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Seasonal variation in the lateral distribution of mayfly nymphs in a boreal river

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Seasonal variations in the lateral distribution of mayfly nymphs were investigated in the North Swedish river Vindelälven; a river with large seasonal differences in water level, current velocity and ice conditions. A total of 22 mayfly species about equally divided between summer and winter species were found along a single transect. At low water level in late summer and autumn most species were distributed over the whole transect. In winter the populations occupying the littoral moved into deeper water, so avoiding the ice. Only very small mortalities were detected in the ice. Prior to the spring flood most characteristically still water species moved to the shallow uppermost littoral while lotic species and the burrowing *Ephemera vulgata* L. did not show the same aggregation near the shore. It is suggested that these lateral movements allow the nymphs to avoid adverse environmental conditions and to exploit food resources over the whole transect.

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Introduction

Unregulated northern rivers are characterized by marked seasonal variations in water flow. During the spring flood large areas are flooded and during minimum flows in winter large areas freeze into the substrate (Olsson 1981). The benthic fauna inhabiting such a biotope has to cope with large seasonal differences in water level, current velocity and ice conditions. In such rivers we would expect to find species with specialized behaviour to cope with these seasonal variations.

Seasonal lateral movements to less exposed places within the habitat is one way of avoiding some of these stresses and would also enable utilization of the food resources in flooded areas. Moon (1935) showed that the benthic animals follow normal fluctuations in water level in lakes by moving towards or from the shore. In rivers, seasonal differences in lateral distribution have been found in plecopteran nymphs (Lillehammer 1965) and trichopteran larvae (Decamps 1967). Harker (1953) found that some ephemeropteran species move to shallower regions during flood, and Ulfstrand (1968a) noted that ephemerellid nymphs spend winter in mid-river. Other studies have shown that some ephemerid species leave the main river and migrate into small tributaries before the peak of the spring flood (Neave 1930, Hayden and Clifford 1974, Olsson and Söderström 1978).

The purpose of the present investigation was to examine seasonal variations in the lateral distribution of mayfly nymphs in a northern river, as part of a larger study on the behaviour of benthic animals in a seasonally fluctuating environment.

Study area

The north Swedish river Vindelälven arises in a mountain area near the Norwegian border. It is 444 km long and joins the River Ume älven 42 km from the Gulf of Bothnia. The mean maximum and minimum discharges at Vindeln (1971–1977) were 1022 $m^3 s^{-1}$ and 31 $m^3 s^{-1}$, respectively (Swedish Meteorological and Hydrological Institute). The area investigated was a slow to moderate flowing part of the river in the boreal coniferous zone at Sirapsbacken 112 km from the sea and 164

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m a.s.l. The spring flood usually has two main peaks, one at the end of May and another around midsummer. There is also a smaller autumn peak in early October (Fig. 1). In 1974 there was an unusually low spring flood, although an extra peak occurred during the summer. The difference in water level between the peak of the spring flood and the late winter minimum is normally about 4 m. The river area is ice-covered from about mid-November until early May. The fall in the water level in winter after the ice cover has formed, combined with low temperatures, causes the substrate to freeze within a 32–35 m broad belt next to the river bank (Fig. 2). The current velocity on two occasions at different distances from the river bank is given in Fig. 3. The substratum in the littoral zone consists of sand with an increasing fraction of organic material towards the bank while the sublittoral zone consists mainly of coarse sand and fine gravel. The vegetation in the geolittoral is dominated by a dense belt of *Carex acuta* L. and in the hydrolittoral by small isoetids and dense stands of elodeids (Olsson 1981). In the sublittoral the vegetation is more scattered consisting of *Potamogeton gramineus* L., *Nitella* spp. and *Isoetes lacustris* L.

Methods

Sampling of the unfrozen substratum of the river was performed with a pole-mounted Ekman grab (225 cm^2). The material was sieved before being analysed (mesh size: 0.6 mm). Evaluation and a more detailed description of the method was given in Olsson (1976).

Samples of ice were chipped from the part of the river frozen to the bottom. Within an area of 500–1000 cm^2 all the overlaying ice down to the sediment was removed (ice samples). Samples were also taken of the frozen sediment beneath the ice with steel cylinders (5 cm deep, 41 cm^2) driven into the frozen mud (steel cylinder samples).

Sampling was performed about once a month from June 1974 to June 1976 (Fig. 2). A total of 530 Ekman, 10 ice, and 97 steel cylinder sample units were taken at different distances along a transect across the river. Distances (m) were measured from a marker at the high water level mark on the river bank.

The nomenclature follows 'Limnofauna Europaea' (Illies 1978), except for *Metretopus alter* Bgtss which has been merged with *M. borealis* Bgtss (Ulfstrand 1968a, Berner 1978). *Heptagenia dalecarlica* Bgtss is treated as a separate species (Saaristo and Savolainen 1980). Electrophoretic analysis indicates that the non-migrating part of *Parameletus* may consist of two species (Jan Nilsson, pers. comm.).

Results

Seasonal abundance

The investigated area supported a diverse number of both lotic and lentic species of mayflies. A total of 22 (possibly 23) species has been found within this single locality (Fig. 4), which is about the same number of species as has been found in the more lotic upper reaches of this river (Ulfstrand 1968a). The highest number was found in May and early June (10–13 species) and the lowest in August (6 species).

Two species, *Ephemera danica* and *E. vulgata,* were semivoltine which has been found elsewhere (Kjellberg 1973, Svensson 1977, Wright et al. 1981).

The univoltine species were about equally divided into summer and winter species. According to Macan (1965) and Clifford (1969) winter species have a short egg diapause, autumn growth and overwinter as fairly large nymphs. This categorization is in general agreement with earlier studies (Ulfstrand 1968b, Kjellberg 1973, Brittain 1974, 1980, Armitage 1976, Barton 1980) and comments will only be given for some problematic species.

Baetis digitatus belonged to the category of winter species. No published information on the nymphal development of this species seems to be available. *Centroptilum luteolum* has in some biotopes been classified as a polyvoltine species (Brittain 1974, cf Macan 1978), but Ulfstrand (1969) found a single emergence period of this species in the headwaters of Vindelälven. No evidence for polyvoltinism was found in the present study. *Ephemerella mucronata* was found to be a winter species which differs from the development proposed by Ulfstrand (1968b) but is in agreement with Bengtsson (1981). *Baetis fuscatus* and *Paraleptophlebia strandii* have not been classified. *B. fuscatus* can have more than one generation per year (Ulfstrand 1968b). The life cy-

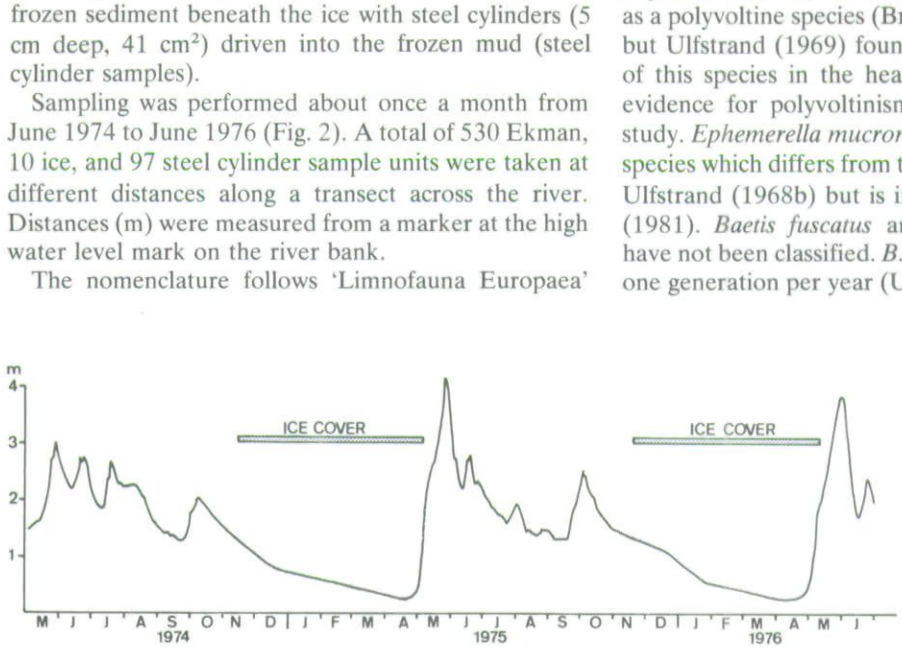

Fig. 1. Seasonal fluctuations of water level, in relation to a fixed point, at Sirapsbacken in the River Vindelälven, 1974–1976.

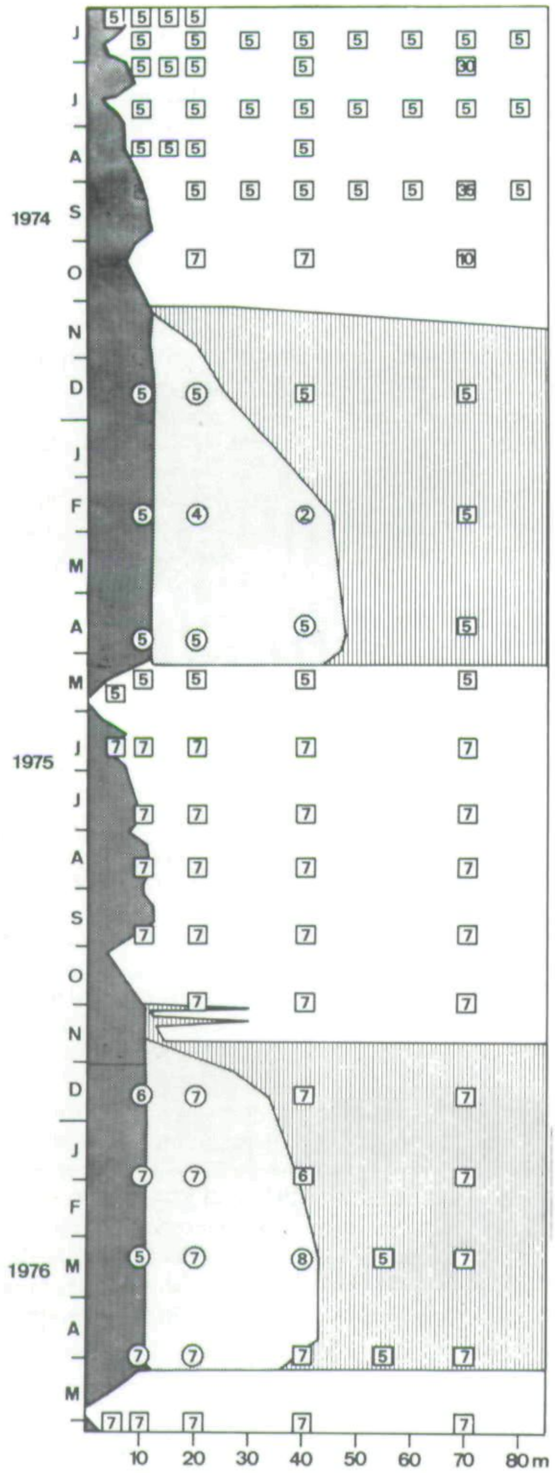

Fig. 2. Seasonal and lateral distribution of ice cover (strippled area), bottom frozen area (grey), and drained area (dark) at Sirapsbacken, the River Vindelälven, 1974–1976. Squares show location and number of Ekman sample units. Circles show location and number of steel cylinder sample units.

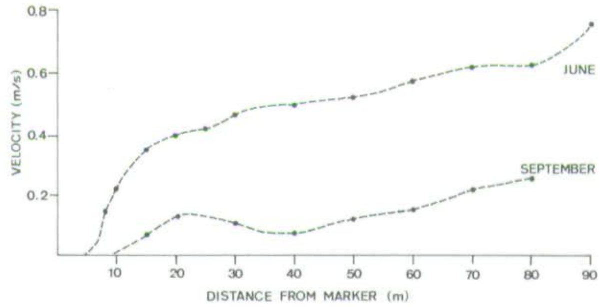

Fig. 3. Current velocity during the spring flood (June) and low water level (September) at Sirapsbacken, the River Vindelälven, 1975.

cle of *P. strandii* is not known. Fulgrown nymphs of *P. strandii* ready to emerge appeared in rather high numbers in the *Carex* belt in July. This was the only time they were caught and nymphal development probably takes place in mid-river.

Lateral distribution

Seasonal inter- and intraspecific differences in lateral distribution were found (Fig. 5). *Leptophlebia vespertina* can be placed in a group of winter species that prefers shallow water. When the new generation appeared in late summer, when the water level was low, the population was distributed over the whole transect. In autumn *L. vespertina* had an increased density near the river margin. As the water level decreased and the substrate began to freeze, the population seemed to be displaced into the sublittoral zone. In mid winter the population was aggregated in a narrow 1–3 cm layer of water beneath the ice. A few dead nymphs of *L. vespertina,* but no other ephemeropteran species, were found in the ice. The ice started to lift off the substratum in late April and *L. vespertina* rapidly colonized the former frozen zone. During the spring flood the whole population was found within the narrow *Carex* belt next to the shore where the nymphs stayed until emergence. *L. marginata* had a similar seasonal distributional pattern. This was also true for *Heptagenia fuscogrisea* with some minor differences: it prefered somewhat deeper water in autumn and did not remain so near the ice during winter.

A second group of winter species, *C. luteolum* and *E. mucronata,* occupied deeper water and performed less pronounced movements. Compared to *L. vespertina, C. luteolum* avoided the ice in winter and was distributed over the whole transect at high water level in spring and did not colonize the shallow *Carex* belt to any greater extent. *E. mucronata* had about the same lateral distribution but was not found in the littoral zone in autumn.

A third group, consisting of *B. digitatus* and the

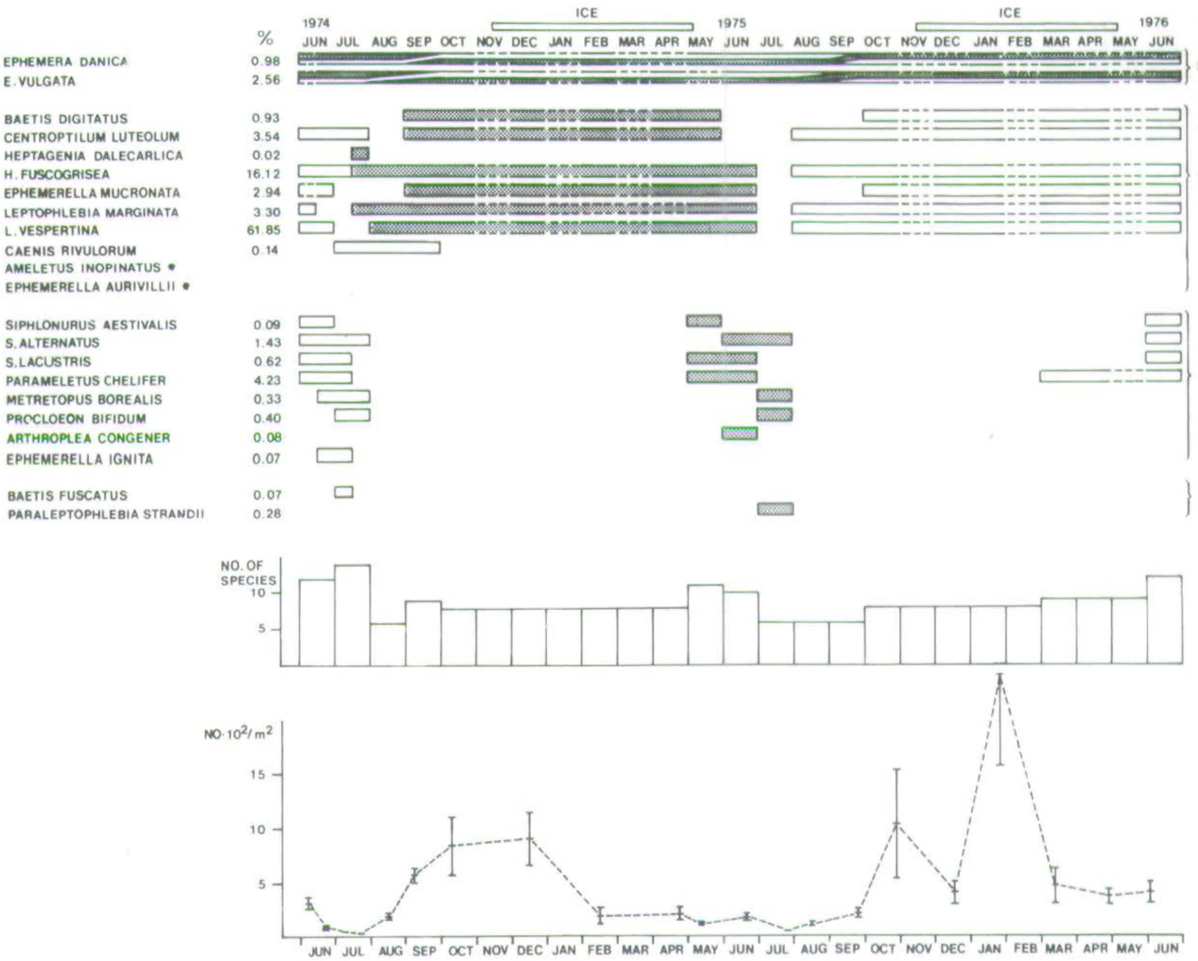

Fig. 4. Seasonal distribution of mayfly nymphs at Sirapsbacken, the River Vindelälven, 1974–1976. SV shows semivoltine species, W winter species and S summer species. Mean number nymphs per m² ± S.E. of the mean is given in the lowest figure. Asterisk indicates species caught by O. Söderström in the same area.

semivoltine species *E. danica,* were stationary in the sublittoral throughout the whole of nymphal development, irrespective of season or water level. The semivoltine species *E. vulgata,* like *E. danica,* did not occupy the littoral zone during the spring flood, but by late summer a new generation had appeared and distributed itself along the whole transect. Older nymphs were only found in the sublittoral zone.

In the category of summer species all those with early development – all the siphlonurids – behaved in a similar way. *Siphlonurus alternatus* appeared as small nymphs in the littoral after the ice had broken up in spring. In 1975 and 1976, when there were normal spring floods, the distribution was totally restricted to the *Carex* belt. The same pattern was found for *S. lacustris, S. aestivalis* and *Parameletus* spp. The presence of a few small nymphs of *Parameletus* spp. during the winter indicates that at least some of the population hatched in the sublittoral zone and later moved to the river bank. The presence of 5 mm long nymphs of *S. aestivalis* in May indicates that this is probably also true for this species. No such indications were found in the other two *Siphlonurus* species.

The late summer species *Procloeon bifidum* and *Metretopus borealis* were only found in mid-summer, when the spring flood had decreased, and then they were distributed over the whole transect. The results are summarized on a seasonal basis in Fig. 6. In summer and autumn most species were distributed over the whole transect (*L. vespertina, L. marginata, E. vulgata, P. bifidum* and *M. borealis*). However *E. mucronata, B. digitatus* and *E. danica* seemed to be exceptions to this and were only found in the sublittoral zone at that time.

In winter *L. vespertina* and *L. marginata* remained very near the ice. Other winter species occupied an area further out in deeper water. No significant losses in the ice were found.

In spring, at high water level, a more obvious division

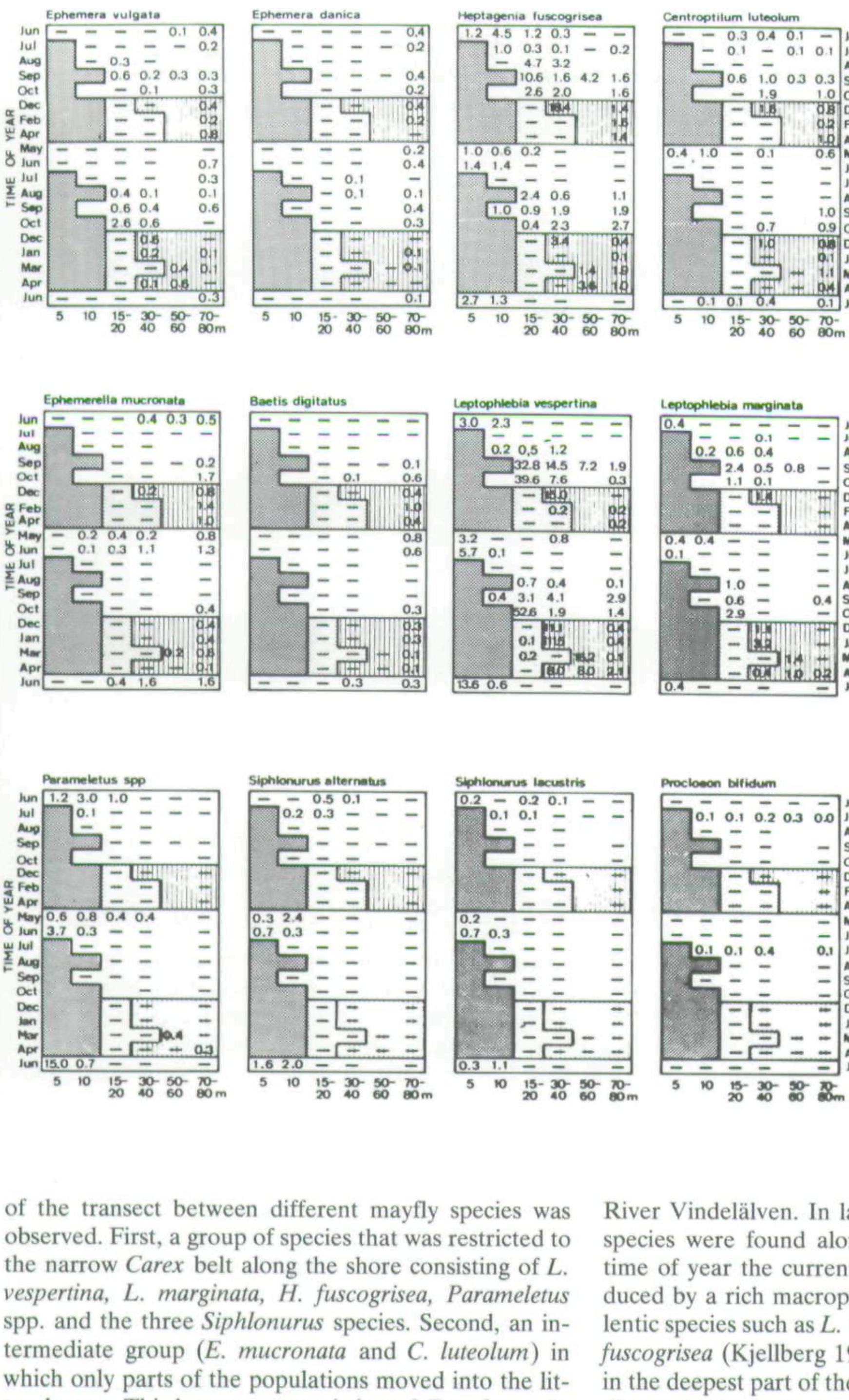

Fig. 5. Lateral distribution of mayfly nymphs at different times of the year at Sirapsbacken, the River Vindelälven, 1974–1976. Mean number nymphs per sample unit is given (compare Fig. 2). The distance (m) out into the river was measured from a high water marker on the river bank.

of the transect between different mayfly species was observed. First, a group of species that was restricted to the narrow *Carex* belt along the shore consisting of *L. vespertina, L. marginata, H. fuscogrisea, Parameletus* spp. and the three *Siphlonurus* species. Second, an intermediate group (*E. mucronata* and *C. luteolum*) in which only parts of the populations moved into the littoral zone. Third, a group consisting of *E. vulgata, E. danica* and *B. digitatus* which stayed in the sublittoral during the spring flood.

Discussion

Both inter- and intraspecific seasonal differences in the lateral distribution of mayfly nymphs are present in the River Vindelälven. In late summer most of the winter species were found along the whole transect. At this time of year the current velocity was low (Fig. 3), reduced by a rich macrophyte vegetation. Even typically lentic species such as *L. vespertina, L. marginata* and *H. fuscogrisea* (Kjellberg 1973, Brittain 1974) were found in the deepest part of the river. Whether this was due to dispersal of eggs by the egg-laying females or by the active swimming of small nymphs is not known.

As the substratum began to freeze during winter the populations or part of the populations occupying the littoral zone moved out into deeper water. Only a few, dead *L. vespertina* were found in the ice probes, indicating that may fly nymphs are not freezing tolerant (see also Olsson 1981). On the other hand, the low number present in the probes indicates that the losses in the ice

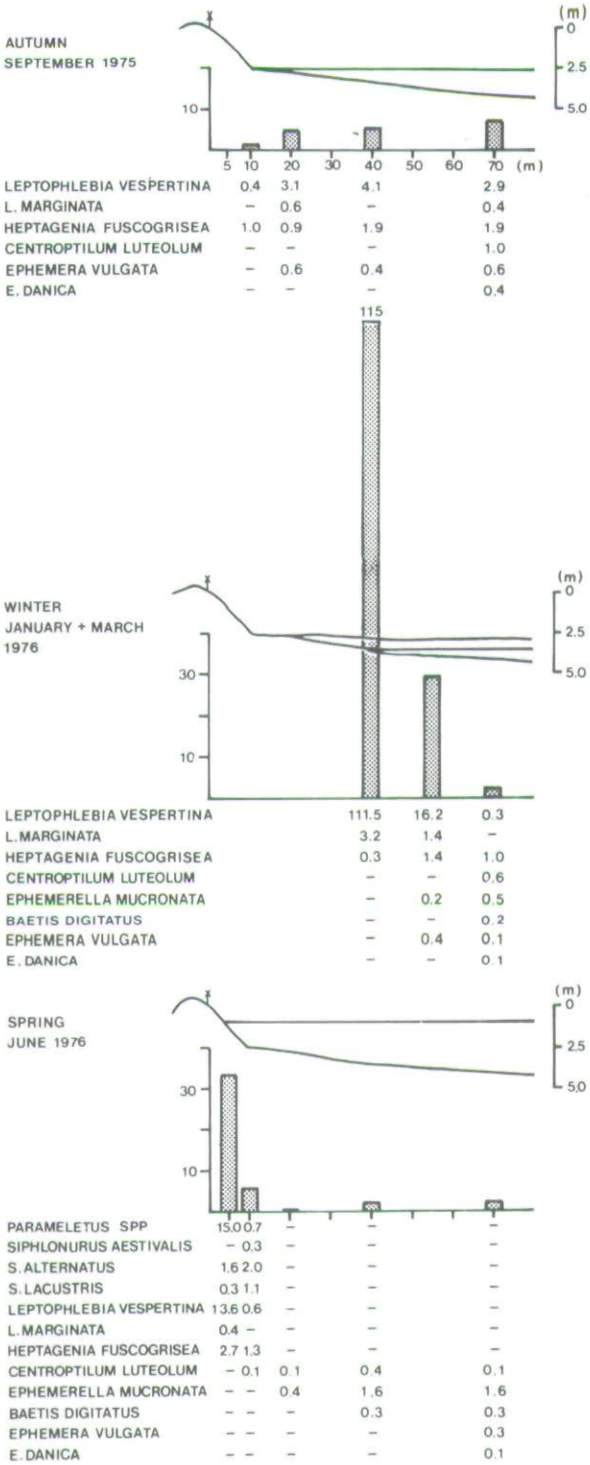

Fig. 6. Lateral distribution of mayfly nymphs in autumn, winter and spring at Sirapsbacken, the River Vindelälven, 1975–1976. Abundance is expressed as mean number per sample unit.

are insignificant. However, other invertebrate species at this locality, such as gastropods, pisids, trichopterans and chironomids are freezing tolerant and at least parts of these populations do overwinter enclosed in the ice (Olsson 1981).

Some ephemerid species kept well away from the ice while *L. vespertina* and *L. marginata* remained very close to it. Obviously this would entail some risk of being trapped in the growing ice. A similar positioning near the ice in *L. vespertina* has been observed in lakes, apparently in relation to a low oxygen content (Brittain and Nagell 1980). In the Vindelälven such distribution occurred without a corresponding low oxygen content. Possibly other factors, such as rich food supply, avoidance of fish predation and interspecific competition might produce the observed distribution.

In spring 1975 and 1976 the water level rose about 4 m within two weeks (Fig. 1). Several of the winter species promptly occupied the uppermost littoral zone (*Carex* belt) before the peak of the spring flood and stayed there till emergence. These species – *L. vespertina, L. marginata* and *H. fuscogrisea* – are all common in lake biotopes (see above). The fact that mainly lentic species perform this behaviour indicates that it might be an adaptation to avoid the rapid current in midriver during the spring flood (Clifford and Boerger 1974, Olsson and Söderström 1978). It would also allow the species to utilize the detritus in the former frozen littoral zone. During the spring flood most of the detritus from the autochthonous production (elodeids and isoetids) is washed away and some of this is deposited in the *Carex* belt.

Also several of the summer species such as *Siphlonurus* spp., common in lentic habitats (Brittain 1980), and *Parameletus* spp. showed the same preference for the uppermost littoral in spring. The presence of summer species shows that even small nymphs – not only nymphs ready to emerge – utilize the uppermost littoral in spring. This differs from the behaviour of plecopteran nymphs (Lillehammer 1965). In fact the main part of the growth of most lentic ephemerid species in the river does occur in this zone. Small nymphs of *S. lacustris* and *S. alternatus* were not found during the winter as they are in lake biotopes (Brittain 1980), but they were quite common in the littoral shortly after the ice had broken up possibly indicating that eggs had overwintered in the ice.

Lotic species (*B. digitatus* and *E. danica*) did not show the same preference for the shallow region. Even during the spring flood they were not found in the littoral. The same is true for the burrowing nymphs of *E. vulgata* which are common in lentic habitats (Kjellberg 1973). *E. mucronata* and *C. luteolum,* common in more lotic habitats (Ulfstrand 1968a), had an intermediate spring distribution with no tendency towards aggregation in the shallow zone.

The results shows that mayfly nymphs, especially several lentic winter species, perform pronounced seasonal lateral movements in this northern river. Changes in the lateral distribution take place mainly twice a year: in early winter when nymphs leave the littoral and move into deeper water in order to avoid the ice; and in spring when nymphs recolonize the littoral.

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