

The function of seasonal habitat shifts in two congeneric mayflies in a boreal river

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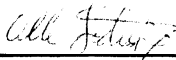
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Title The function of seasonal habitat shifts in two congeneric mayflies in a boreal river			
<p>Abstract Unregulated North Swedish rivers show large seasonal variations in their physical characteristics. During winter the whole littoral zone freezes solid, and in spring the water flow increases rapidly and the same areas become flooded. The two mayflies <i>Parameletus chelififer</i> and <i>P. minor</i> are common in the North Swedish river Vindelälven. They probably pass through a dormant egg stage in its mid-stream section. The first tiny nymphs appeared in January to March, but they did not become abundant until the ice broke up in May. At this time they migrated rapidly to the flooded upper littoral, some continuing into the tributaries. During the migration phase, both species used chemoreception to orient themselves towards the flooded areas. The shoreward migration allowed the nymphs to avoid high current velocity, and to utilize unexploited food resources. The two species differed with respect to utilization of the upper littoral. Most <i>P. chelififer</i> nymphs colonized a seasonal stream, while the <i>P. minor</i> nymphs were equally abundant at the river margin as in a seasonal stream. Both temperature and food quality differed between the river margin and the seasonal stream. Compared to <i>P. minor</i> specimens, those of <i>P. chelififer</i> showed a somewhat higher optimum temperature, and they gained advantage of the higher food quality observed in the seasonal stream. <i>P. chelififer</i> specimens colonizing a seasonal stream had higher growth rate, higher fecundity, and probably also advanced emergence as well as larger adult size compared with those remaining at the river margin. In addition mortality from fish predation may be lowered by utilizing shallow seasonal streams. Specimens of <i>P. minor</i> had higher growth rate, larger adult size and advanced emergence in the seasonal stream compared with those at the river margin. Nevertheless, fecundity was equal in both habitats and the mortality caused by predation seemed almost similar in both habitats. In most years <i>P. chelififer</i> specimens utilizing the seasonal stream thus obtain a higher fitness than those utilizing the river margin. In <i>P. minor</i> this difference was not so pronounced. However, due to mortality risks caused by an early desiccation of the seasonal stream, the long-term reproductive output of the two species probably varies irregularly in the two habitats.</p>			
<p>Key words Habitat utilization, diel activity, orientation, predation, life-history, temperature, food quality, mayflies, <i>Parameletus chelififer</i>, <i>Parameletus minor</i>.</p>			
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LIST OF PAPERS

The dissertation is based on the six papers listed below. References to these publications are made by using the Roman numerals.

- I. Olsson, T.I. and Söderström, O. 1978. Springtime migration and growth of *Parameletus chelifer* (Ephemeroptera) in a temporary stream in northern Sweden. - *Oikos* 31:284-289.
- II. Söderström, O. 1988. Changes in distribution and behaviour of two congeneric mayflies in a boreal river and its seasonal tributaries. - *Hydrobiologia* (accepted).
- III. Söderström, O. 1988. Environmental cues used in upstream orientation by *Parameletus chelifer* and *P. minor* (Ephemeroptera) nymphs; an experimental study. - *Hydrobiologia* (in press).
- IV. Söderström, O. and Nilsson, A.N. 1987. Do nymphs of *Parameletus chelifer* and *P. minor* (Ephemeroptera) reduce mortality from predation by occupying temporary habitats? - *Oecologia* (Berlin) 74:39-46.
- V. Söderström, O. and Johansson, A. Effect of different habitat use on growth, emergence, adult size, fecundity and parasitism in *Parameletus chelifer* and *P. minor* (Ephemeroptera). - Manuscript.
- VI. Söderström, O. Effects of temperature and food quality on life history parameters in *Parameletus chelifer* and *P. minor* (Ephemeroptera); a laboratory study. - Manuscript.

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Introduction

Mobile animals often shift between habitats. Most natural environments are heterogenous and fluctuate in one way or another. Consequently the suitability of a habitat for an organism may vary over its life-cycle. The animal then obviously benefits from being able to change habitats. Besides from abiotic factors also inter- and intraspecific interactions can exclude individuals from certain habitats (Partridge 1979). A seasonally recurrent habitat is often at the beginning a more or less empty niche in which suitability increases to a maximum soon after appearance, and then it declines to zero at disappearance (Baker 1978). The suitability of such a habitat to a potential inhabitant depends on habitat parameters and on life history characters of the colonist.

Individuals living in a seasonal environment frequently migrate. The major function of their migration is to colonize new habitats with an expected higher suitability (Fretwell 1972, Southwood 1962, 1977, Baker 1978, Dingle 1980). A colonist need to have certain attributes to properly find and utilize new habitats. Although not necessary, it is advantageous if the colonist can use some environmental cue(s) to find the habitat. Fast migration and a short generation time should also be favourable (Levontin 1965). It has been suggested that the timing of the migration may be linked to a particular ontogenetic stage (Baker 1978, Meier and Fivizzani 1980), while the orientation of the migration may be inherited and/or learned (Partridge 1979).

Mayflies constitute an important part of the benthic invertebrate fauna in unregulated North Swedish rivers (Olsson 1976). The life span of mayflies varies from about a month up to about 3 years (Brittain 1982). Most of the life is spent in the aquatic environment, either as eggs or as nymphs. In some species the eggs hatch immediately after oviposition, whereas the egg stage in other species takes about 10-11 months (Brittain 1982). In some species a true diapause is established. Emergence from nymph to adult takes place either from the water surface or from stones and vegetation along the

shore. In most species the terrestrial adult stages comprise subimagos and imagoes. Production of eggs and sperm is completed in the final nymphal instar but eggs and sperm become physiologically mature in the subimago stage. Adult mayflies do not eat and their life span varies from some hours up to two weeks. The mating behaviour of mayflies usually includes the formation of dense swarms of males. The females fly into the swarms and mating occurs almost immediately. Oviposition takes place at the water surface or in the water where all or a few eggs at a time are released (Brittain 1982).

Study area

The field work was carried out in the unregulated river Vindelälven at Sirapsbacken and in an adjacent seasonal stream and pond in northern Sweden (64°22'N, 19°28'E). The river rises in the Scandian mountain chain and the seasonal fluctuations in water flow are very large. The mean minimum and maximum flows in the studied area were 30 and 956 m³s⁻¹, respectively, between 1971 and 1986 (data from the Swedish Meteorological and Hydrological Institute). The river is covered with ice from the middle of November until the first half of May. During this period water velocity decrease and the littoral zone is succesively frozen solid as the water level retreats. At the end of the winter the frozen zone form a 40 to 50 m wide belt along the river margins (II, Olsson 1981). During spring, water velocity and water level rapidly increase, and the littoral zone is flooded. The spring flood usually has two peaks; one at the end of May and another in the middle of June. Sometimes the two spring floods coincide. The seasonal water level amplitude is normally about 4 m, with a maximum at the end of May or in June and a minimum in mid-April. The vegetation along the river margin is dominated by *Carex acuta* L.

The adjacent stream and pond, situated on an alluvial meadow, are classed as seasonal according to the major classes of wetlands recognized by Stewart and Kantrud (1971). The

seasonal stream is about 300 m long and 0.5 - 1 m wide, connecting the pond and the river. In most years the seasonal stream and pond become a part of an extensive river lagoon at the time of spring peak flood. They usually dry out in late June or mid-July. The vegetation in the seasonal stream and pond is dominated by *Calamagrostis canescens* (Web.) Roth. and *Deschampsia caespitosa* (L.).

Status and biology of the species studied

In 1908 and 1909 S. Bengtsson first described the mayfly species *Parameletus chelifer* and *P. minor*. Since then there has been some confusion whether one or two species of *Parameletus* occur in Fennoscandia, and also about the validity of the generic name. However, the validity of the generic name *Parameletus* Bengtsson, 1908 was established by Hubbard (1977). Recently Söderström and Nilsson (1986) showed that *Parameletus chelifer* and *P. minor* are two separate species. They are morphologically very similar and they are frequently found in the same habitat. The study of springtime migration of *Parameletus chelifer* (I) unfortunately included both *P. chelifer* and *P. minor*.

The first tiny nymphs of *Parameletus chelifer* Bengtsson and *P. minor* (Bengtsson) appear in the mid-stream section of the river Vindelälven in late winter to early spring (II). When the ice breaks up they migrate to the river margins as well as into seasonal streams (II). Nymphs of *P. chelifer* and *P. minor* are fine particulate detritivores (V). Individuals of both species are able to orient by specifically different environmental cues (III). After completed nymphal development both species have a short emergence period (V). Although I have not seen the swarming of these species, Brinck (1957) reported that it took place above the mid-stream section of rivers. After mating females probably deposit their eggs in the mid-stream section of the river.

Dormancy

During environmental conditions which do not permit the individual to escape elsewhere, it is advantageous to be in a dormant stage (Southwood 1977). In cold temperate areas, arrested development during winter is often regarded as an adaptation to severe environmental conditions which may otherwise incur low survival rates (Grüm 1975, Danks 1987).

Although intense sampling was performed during autumn and winter I did not find nymphs of *Parameletus chelifera* and *P. minor* until January, then in very low numbers. Not until the ice broke up nymphs of both species became abundant. Thus, a period of 6-10 months had passed since the eggs were deposited (II). Illumination beneath the snow and the ice increased markedly shortly after 8 March in 1981, when the sun reached this part of the river (Fig. 1). Water temperature did not increase until 5 May (Fig. 1). At this time, the mean body length (\pm 95% C.I.) of nymphs of *P. chelifera* and *P. minor* was 4.7 ± 0.28 mm (n=29) and 5.6 ± 0.16 mm (n=68), respectively.

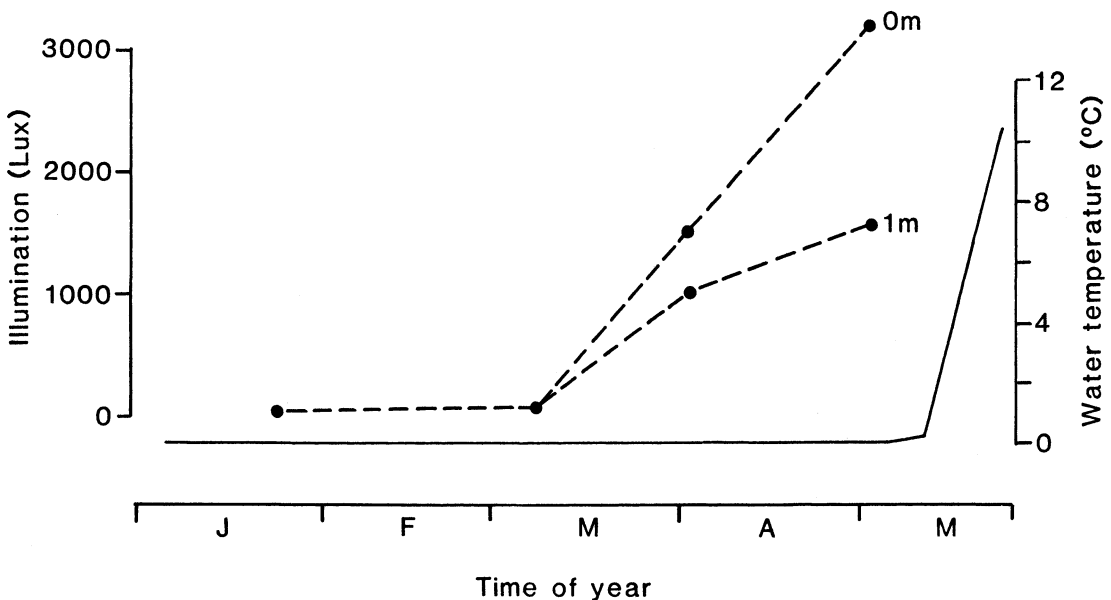


Fig. 1. Illumination (lux, broken lines) at two depths (0 and 1 m) below the ice 70 m out from the river bank and water temperature (solid line, data from the Swedish Meteorological and Hydrological Institute) during the winter of 1981.

This is about half the size of full grown nymphs. Thus, if the eggs had passed through a dormant stage, the increase in illumination intensity and/or daylength is likely to have been involved in terminating this stage. Water temperature apparently rose too late to be influential (cf. Fig. 1). I find it very likely that egg dormancy occurs in these two species. Similar evidence comes from North American *Parameletus* spp. (Edmunds et al. 1976, Clifford 1982). The nymphal size of *P. chelifera* and *P. minor* at the time when the upper littoral and the seasonal stream thawed in spring indicates that the eggs were deposited near mid-stream and not in the littoral. A reason for this may be that the eggs are not cold-hardy as also indicated for *Siphonurus aestivalis* Etn. (Olsson 1983).

Migration

In the definition of migration some authors have included long-distance round trip movements (e.g. Endler 1977). Recent studies define migration as "the act of moving from one spatial unit to another" (Baker 1978), or as "specialized behaviour especially evolved for the displacement of the individual in space" (Dingle 1980).

In late winter, nymphs of *P. chelifera* and *P. minor* move from the deeper parts of the river to shallow areas close to the ice border at the river margin (II). When the ice breaks up they rapidly colonize the uppermost littoral at the river margin as well as seasonal streams (I and II). This may be adaptive for several reasons. By the shoreward spring migration nymphs of both species leave a habitat with a high current velocity and a poor food supply, and colonize habitats with markedly lower velocities and rich food supplies (Fig. 2). The major reasons proposed in this thesis for such movements are a) search for unexploited resources (e.g. food, I, II and V), and b) escape from unfavourable abiotic and biotic conditions (e.g. high water velocity and heavy predation pressure, I, II and IV) (see also Söderström 1987 for review). After emergence and mating, females of *P.*

chelifer and *P. minor* have to fly back to the main river for oviposition (see discussion on dormancy). Thus, both species perform true migrations.

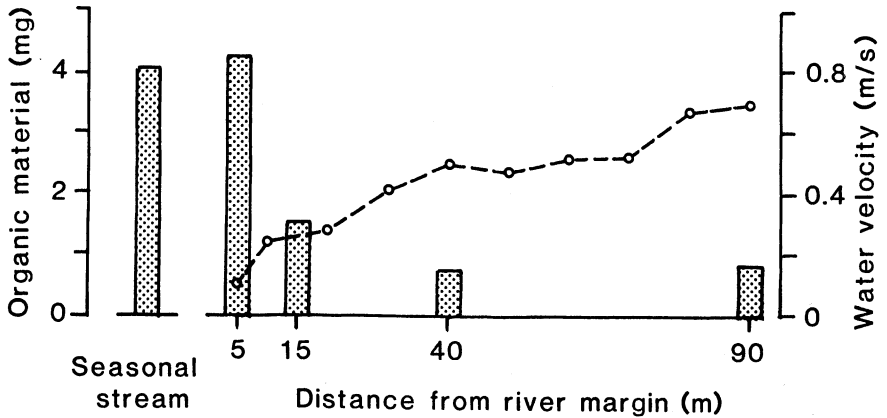


Fig. 2. Dry weight of organic material (shaded bars) in the upper two cm of bottom sediment at different parts of the river Vindelälven in the spring of 1983. Samples of organic material in the seasonal stream and at the 5 metre point in the river were taken in the spring of 1985. The broken line shows the current velocity in different parts of the river during spring flood in 1979. Measurements were made 20 cm below the water surface. Current velocity in the seasonal stream was below 5 cm per second.

The suitability of seasonal habitats usually declines rapidly (Baker 1978). Hence rapid colonization seems advantageous. The nymphs of *P. chelifera* and *P. minor* colonize the seasonal stream in vast numbers each spring (I,II). Experimental studies showed that *P. chelifera* and *P. minor* used gradients in pH and DOM, respectively, as cues for their orientation towards the seasonal habitats (III). After having reached the stream the nymphs lost their capacity to detect differences in water quality. Then they oriented by a temperature gradient (III). The upstream migration behaviour is limited to a short period in spring. The timing of this migration period seem to differ between the two species, *P. chelifera* have a somewhat earlier migration than does *P. minor* (III).

Differences in mortality from predation

In a predator-prey situation, natural selection will favour individuals of the prey population that are better able to escape predation. However selection on predators favours new adaptations to increase the predator's efficiency. Thus two selective forces will continually interact with one another (Pianka 1983). Aquatic insects have evolved a wide variety of antipredator behaviours to decrease the probability of being found and/or consumed (Peckarsky 1984).

Nymphs of *P. chelifera* and *P. minor* are consumed by a variety of fish and invertebrate predators (IV). The invertebrate predators were about equally abundant at the river margin as in the seasonal pond. Fish predators visited the seasonal stream and pond only during the short time of peak flood, whereas they were continuously present at the river margin.

Laboratory experiments showed that invertebrate predators consumed less *Parameletus* nymphs than expected from their relative abundance in a situation corresponding to that in the seasonal pond. However, in a situation corresponding to that at the river margin invertebrate predators consumed *Parameletus* nymphs in proportion to their relative abundance (IV). This difference was probably due to the much higher abundance of mosquito larvae in the seasonal pond than at the river margin (IV). The consumption of nymphs of *P. chelifera* and *P. minor* by fish was generally lower in the seasonal pond than at the river margin. However pike (*Esox lucius* L.) temporarily increased the predatory pressure in the pond markedly (IV).

Nocturnal activity has been interpreted as an antipredator behaviour (Thorne 1969, Allan 1978, Townsend 1980). Small nymphs of *P. chelifera* and *P. minor* showed a nocturnal activity at the river margin while they adopted a diurnal activity pattern as soon as they entered the seasonal stream (I,II). However, at the same time as fish utilized the seasonal stream (during peak flood) *P. chelifera* and *P. minor* shifted back to nocturnal activity. As nymphs of *P. chelifera* and *P. minor* used chemoreception for orientation (III) they

may detect fish by chemoreception. It has been suggested that other mayfly species avoid stonefly predators by chemical stimuli (Peckarsky 1980). However, other mechanisms such as long-range detection of mechanical waves could be involved (Peckarsky 1984).

At the river margin nymphs of *P. minor* were consumed according to expectance, while nymphs of *P. chelifera* were consumed by fish in a higher proportion than expected. This difference may be due to a more cryptic behaviour of *P. minor*. Specimens of *P. minor* had a lower temperature "optimum" than those of *P. chelifera* (VI). Thus, at the river margin, nymphs of *P. minor* can live and maintain a high growth rate in the cooler water within the dense vegetation. To achieve a high growth rate nymphs of *P. chelifera* are forced out to more exposed places with higher temperature but also with a higher risk of being captured by fish. Almost no individuals of *P. chelifera* emerged at the river margin although they were fairly abundant here a few weeks before emergence (V). Thus, nymphs of *P. minor* and especially *P. chelifera* seemed to reduce mortality from fish predation by colonizing the seasonal stream.

Intraspecific differences in growth and reproduction

The habitat utilized for growth and emergence affected survival and reproductive success of both *P. minor* and *P. chelifera*. By utilizing the seasonal stream, specimens of *P. minor* obtained a higher growth rate, a shortening in developmental time and larger adult size compared to those at the river margin (V). However, fecundity was equal at both sites (V). Both temperature and food quality were crucial for most life history parameters of *P. minor* (VI). However, as *P. minor* specimens seemed to have an optimum temperature for growth and reproduction at about +10°C, the water in the seasonal stream may have been too warm. This together with the small effect of food quality within the range observed in the field, may explain why no difference in fecundity was obtained.

If the product of fecundity and chance of survival is a good estimate of fitness, specimens of *P. minor* should obtain a higher fitness in some years by utilizing the seasonal stream (cf IV). Further, if males emerging from both habitats should participate in the same swarms, males from the seasonal stream should probably obtain a higher mating success due to larger size (V).

Specimens of *P. chelifera* grew faster and probably obtained larger adult size by utilizing the seasonal stream than by utilizing the river margin. Further, fecundity was higher in the seasonal stream compared to at the river margin. Specimens of *P. chelifera* seemed to have an optimum temperature for growth and reproduction at about +15°C (VI). The water temperature in the seasonal stream seldom reached too high values. Food quality was crucial to many life history parameters in *P. chelifera*, also in the range observed in the field (V and VI). By utilizing the seasonal stream, *P. chelifera* gained the advantages of a more optimal water temperature and of a higher food quality. Survival rates were probably also increased by leaving the river margin (IV). Thus a higher fitness was reached in the seasonal stream in all years studied. Given the same assumption as for *P. minor*, males of *P. chelifera* from the seasonal stream should obtain a higher mating success than those from the river margin.

Interspecific differences in adaptations to the seasonal habitats

Except differences in adult size (*P. chelifera* being larger) and fecundity (*P. chelifera* producing more eggs) the very similar mayflies *P. chelifera* and *P. minor* showed separate emergence periods (V). Temporal separation may be expected in such closely related species living in the same habitat (Pianka 1983), which has also been found in other closely related mayflies (Brittain 1978). Nymphs of *P. chelifera* and *P. minor* used different environmental cues for orientation, directing them to their areas of suitable growth (III). Nymphs of *P. minor* utilized the two habitats equally frequent, while

the vast majority of *P. chelifera* nymphs utilized the seasonal stream. These differences were probably related to interspecific differences with respect to optimum water temperature, food demand and vulnerability to predators (IV, V and VI). Specimens of *P. chelifera* had a higher optimum temperature and they seemed to gain more from a somewhat higher food quality. They probably also obtained a higher survival rate by utilizing the seasonal stream compared with *P. minor* specimens.

Only *P. chelifera* was found to be infested by mermithid nematodes. All females and probably all males infested were sterile. These specimens survived, emerged and they probably also participated in the mating. The nematode not only caused a great reduction in fecundity of infested females. It could also affect the reproductive success of uninfested males and females if uninfested males mate with sterile females and vice versa.

Both habitats showed a high predictability but differed with respect to constancy (cf. Stearns 1981), the seasonal stream showed a lower constancy. Thus, individuals utilizing the seasonal stream are exposed to a high mortality risk due to desiccation. In most years *P. minor* specimens were more or less unaffected by desiccation while those of *P. chelifera* suffered a high mortality in some years caused by their longer developmental period (V). In extreme years, when the seasonal stream dries up too early, almost all *P. chelifera* individuals are likely to die before emergence. Only those few remaining in the river will have a chance to emerge. As many individuals remain in the river the effect of desiccation will be less drastic for the *P. minor* population. In 1987 the seasonal stream dried out twice in May, but it was later refilled with rain water and with water from a late spring peak flood. In this exceptional year all *P. minor* and *P. chelifera* specimens that colonized the seasonal stream in early May died. Only those colonizing late, at the peak flood, seemed to survive. Thus the long-term reproductive output of the two species will probably vary irregularly between the two habitats.

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References

- Allan, J.D. 1978. Trout predation and the size composition of stream drift. - *Limnology and Oceanography*. 23:1231-1237.
- Baker, R.R. 1978. The evolutionary ecology of animal migration. Holmes and Meier Publ., Inc., New York, 1012 pp.
- Bengtsson, S. 1908. Berättelse öfver en resa i entomologiskt syfte till mellersta Sverige sommaren 1907. - *K. svenska Vetensk. Akad. Årsb.* 6:237-246.
- ". 1909. Beiträge zur Kenntnis der paläarktischen Ephemeriden. - *Acta Univ. Lund, (N.F.), Afd. 2, 5(4):*1-19.
- Brinck, P. 1957. Reproductive system and mating in Ephemeroptera. - *Opusc. Ent.* 22(1): 1-37.
- Brittain, J.E. 1978. The Ephemeroptera of Ovre Heimdalsvatn. - *Holarct. Ecol.* 1:239-254.
- ". 1982. Biology of mayflies. - *Ann. Rev. Entomol.* 27:119-147.
- Clifford, H. F. 1982. Life cycles of mayflies (Ephemeroptera), with special reference to voltinism. - *Quaestiones Entomologicae* 18:15-90.
- Danks, H.V. 1987. Insect dormancy: an ecological perspective. Biological Survey of Canada Monograph Series No. 1. Biological Survey of Canada (Terrestrial Arthropods), National Museum of Natural Sciences, Ottawa. 437 pp.
- Dingle, H. 1980. Ecology and evolution of migration. In: Gauthreaux, S.A.Jr. (Ed.), Animal migration, orientation, and navigation. Acad. Press, New York, 1-101.
- Edmunds, G.F.Jr., Jensen, S.L. and Berner, L. 1976. The mayflies of North and Central America. University of Minnesota Press. Minneapolis 330 pp.
- Endler, J.A. 1977. Geographic variation, speciation and clines. Princeton Univ. Press, New Jersey 248 pp.
- Fretwell, S.D. 1972. Populations in a seasonal environment. Princeton Univ. Press, Princeton, New Jersey. 217 pp.
- Grüm, L. 1975. Mortality patterns in carabid populations. - *Ekol. Pol.* 23:649-665.
- Hubbard, M. D. 1977. The validity of the generic name *Parameletus* Bengtsson (Ephemeroptera: Siphonuridae). - *Proc. ent. Soc. Wash.* 79:409-410.
- Levontin, R.C. 1965. Selection for colonizing ability. In: Baker, H.G. and G.L. Stebbins, (Eds.), The genetics of colonizing species. Acad. Press, New York, 79-91.
- Meier, A.H. and Fivizzani, A.J. 1980. Physiology of migration. In: Gauthreaux, S.A.Jr. (Ed.), Animal migration, orientation, and navigation. Acad. Press. New York, 225-282.
- Olsson, T.I. 1976. Benthos inventories in rivers by means of the Ekman grab. A study of the method with recommendations. - National Swedish Environmental Protection Board PM 749 (in Swedish with English summary).
- ". 1981. Overwintering of benthic macroinvertebrates in ice and frozen sediment in a North Swedish river. - *Holarct. Ecol.* 4:161-166.

- "- . 1983. Seasonal variation in lateral distribution of mayfly nymphs in a boreal river. - *Holarct. Ecol.* 6:333-339.
- Partridge, L. 1979. Habitat selection. In: Krebs, J.R. and N.B. Davies, (Eds.), *Behavioural ecology an evolutionary approach*. Blackwell Sci. Publ., Oxford, 351-376.
- Peckarsky, B.L. 1980. Predator-prey interactions between stoneflies and mayflies: Behavioural observations. - *Ecology* 61: 932-943.
- "- . 1984. Predator-prey interactions among aquatic insects. In: Resh, V.H. and Rosenberg, D.M.(Eds.), *The ecology of aquatic insects*. Praeger Publ., New York. 196-254.
- Pianka, E.R. 1983. *Evolutionary ecology*. Harper and Row Publ., New York, third edition 415 pp.
- Southwood, T.R.E. 1962. Migration of terrestrial arthropods in relation to habitat. - *Biol. Rev.* 37:171-214.
- "- . 1977. Habitat, the template for ecological strategies? - *J. Anim. Ecol.* 46:337-365.
- Stearns, S.C. 1981. On measuring fluctuating environments: Predictability, constancy, and contingency. - *Ecology* 62(1):185-199.
- Stewart, R.E. and Kantrud, H.A. 1971. Classification of natural ponds and lakes in the glaciated prairie region. - USDI, FWS. Resource publ. 92, 57 pp.
- Söderström, O. 1987. Upstream movements of invertebrates in running waters - a review. - *Arch. Hydrobiol.* (in press).
- Söderström, O. and Nilsson, J. 1986. Redescription of *Parameletus chelififer* Bengtsson and *P. minor* (Bengtsson), with keys to nymphs and adult stages of the Fennoscandian species of Siphonuridae (Ephemeroptera). - *Ent. Scand.* 17:107-117.
- Thorne, M.J. 1969. Behaviour of the caddisfly larva *Potamophylax stellatus* (Curtis)(Trichoptera). - *Proc. R. ent. Soc. London (A)*. 44:91-110.
- Townsend, C.R. 1980. *The ecology of streams and rivers*. Studies in Biology no 122. Edward Arnold London 68 pp.