

Environmental cues used in upstream orientation by *Parameletus chelififer* and *P. minor* (Ephemeroptera) nymphs; an experimental study

Olle Söderström

Dept. of Animal Ecology, University of Umeå, S-901 87 Umeå/Sweden

Received 17 November 1986; in revised form 13 May 1987; accepted 4 June 1987

Key words: Ephemeroptera, upstream orientation, pH, DOM, temperature

Abstract

Experiments using a plexiglass Y-maze fluvium showed that nymphs of *Parameletus chelififer* and *Parameletus minor* each used different environmental cues to orient. *P. chelififer* nymphs reacted to pH while nymphs of *P. minor* were very sensitive to concentration of dissolved organic matter. The capacity to detect these water quality differences was lost as soon as the nymphs reached seasonally submerged areas suitable for growth at the margin of the river. When nymphs of both species had reached their growing areas, water temperature became the crucial cue for orientation.

Introduction

In a patchy environment it is advantageous to an organism to have the capacity to discriminate among the stimuli surrounding it. For aquatic invertebrates, such stimuli include water temperature and differing chemical substances. The seasonal distribution of many aquatic invertebrates in temperate areas seems to be largely governed by variations in temperature (Clampitt, 1972; Horst & Costa, 1975; Boag & Bentz, 1980; Olsson, 1982 and 1983). Many aquatic invertebrates have the capacity to detect and orient towards distant food sources by olfactory and/or gustatory receptors (Van Dongen, 1956; Michelson, 1960; Kohn, 1961; Kleerekoper & Mogensen, 1963; Castilla & Crisp, 1970; Jager, 1971; Townsend, 1973; Burdosh *et al.*, 1982; Thomas, 1982; Sterry *et al.*, 1983 and Brönmark, 1985).

Olfactory receptors may also be used to detect predators (Kohn, 1961; Castilla & Crisp, 1970; Peckarsky, 1980; Townsend & McCarthy, 1980; Williams & Moore, 1982 and 1985, Croll, 1983; Andersson *et*

al., 1986) as well as conspecifics (Williams & Moore, 1985).

Animals that use temporary habitats as areas for growth and emergence must colonize them quickly as the suitability of these habitats usually declines rapidly (Baker, 1978). In northern Scandinavia nymphs of two mayflies, *Parameletus chelififer* Bengtsson and *P. minor* (Bengtsson), colonize temporary habitats such as seasonal stream in the hundreds of thousands each spring (Olsson & Söderström, 1978). The high water temperature and rich food supply in the seasonal stream allows faster growth than in the river (Olsson & Söderström, 1978). As this springtime migration is so pronounced, it would appear probable that the nymphs have receptors which make them capable of quick and accurate orientation toward these temporary feeding areas.

The purpose of the present study was to examine which if any environmental cues nymphs of *P. chelififer* and *P. minor* use when orienting to seasonal streams and whether the propensity to migrate was affected by season.

Material and methods

Experiments were carried out at Sirapsbacken (64°22'N, 19°28'E) on the river Vindelälven in northern Sweden. On this part of the river, several small seasonal streams flowed into the main river. Some of them drained alluvial meadows. These latter streams were fed by the snow melt in the beginning of spring (early May) and later by the rising water of the main river (mid May to mid June). They dried up completely in late June to mid July. The seasonal stream and the surrounding section of the river Vindelälven where nymphs were collected and field experiments were performed were described by Olsson & Söderström (1978) and Olsson (1983). During early spring this seasonal stream was more acid and had a higher loading of organic carbon than had the main river (cf. Fig. 2).

All experiments were performed in a plexiglass Y-maze fluvium (Fig. 1). Water from two 25 l plastic headboxes ran into the fluvium. The water flow through both inlets was equal at an average of 1.15 l/min. through each arm during a trial. In the field the headboxes were placed in a box isolated with styrolite. Behind the headboxes a black plastic sheet (1 m high and 3 m long) was mounted to avoid interference from landmarks. To exclude possible interference from celestial cues, some experiments were performed in the laboratory.

Water from the headboxes was run for one minute before the nymphs were placed at the end of the common down-channel (A in Fig. 1). The nymphs were kept outside of the common down-channel by a plastic door for one minute before the start of each trial. When the nymphs had passed half the length of each arm (L in Fig. 1), they were counted and removed from the channel. Each trial lasted for 20 min, and nymphs that were downstream of line L after that time were regarded as non-migrating. In experiment no. 2 the proportion of migrating number of nymphs relative to total number in each species was examined in all trials. In all other experiments only nymphs that made a choice were considered.

The nymphs were caught by a handnet in the main river and in the seasonal stream respectively. Nymphs from the river had not been exposed to water from the seasonal stream.

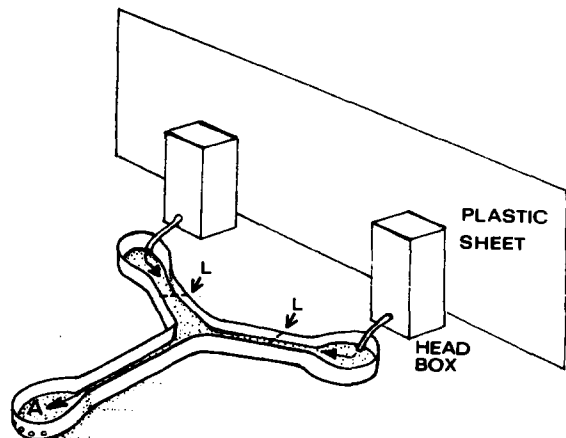


Fig. 1. The Y-maze fluvium used in the experiments. A: starting point for the nymphs at the beginning of each trial, L: line which nymphs had to pass before they were considered as making a choice.

The field experiments were carried out between 14 and 19 May, 1981, 6 and 9 May, 1983, and 10 and 11 May, 1986. These periods were at the beginning of the migration phase of the nymphs. Each experiment was conducted within half an hour after the nymphs were collected.

The laboratory experiments were carried out between 31 May and 14 June in 1983, which was late with respect to the migration phase (Olsson & Söderström, 1978). Nymphs used in the laboratory experiments were taken to the laboratory within two hours after they were collected. They were kept overnight at +10°C and the experiments started the next day.

Either 50 or 100 specimens were used in each trial. After each trial the nymphs were preserved in 70% alcohol for later identification. Nymphal identification followed Söderström & Nilsson (1986).

To investigate the nymphal reaction to different water qualities, water used was from the river Vindelälven, from the nearby seasonal stream, Umeå tap water, from lake Hamptjärn, and peat moss water (cf. Fig. 2). Peat moss water was prepared by mixing approximately one kg peat moss (wet weight) with 10 l of Umeå tap water for 12 hours. This water was filtered through a 90 µm filter and 2 l of this extract was diluted with 23 l of Umeå tap water.

Experiment no. 1 was conducted to examine possible errors in the experimental design. Thirteen trials were carried out to evaluate the nymphal

choice in relation to left and right arm and headbox 1 and 2, respectively, of the fluvium. Testwater and nymphs were from the main river. These trials were performed both in 1981 and in 1983.

Experiment no. 2 was conducted on both species to evaluate the rate of migration in early (7 and 8 May) and late (31 May) spring 1983. Experimental water and nymphs were taken from the main river.

In experiment no. 3 the effects of acidity were investigated. Nymphs from the main river were exposed to natural river water (pH 6.4, DOM 30.2) and acidified river water (pH 5.8, DOM 30.2). Acidification was accomplished by the addition of sulphuric acid. Artificially acidified water corresponded to water from the seasonal stream (pH 5.8.).

Experiment no. 4 was performed in 1986 to examine the effect of dissolved organic material (DOM) on the nymphal choice. Nymphs from the main river were exposed to natural water from the seasonal stream (pH 5.8, DOM 52.1) and acidified river water (pH 5.8, DOM 30.2).

Experiment no. 5 was performed to examine the combined effect of pH and DOM. Nymphs and experimental water were taken from the seasonal stream (pH 5.8, DOM 52.1) and from the main river (pH 6.4, DOM 30.2). During 1983 a laboratory experiment with nymphs of *P. minor* from the main river was also performed. In this latter experiment nymphs were exposed to water from five different sources.

In experiment no. 6 nymphal choice with respect to water temperature was examined in 10 trials. In each trial water with natural and aberrant temperature was offered. The aberrant temperature in each successive trial with nymphs and water from the main river was respectively +0.5 °C, +1.5 °C, +3.1 °C, +5.4 °C and +8.1 °C above the field temperature. The aberrant temperature in each successive trial with nymphs and water from the seasonal stream was respectively +1.0 °C, +3.4 °C, +5.0 °C, +7.0 °C and +8.6 °C above the field temperature.

Results

When the fluvium was examined (experiment

no. 1), neither bias towards any direction or headbox (both species; χ^2 -test, $P > 0.05$) nor between years (both species; χ^2 -test, $P > 0.05$) was found. When results under similar conditions for those nymphs making choice from the field and the laboratory experiments were compared, no significant difference was observed (both species; χ^2 -test, $P > 0.05$). Thus, in the following, experiments conducted in the field and in the laboratory as well as during different years will be treated together.

From experiment no. 2 it was apparent that *P. minor* nymphs moved upstream intensively both in early and late spring (mean 90% and 78% respectively, $\chi^2 = 0.8$, $P > 0.05$). Nymphs of *P. chelifera* showed a markedly lower rate of migration in late compared with early spring (mean 18% and 74% respectively, $\chi^2 = 30.7$, $P < 0.001$).

When nymphs of *P. chelifera* from the main river were exposed to normal and acidified river water (experiment no. 3), they were significantly more prone to move upstream through the acid water arm ($\chi^2 = 4.4$, $P < 0.05$) while nymphs of *P. minor* did not show any such preference ($\chi^2 = 0.3$, $P > 0.05$) (Fig. 2a).

In experiment no. 4, nymphs of *P. minor* from the main river preferred water with a high loading of DOM ($\chi^2 = 4.2$, $P < 0.05$) while nymphs of *P. chelifera* did not show any such preference ($\chi^2 = 1.6$, $P > 0.05$) (Fig. 2b).

In experiment no. 5, nymphs of both *P. chelifera* and *P. minor* collected in the main river showed significant attraction to water from the seasonal stream rather than from the main river (*P. chelifera* $\chi^2 = 3.9$, $P < 0.05$; *P. minor* $\chi^2 = 30.6$, $P < 0.001$) (Fig. 2c). Nymphs of *P. minor* collected in the main river showed a significant attraction to water from the seasonal stream, lake Hamptjärn and peat moss water compared with Umeå tap water ($P < 0.001$ in all experiments (Fig. 2d–f). These later experiments were performed in the laboratory and were only performed on *P. minor* as *P. chelifera* nymphs showed a significant decrease in rate of upstream migration during late spring. None of the nymphs collected in the seasonal stream showed any preference between the two water qualities offered (*P. chelifera* $\chi^2 = 2.6$, $P > 0.05$; *P. minor* $\chi^2 = 0.9$, $P > 0.05$) (Fig. 3a).

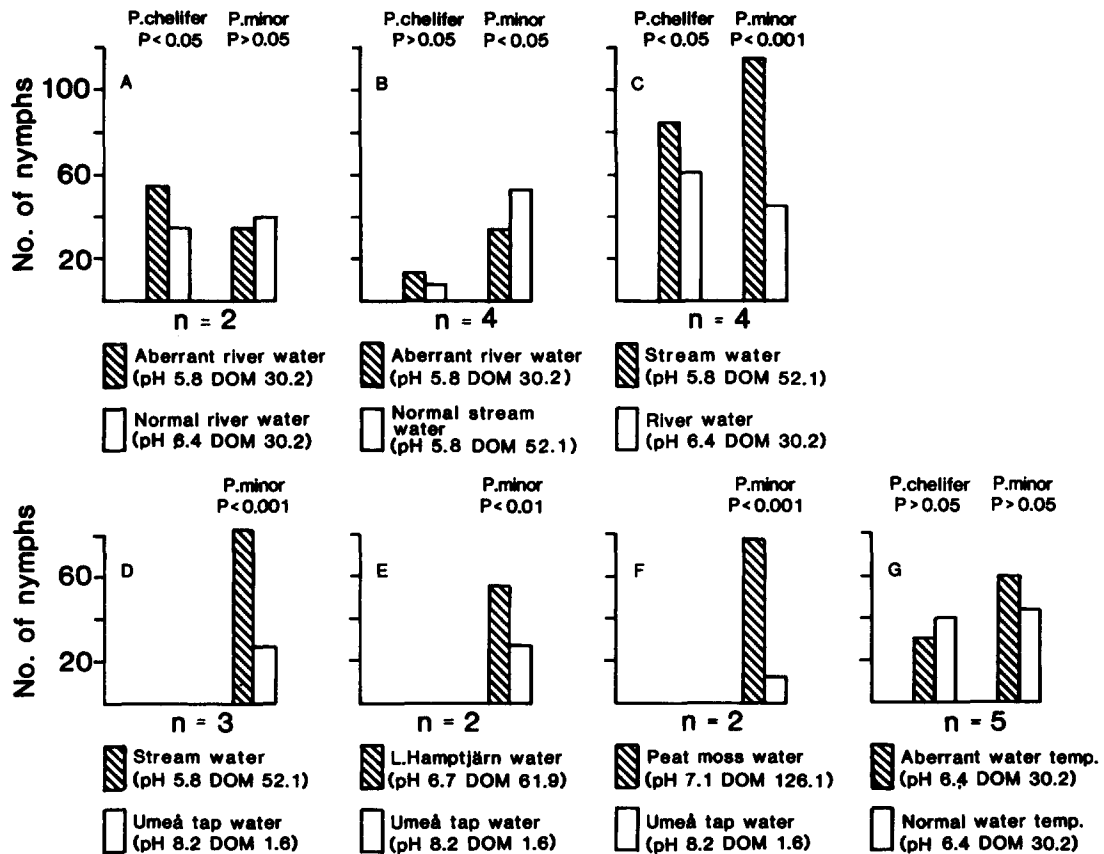


Fig. 2. Effect of water quality and temperature on orientation of nymphs taken from the river. The bars represent sum of all trials (=n) in each experiment. Levels of significance from χ^2 -tests are given. A: Effect of pH, B: Effect of DOM, C–F: Combined effect of pH and DOM, G: Effect of water temperature (Normal temp; 7.5 °C, Aberrant temp; 7.5 +0.5 – 8.1 °C).

In experiment no. 6 none of the nymphs of either species taken from the river showed any preference to any temperature in the five separate trials ($P > 0.05$ in all trials for both species). Consequently, no significant correlation between the nymphs' choice and ΔT (ΔT = aberrant water temperature minus natural water temperature) could be found. When all trials were taken together, no preference to any temperature could be found (*P. chelifera* $\chi^2 = 1.2$, $P > 0.05$; *P. minor* $\chi^2 = 2.4$, $P > 0.05$) (Fig. 2g).

Nymphs of both species taken from the seasonal stream showed a significant attraction to water of natural temperature in the five separate trials ($P < 0.05$ in all trials for both species). Consequently, when all five trials were taken together, nymphs of both species were attracted to natural water temperature (*P. chelifera* $\chi^2 = 24.1$, $P < 0.001$; *P. minor* $\chi^2 = 43.3$, $P < 0.001$) (Fig. 3b). No significant corre-

lation between nymphs' choice and ΔT could be found.

Discussion

The rate of upstream migration of *P. minor* nymphs late in the spring of 1983 was only slowed down to about 75% of the early spring values. In *P. chelifera* nymphs, on the other hand, the rate of migration was markedly reduced in late spring 1983. These results indicated that the migration occurred earlier in *P. chelifera* than in *P. minor*. This would imply that *P. chelifera* nymphs colonize the seasonal stream in greater numbers before *P. minor* nymphs do so, which seems to be confirmed by other data (Söderström unpubl.).

Although the timing of the migration period

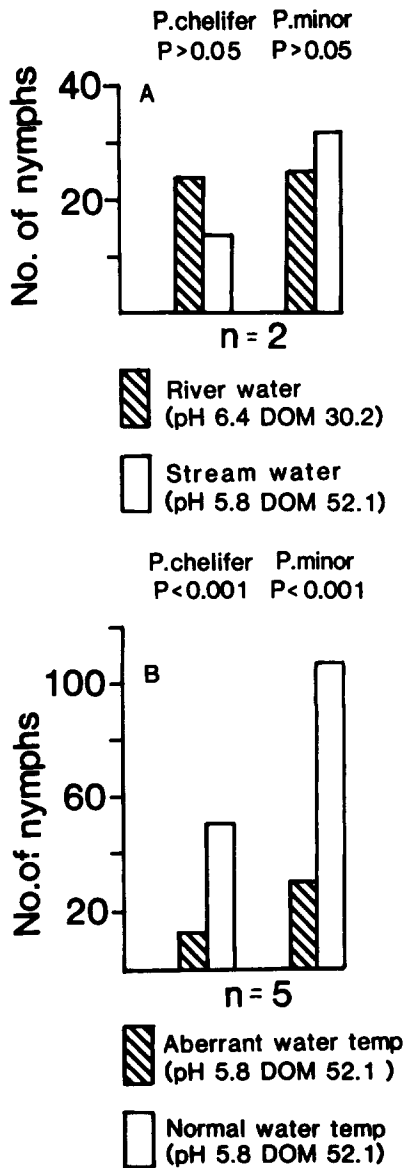


Fig. 3. Effect of water quality and temperature on orientation of nymphs taken from the seasonal stream. The bars represent sum of all trials (=n) in each experiment. Level of significance from χ^2 -test are given. A: Combined effect of pH and DOM, B: Effect of water temperature (Normal temp; 9.5°C, Aberrant temp; 9.5+1.0 – 8.5°C).

differed between the two species, upstream migration of each was limited to a short period during spring. It has been shown that the period of heavy upstream migration is restricted to a short period during the year for many aquatic invertebrates

(Neave, 1930; Hayden & Clifford, 1974; Olsson & Söderström, 1978).

The major reasons for upstream migration seems to be: 1) search for unexploited resources such as food and/or space (e.g. Bishop & Hynes, 1969; Olsson & Söderström, 1978), 2) search for suitable emergence, puppation or mating sites (e.g. Hultin *et al.*, 1969; Otto, 1971; Goedmaker & Pinkster, 1981) and 3) avoidance of unfavourable abiotic conditions e.g. (Hayden & Clifford, 1974; Olsson & Söderström, 1978).

Behavioural shifts leading to upstream movements may be governed by an annual physiological rhythm. In *P. chelifera* and *P. minor* an annual rhythm should prepare the nymphs for migrational response as soon as the seasonal streams become available to colonization.

Nymphs of *P. chelifera* from the river showed a significant attraction to acidified water whereas no reaction was found in nymphs of *P. minor* (Fig. 2a). On the other hand nymphs of *P. minor* collected in the river showed a significant attraction to water with the highest content of DOM while nymphs of *P. chelifera* were unaffected (Fig. 2b). Thus there appears to be species-specific chemoreception for orientation. The response to water with a high load of DOM shown by nymphs of *P. minor* was not restricted to water taken from the seasonal stream (Fig. 2e–f). Although there was a great variation in pH of the testwaters in these experiments, pH did not influence the *P. minor* results (cf. Fig. 2a).

The reactions to either pH or DOM have essentially the same effect, serving to orient the nymphs to their food supply. To achieve fast growth, both species, which feed by collecting fine particulated organic matter (FPOM) (Söderström & Johansson unpubl.), prefer areas with high loading of organic matter (Olsson & Söderström 1978). FPOM is converted to DOM (Cummins *et al.*, 1973) by microbial metabolism. Water naturally rich in DOM is often found to have low pH values (Wetzel, 1983). Thus it seems very reasonable to believe that nymphs of *P. chelifera* and *P. minor* have developed sensory mechanisms to accurately detect areas rich in food.

Thomas (1982) showed that the reactions of *Biomphalaria glabrata* (Say) (Gastropoda) to certain amino acids and plant chemicals were partially linked to

the age of the animal. In nymphs of *P. chelifera* and *P. minor* age and/or physiological status seemed crucial. As soon as these nymphs had reached areas suitable for growth, they did not react to high loadings of DOM or low pH values (Fig. 3a).

The effect of temperature with respect to orientation of *P. chelifera* and *P. minor* nymphs differed depending on the migrational stage of the nymphs. To nymphs in their premigrational stage i.e., those taken from the river, temperature had no effect on choice (Fig. 2g). Nymphs in a postmigrational stage, on the other hand, reacted heavily to temperature (Fig. 3b). A temperature regime close to that at the collection site was preferred.

In the premigrational stage, nymphs of *P. chelifera* and *P. minor* seemed prepared to make a habitat shift. It seems reasonable that temperature should not be factor in the search of habitats suitable for growth. Temperature of the seasonal habitats, which these nymphs colonize, vary a great deal during early spring (Olsson & Söderström, 1978; Söderström unpubl.).

Temperature has been shown to act as a trigger for the seasonal as well as the diel activity pattern of upstream movements in three gammarid species (Goedmaker & Pinkster, 1981). Temperature may also affect habitat selection. Costa (1966) and Gebczynski (1965) have demonstrated species specific differences in preferred temperature regimes in two decapods and two pulmonata snails, respectively.

It has been shown that most life-history parameters are significantly affected by temperature (Vannote & Sweeney, 1980). Temperature can directly affect rates of feeding, assimilation and respiration (Vannote & Sweeney, 1980; Sweeney & Vannote, 1981), or have an indirect effect by altering the quantity and quality of food available (Cummins & Klug, 1979). As the individual grows, the physiological status will change, which may lead to a change in the optimal temperature (Lutz, 1974; Iversen, 1979).

Nymphs of *P. chelifera* and *P. minor* collected in the seasonal stream have just reached habitats suitable for growth. Postmigrational nymphs of *P. chelifera* and *P. minor* which have recently reached the strams may still be physiologically adapted to the temperature regime in the main river. This may be the reason why they avoid high temperatures. The

acclimation to the higher temperature that often prevails in the seasonal stream probably taken some time. Heiman & Knight (1972) have shown that nymphs of the stonefly *Paragnetina media* Walker acclimates to increasing temperature at approximately 5 °C per day. Alternatively, the nymphs never acclimate to this high amplitude temperature regime.

Concluding remarks

From these experiments it is obvious that nymphs of *P. chelifera* and *P. minor* have the ability to use different cues to orient. Nymphs of *P. chelifera* have chemoreceptors to detect the pH regime, while nymphs of *P. minor* have chemoreceptors to detect the content of DOM. The capacity to detect differences in water quality is lost as soon as the nymphs have reached areas suitable for growth. For both species when they have reached suitable growth areas, water temperature also acts as a cue for orientation. I propose that through these stimuli nymphs of *P. chelifera* and *P. minor* have the capacity to orient to habitats with a plentiful supply and/or high quality of food.

Acknowledgements

I am grateful to Prof. C. Otto for his valuable comments on the manuscript; Å. Nordström, H. Söderberg and A. Johansson for their assistance in the field; G. Marklund for drawing the figures; and J. Clarke for improving the English. This investigation has been supported by grants from Helge Ax:son Johnsons stiftelse, Stockholm and Långmanska kulturfonden, Stockholm.

References

- Anderson, K. G., C. Brönmark, J. Herrmann, B. Malmqvist, C. Otto, & P. Sjöström, 1986. Presence of sculpins (*Cottus gobio*) reduces drift and activity of *Gammarus pulex* (Amphipoda). *Hydrobiologia* 133: 209–215.
- Baker, R. R., 1978. The evolutionary ecology of animal migration. Holmes and Melew Publ. Inc. New York 1012 pp.

- Bishop, J. E. & H. B. N. Hynes, 1969. Upstream movements of the benthic invertebrates in the Speed River, Ontario, J. Fish. Res. Bd. Canada. 26: 279–298.
- Boag, D. A. & J. A. Bentz, 1980. The relationship between simulated seasonal temperature and depth distributions in the freshwater pulmonate, *Lymnea stagnalis*. Can. J. Zool. 58: 198–201.
- Brönmark, C., 1985. Interactions between macrophytes, epiphytes and herbivores: an experimental approach. Oikos. 45: 26–30.
- Burdosh, M., G. A. Robilliard, K. Tarbox & C. L. Beehler, 1982. Chemoreception in an arctic amphipod crustacean: A field study. J. exp. mar. Biol. Ecol. 62: 261–269.
- Castilla, J. C. & D. J. Crisp, 1970. Responses of *Asterias rubens* to olfactory stimuli. J. mar. biol. Ass. U.K. 50: 829–847.
- Clampitt, P. T., 1972. Seasonal migrations and other movements in Douglas lake pulmonate snails. Malacological Rev. 5: 11–12.
- Costa, H. H., 1966. Thermal sensitivity and responses in two species of freshwater *Caridina*. Hydrobiologia 28: 583–588.
- Croll, R. P., 1983. Gastropod chemoreception. Biol. Rev. 58: 293–319.
- Cummins, K. W. & M. J. Klug, 1979. Feeding ecology of stream invertebrates. Ann. Rev. Ecol. Syst. 10: 147–172.
- Cummins, K. W., R. C. Petersen, F. O. Howard, J. C. Wuycheck & V. I. Holt, 1973. The utilization of leaf litter by stream detritivores. Ecology 53: 336–345.
- Gebczyn'ski, M., 1965. Preferendum termiczne s'limakow slodkowodnychzatozcka rogowego (*Planorbis corneus rubra* L.) i blotniarki stawowej (*Limnea stagnalis* L.). Zesz. nauk. Univ. Jagiellansk. 9: 87–96.
- Goedmaker, A. & S. Pinkster, 1981. Population dynamics of three Gammarid species (Crustacea, Amphipoda) in a French chalk stream Part III. Migration. Bijdragen tot de Dierkunde 51: 145–180.
- Hayden, W. & H. F. Clifford, 1974. Seasonal movements of the mayfly *Leptophlebia cupida* (Say) in a brown-water stream of Alberta, Canada. Am. Midl. Nat. 91: 90–102.
- Heiman, D. R. & A. W. Knight, 1972. Upper-lethel-temperature reations of the nymphs of the stonefly, *Paragnetina media*. Hydrobiologia 39: 479–493.
- Horst, T. J. & R. R. Costa, 1975. Seasonal migration and density patterns of the fresh water snail *Ammicola limosa*. Nautilus. 89: 56–59.
- Hultin, L., B. Svensson & S. Ulfstrand, 1969. Upstream movements of insects in a south Swedish small stream. Oikos 20: 553–557.
- Iversen, T. M., 1979. Laboratory energetics of larvae of *Sericostoma personatum* (Trichoptera). Holarct. Ecol. 2: 1–5.
- Jager, J. C., 1971. A quantitative study of a chemoresponse to sugars in *Lymnaea stagnalis* (L.). Neth. J. Zool. 21: 1–59.
- Kleerekoper, H. & J. Mogensen, 1963. Role of olfaction in the orientation of *Petromyzon marinus*. I. Response to a single amine in prey's body odor. Physiol. Zool. 36: 347–360.
- Kohn, A. J., 1961. Chemoreception in gastropod molluscs. Am. Zool. 1: 291–308.
- Lutz, P. E., 1974. Effects of temperature and photoperiod on larval development in *Tetragoneuria cynosura* (Odonata: Libellulidae). Ecology. 55: 370–377.
- Michelson, E. H., 1960. Chemoreception in the snail *Australorbis glabratus*. Am. J. trop. Med. Hyg. 9: 480–487.
- Neave, F., 1930. Migratory habits of the mayfly *Blasturus cupidus* Say. Ecology 11: 568–576.
- Olsson, T. I., 1982. Lateral movements versus stationary – adaptive alternatives in benthic invertebrates to the seasonal environment in a boreal river. Dissertation. Dept. of Animal Ecology, Univ. of Umeå, S-901 87 Umeå, Sweden.
- Olsson, T. I., 1983. Seasonal variation in the lateral distribution of mayfly nymphs in a boreal river. Holarct. Ecol. 6: 333–339.
- Olsson, T. I. & O. Söderström, 1978. Springtime migration and growth of *Parameletus chelifer* (Ephemeroptera) in a temporary stream in northern Sweden. Oikos 31: 284–289.
- Otto, C., 1971. Growth and populations movements of *Potamophylax cingulatus* (Trichoptera) larvae in a south Swedish stream. Oikos 22: 292–301.
- Peckarsky, B. L., 1980. Predator-prey interactions between stoneflies and mayflies: behavioural observations. Ecology 61: 932–943.
- Sterry, P. R., J. D. Thomas, & R. L. Patience, 1983. Behavioural responses of *Biomphalaria glabrata* (Say) to chemical factors from aquatic macrophytes including decaying *Lemna paucicostata* (Hegelm ex Engelm). Freshw. Biol. 13: 465–476.
- Sweeney, B. W. & R. L. Vannote, 1981. *Ephemerella* mayflies of White Clay Creek: Bioenergetic and ecological relationships among six coexisting species. Ecology 62: 1353–1369.
- Söderström, O & J. Nilsson, 1986. Redescription of *Parameletus chelifer* Bentsson and *P. minor* (Bengtsson), with keys to the nymphal and adult stages of the Fennoscandian species of Siphonuridae (Ephemeroptera). Ent. Scand. 17: 107–117.
- Thomas, J. D., 1982. Chemical ecology of the snail hosts of schistosomiasis: snail-snail and snail-plant interactions. Malacologia 22: 81–91.
- Townsend, C. R., 1973. The food-finding orientation mechanism of *Biomphalaria glabarata* (Say). Anim. Behav. 21: 544–548.
- Townsend, C. R. & T. K. McCarthy, 1980. On the defence strategy of *Physa fontinalis* (L.), a freshwater pulmonate snail. Oecologia. 46: 75–79.
- Van Dongen, A., 1956. The preference of *Littorina obtusata* for fucaecae. Arch. Neerl. Zool. 11: 373–386.
- Vannote, R. L. & B. W. Sweeney, 1980. Geographic analysis of thermal equilibria: A conceptual model for evaluating the effect of natural and modified thermal regimes on aquatic insects communities. Am. Nat. 115: 667–695.
- Wetzel, R. G., 1983. Limnology. Saunders College Publ. Philadelphia 767 pp.
- Williams, D. D. & K. A. Moore, 1982. The effect of environmental factors on the activity of *Gammarus pseudolimnaeus* (Amphipoda). Hydrobiologia 96: 137–147.
- Williams, D. D. & K. A. Moore, 1985. The role of semiochemicals in benthic community relationships of the lotic amphipod *Gammarus pseudolimnaeus*: a laboratory analysis. Oikos 44: 280–286.