on the types of daily change observed in taxonomic groups of insects. Bull. Freshwat. Fish. Res. Lab., Tokyo 9: 13-24.

Ulfstrand, S., 1968. Benthic communities in Lapland streams. Oikos Suppl. 10: 1-120.

Waters, T. F., 1965. Interpretation of invertebrate drift in streams. Ecology 46: 327-334.

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