

Do nymphs of *Parameletus chelififer* and *P. minor* (Ephemeroptera) reduce mortality from predation by occupying temporary habitats?

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Summary. The possible effect of predation on the habitat selection of nymphs of the two mayfly species *Parameletus chelififer* Bengtsson and *P. minor* (Bengtsson) was investigated for different habitats of a North Swedish boreal river. In spring, these two species migrate to river margins and subsequently, in different proportions, to adjacent seasonal ponds. Feeding rates on mayfly nymphs and mosquito larvae by some dytiscid beetles and larvae, a corixid waterbug and a caddisfly larva were studied in the laboratory. In the seasonal pond, the consumption rate of invertebrate predators on *Parameletus* nymphs was below that expected from their relative abundance, and mosquito larvae were preferred. At the river margin, where mosquito larvae were absent, *Parameletus* nymphs were consumed in agreement with their relative abundance. The absolute abundance of macroinvertebrate predators was similar at the river margin and in the pond. Fish predators visited the seasonal pond only during a short time of flood, while at the river margin their presence was continuous. In the seasonal pond, minnow and roach consumed nymphs of both *P. chelififer* and *P. minor* in a lower proportion than expected. At the river margin, nymphs of *P. chelififer* were consumed by minnow and ten-spined stickleback in a higher proportion than expected. Nymphs of *P. minor* were consumed according to expectation. Imagines of *P. minor* emerged early, and nymphs were equally abundant in the river and in the seasonal pond. In contrast, almost all nymphs of *P. chelififer* migrated to the seasonal pond. The later emergence of *P. chelififer* would probably result in a very high mortality from predation if it remained at the river margin.

Key words: Mayfly nymphs – Predators – Consumption rate – Habitat shift – Boreal river

Many aquatic insects change habitat during their larval development, and seasonally short-lived wetlands are often exploited in this way. Such habitat shifts may be realized in response to short supply of important resources such as food and pupation or emergence sites. Alterations in environmental parameters, such as water temperature and current, may also be important. Some stoneflies and the mature larvae of the caddisfly *Potamophylax cingulatus* (Steph.) change habitat in their search for suitable pupation or emergence sites (Lillehammer 1965, Otto 1971). Hayden and Clifford (1974) suggested that the mayfly *Leptophlebia cupida* (Say) avoids the increasing current in a main river

by colonizing tributaries. The same explanation was partly put forward for the shoreward spring migration observed in the mayfly species *Parameletus chelififer* Bengtsson (Olsson and Söderström 1978, Söderström 1987), also including *P. minor* (Bengtsson) (Söderström and Nilsson 1986). Other possible ultimate explanations for this behaviour in these two mayfly species may include an avoidance of fish and invertebrate predation, an exploitation of abundant food supplies and a search for water temperatures optimal for nymphal development (Olsson and Söderström 1978; Olsson 1983; Söderström unpublished work).

The shoreward spring migration observed in *P. chelififer* and *P. minor* also involves the colonization of seasonal tributaries and ponds (Olsson and Söderström 1978; Söderström unpublished work). Especially in *P. chelififer* this process is very pronounced. In a seasonal pond, a shortening of the nymphal period and an earlier emergence were observed relative to the river habitat (Söderström and Johansson unpublished work). In *P. chelififer* mature nymphs from a seasonal pond also grew larger. Given these advantages, it is remarkable that only a small proportion of the nymphs of *P. minor* migrate to seasonal ponds. The relative importance of different mortality factors in the two habitats could be decisive. In seasonal ponds, interannual variation of duration imposes a risk due to desiccation. Further, a wide range of both invertebrate and vertebrate predators feed on mayfly nymphs (Hynes 1970; Macan 1970; Brittain 1982; Blois 1985; Nilsson 1986a). Generally, aquatic insect predators feed on all sizes and types of prey within the range that they can handle (Peckarsky 1984). In the seasonal pond, dytiscid beetles and larvae are the dominating predators (Nilsson 1986a). In the river, a diverse set of plecopteran, odonatan, hemipteran and coleopteran predators are present. Fish predation should be a serious threat, especially in the river.

The aim of the present study is to estimate the impact of predation on nymphs of *Parameletus chelififer* and *P. minor* at a river margin and in a seasonal pond.

Study area

The area investigated (Fig. 1) is situated in a slow-flowing part of the river Vindelälven, near the village Sirapsbacken (64°22' N, 19°28' E), in northern Sweden. The annual and the seasonal fluctuations in discharge are pronounced. The maximum flow (daily record) during 1971–1986 varied from 579 to 1,484 m³/s, and the difference between mean minimum and maximum flow (daily record) from 30 to 956 m³/s (data from the Swedish Meteorological and Hydrological

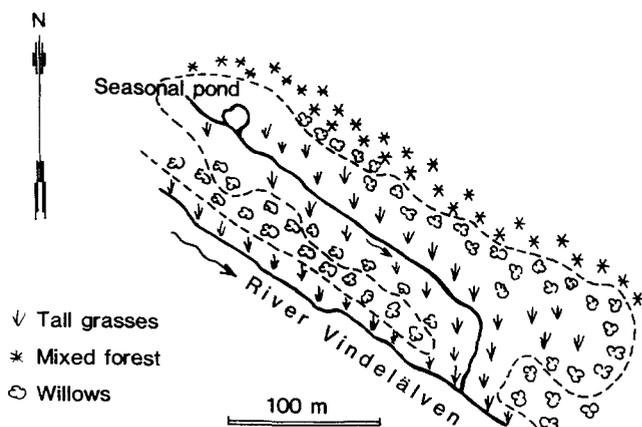


Fig. 1. Map of the seasonal pond and river margin studied. The solid line marks the outline of the pond, the seasonal stream and the river margin in early May, and the broken line shows the approximate extension of the river during spring flood

Institute, SMHI). Normally, the river is ice-covered and the upper littoral zone is frozen solid from mid November to mid May. The adjacent seasonal pond, situated on an alluvial meadow, is connected to the river by a small stream about 300 m long and 0.5–1 m wide. The stream carries melt water from late April to early May. The peak flood of the river is from late May to early June. In most years the river flood reaches the pond which then becomes the innermost part of an extensive river lagoon. The pond usually dries out in late June or mid July. Field observations together with data from SMHI for 1977 to 1986 show that the predictability of the seasonal pond is very high (0.91 according to Stearns, 1981). Contingency shows an intermediate value (0.54) while constancy is low (0.38) (Stearns op. cit.).

Material and methods

Field data

Fish predators were sampled in two ways. On 18 May 1979 and 21 May and 1 June 1986, during the river flood, three gill-nets (mesh size 37 mm) were used in the river lagoon. On 18 May 1979, three gill-nets were also operating in the river. On 9 and 17 June 1986, fish were collected with a handnet (mesh size 0.5 mm), used with equal efforts close to the river margin and in the seasonal pond on each occasion. Fish smaller than 50 mm were preserved in 95% ethanol, and stomachs of larger fish were removed and preserved. The total length of each fish was measured. The maturity of eggs and sperms were noted during 1986. The total number of *P. chelifera* and *P. minor* nymphs consumed by all minnows and ten-spined sticklebacks was tested by a X^2 -test (2×2 contingency table, Siegel 1956). In these tests, the total number of *P. chelifera* and *P. minor* nymphs from the handnet samples (see below) on the corresponding dates at the river and pond margins were used as the expected numbers.

The relative abundance of different macroinvertebrates at the river and pond margins was estimated from samples taken with a handnet (mesh size 0.5 mm) at four occasions from 13 May to 17 June 1986. At two occasions (9 and 17 June) seven Ekman grab samples (225 cm²) were taken to estimate the absolute abundance of different macroinver-

tebrates at the river and pond margins. The differences in absolute abundance, both between 9 and 17 June within habitats, and between habitats on the same dates, as observed in the Ekman grab samples, was tested by the Mann-Whitney *U*-test (Siegel 1956).

Laboratory experiments

Two sets of predation experiments were performed in the laboratory in May–June 1986. All predators and prey used in these experiments were collected at the river margin and in the adjacent seasonal pond. A sample of mosquito pupae were collected in the pond on 5 June and the emerging adults mainly belonged to *Aedes communis* (DeG.), but a few specimens of *A. intrudens* Dyar were also found.

The first set of experiments was designed to estimate prey selection and consumption rates of nine predator species. Here small aquaria (203 × 100, height 65 mm) filled with 400 cm³ water under a 18:6 h light-dark cycle were used. Water depth was 24 mm, and five stems of *Polytrichum* sp moss were used as a substrate in each aquarium. Water temperature ranged from 11 to 14° C and each experiment lasted for 24 h. At the start, a single predator (starved for at least 24 h) was introduced into an aquarium containing either 100 or 200 prey individuals. In the first prey situation, (72 *Parameletus* spp, 23 *Leptophlebia vespertina* (L.) and five *Heptagenia fuscogrisea* (Retz.) (Ephemeroptera nymphs)), the relative composition was equal to, and the absolute abundance 4.6 times that observed at the river margin on 9 June. In the second prey situation, (100 Culicidae, 72 *Parameletus* spp, 23 *L. vespertina* and five *H. fuscogrisea*), both the relative composition and the absolute abundance were equal to that observed in the seasonal pond on 9 June. For identification and counting purposes, predator and the prey still alive were preserved in 70% ethanol. Between two and five trials were performed for each predator.

The second set of predation experiments was designed to estimate encounter, attack and capture rates for two common species of dytiscid larvae. The two dominating invertebrate taxa in the pond, Culicidae and *Parameletus* spp, were used as prey in these experiments. These trials were conducted in small round vials (diameter 66, height 50 mm) filled with 50 cm³ of water and with a moss stem added. The water depth was 27 mm. Water temperature ranged from 12 to 22° C and each trial lasted for 12–76 min. At the start of each trial a predator (starved for at least 24 h) was introduced to a vial with five culicid larvae and five *Parameletus* nymphs. Upon consumption a new prey item was added. The predators used in these experiments were 3rd-instar larvae of *Agabus erichsoni* Gemm. & Har. (seven experiments) and *Colymbetes paykulli* Er. (six experiments). Number of encounters, attacks and captures per hour and capture efficiency (number of captures per number of attacks) for Culicidae and *Parameletus* spp for each predator species was tested by the Mann-Whitney *U*-test (Siegel 1956).

Results

Predator abundance

Fish species such as pike (*Esox lucius* L.), roach (*Rutilus rutilus* (L.)), minnow (*Phoxinus phoxinus* (L.)) and ten-spined stickleback (*Pungitius pungitius* (L.)) were all com-

Table 1. Numbers and total length (range) of the fish captured by gill-nets and a handnet at the river margin and in the seasonal pond. Asterisks denote that gill-nets were used

| Species | | Seasonal pond | | | | | River | | |
|----------------------------|-------------|-----------------|-----------------|-----------------|----------------|-----------------|-----------------|----------------|-----------------|
| | | 1979 18 May* | 1986 21 May* | 1986 1 June* | 1986 9 June | 1986 17 June | 1979 18 May* | 1986 9 June | 1986 17 June |
| <i>Esox lucius</i> | number | 5 | 8 | 2 | 0 | 0 | 2 | 0 | 0 |
| | length (mm) | 180–360 | 450–550 | 460–650 | | | 165–540 | | |
| <i>Phoxinus phoxinus</i> | number | – | – | – | 31 | 0 | – | 27 | 23 |
| | length (mm) | | | | 18–32 | | | 17–48 | 19–41 |
| <i>Pungitius pungitius</i> | number | – | – | – | 0 | 0 | – | 8 | 3 |
| | length (mm) | | | | | | | 31–46 | 36–38 |
| <i>Rutilus rutilus</i> | number | 15 | 0 | 4 | 0 | 16 | 5 | 0 | 0 |
| | length (mm) | 116–270 | | 140–185 | | 22–38 | 99–215 | | |

Table 2. Relative abundance of macroinvertebrates captured by handnet sampling in the seasonal pond and at the river margin at different dates in 1986. Total number of macroinvertebrates captured indicated by *n*

| | Seasonal pond | | | | River | | | |
|-------------------------------|---------------|--------|--------|---------|--------|--------|--------|---------|
| | 13 May | 1 June | 9 June | 17 June | 13 May | 1 June | 9 June | 17 June |
| <i>Asellus aquaticus</i> | 0.2 | 0.1 | 0.2 | 0.6 | 0.2 | 0.9 | 9.4 | 8.2 |
| <i>Ameletus inopinatus</i> | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0.6 |
| <i>Parameletus chelifera</i> | 21.7 | 16.3 | 16.7 | 19.6 | 44.8 | 2.7 | 1.0 | 0.1 |
| <i>P. minor</i> | 16.3 | 5.1 | 2.2 | 1.6 | 20.7 | 31.2 | 22.4 | 5.0 |
| <i>Siphonurus aestivalis</i> | 0 | 1.2 | 0 | 0.4 | 1.3 | 0.3 | 0.1 | 0 |
| <i>S. alternatus</i> | 0 | 3.1 | 0.4 | 1.3 | 0 | 0.9 | 1.1 | 0.4 |
| <i>S. lacustris</i> | 0 | 2.4 | 0.4 | 1.9 | 0.7 | 4.7 | 1.7 | 0.4 |
| <i>Centroptilum luteolum</i> | 0 | 0 | 0 | 0 | 0 | 0.3 | 0 | 0 |
| <i>Heptagenia fuscogrisea</i> | 2.9 | 5.8 | 8.9 | 2.2 | 2.6 | 24.4 | 25.8 | 34.6 |
| <i>Ephemerella mucronata</i> | 0 | 0 | 0 | 0 | 0 | 0.1 | 1.6 | 2.1 |
| <i>Leptophlebia marginata</i> | 0.2 | 0.1 | 0.1 | 0 | 0.2 | 0.1 | 2.1 | 0 |
| <i>L. vespertina</i> | 7.3 | 14.1 | 26.2 | 49.6 | 28.7 | 31.9 | 20.5 | 24.2 |
| Trichoptera, non predators | 0.8 | 0.8 | 1.3 | 0 | 0 | 1.5 | 8.1 | 4.9 |
| Chironomidae | 0.2 | 0.3 | 9.0 | 7.1 | 0.2 | 0.1 | 0.3 | 1.6 |
| Culicidae | 50.4 | 50.0 | 32.1 | 12.2 | 0 | 0 | 0 | 0 |
| macroinv. predators | 0.2 | 0.8 | 0.9 | 1.0 | 0.2 | 0.3 | 5.4 | 13.5 |
| other macroinv. | 0 | 0.1 | 1.5 | 2.6 | 0.2 | 0.3 | 0.5 | 4.4 |
| <i>n</i> | 516 | 1850 | 2993 | 2154 | 453 | 737 | 934 | 817 |

mon at the river margin. All species, except ten-spined stickleback, were also found in the seasonal pond when flooded by the river (Table 1). Small roaches were only captured in the seasonal pond on 17 June 1986. Equal efforts of handnet sampling in the river and the seasonal pond on 9 June 1986 gave similar abundancies of minnow (Table 1).

The relative abundance of invertebrate predators varied between 0.2 and 13.5% of the total fauna in the river (Table 2). On 13 May and 1 June, coleopterans dominated but later trichopterans, heteropterans and plecopterans became abundant. The absolute abundance of invertebrate predators was 63 and 101 inds m^{-2} (9 and 17 June, respectively) at the river margin (Table 3), and this difference is not significant (Mann-Whitney *U*-test, $P > 0.05$).

In the seasonal pond the relative abundance of invertebrate predators varied between 0.2 and 1.0% of the total fauna (Table 2). Coleopterans dominated throughout the investigation period. Here, the absolute abundance was 50 and 88 inds m^{-2} on 9 and 17 June, respectively (Table 3), and this difference is not significant (Mann-Whitney *U*-test, $P > 0.05$). No significant difference in abundance of total

numbers of invertebrate predators between the river and the seasonal pond was observed (Mann-Whitney *U*-test, $P > 0.05$ for both sampling dates).

Abundance of potential prey

In the river, nymphs of *Parameletus chelifera* were very abundant on 13 May but later they became rare (Table 2). *P. minor* and *Leptophlebia vespertina* were equally abundant throughout the study period, except on 17 June when *P. minor* showed a lower relative abundance. *Heptagenia fuscogrisea*, in conformity with the trichopteran larvae and *Asellus aquaticus* (L.), seemed to colonize the upper littoral of the river later than did the other common mayfly species. Culicid larvae were never observed at the river margin. At the river margin, the absolute abundance of non-predatory invertebrates, mainly mayfly nymphs, was 1,021 and 601 inds m^{-2} on 9 and 17 June, respectively (Table 3). This difference is not significant (Mann-Whitney *U*-test, $P > 0.05$).

Culicid larvae were the most abundant prey organisms

Table 3. Absolute abundance of macroinvertebrates from Ekman grab samples in the seasonal pond and at the river margin on 9 and 17 June, 1986 (ad = adult, L = larva, P = pupa). A total of seven Ekman grab samples were taken at each site and date

| | Seasonal pond | | | | | | River | | | | | |
|----------------------------------|---------------|-------------|----------------------|-------------|-------------|----------------------|-------------|------------|----------------------|-------------|------------|----------------------|
| | 9 June | | | 17 June | | | 9 June | | | 17 June | | |
| | Mean | S.D. | ind. m ⁻² | Mean | S.D. | ind. m ⁻² | Mean | S.D. | ind. m ⁻² | Mean | S.D. | ind. m ⁻² |
| <i>Asellus aquaticus</i> | 0.9 | 1.5 | 38 | 0.1 | 0.4 | 6 | 2.6 | 2.2 | 114 | 1.6 | 3.3 | 70 |
| <i>Ameletus inopinatus</i> | | | | | | | | | | 0.1 | 0.4 | 6 |
| <i>Parameletus chelifera</i> | 45.7 | 11.7 | 2032 | 11.1 | 8.2 | 495 | 0.4 | 0.8 | 19 | | | |
| <i>P. minor</i> | 6.3 | 1.6 | 279 | 1.0 | 1.0 | 44 | 6.0 | 2.2 | 267 | 0.9 | 1.2 | 38 |
| <i>Siphonurus alternatus</i> | 0.3 | 0.8 | 13 | 1.3 | 1.4 | 57 | | | | 0.1 | 0.4 | 6 |
| <i>S. lacustris</i> | 0.3 | 0.5 | 13 | 1.0 | 1.8 | 44 | 0.1 | 0.4 | 6 | | | |
| <i>Heptagenia fuscogrisea</i> | 18.9 | 10.1 | 838 | 1.4 | 0.8 | 64 | 5.1 | 1.7 | 229 | 5.1 | 3.9 | 228 |
| <i>Ephemerella mucronata</i> | | | | | | | 0.6 | 1.1 | 25 | 0.4 | 0.8 | 19 |
| <i>Leptophlebia marginata</i> | 0.1 | 0.4 | 6 | | | | 0.9 | 0.7 | 38 | | | |
| <i>L. vespertina</i> | 55.9 | 35.3 | 2483 | 24.7 | 15.6 | 1098 | 5.3 | 4.9 | 235 | 3.1 | 2.2 | 140 |
| <i>Amphinemura</i> sp | | | | | | | 0.1 | 0.4 | 6 | 0.6 | 1.5 | 25 |
| Limnephilidae | 5.6 | 3.7 | 248 | | | | 1.7 | 1.1 | 76 | 0.9 | 1.2 | 38 |
| Chaoboridae P | 0.1 | 0.4 | 6 | | | | | | | | | |
| Chironomidae L | 13.0 | 9.3 | 578 | 7.0 | 3.9 | 311 | 0.1 | 0.4 | 6 | 0.6 | 0.8 | 25 |
| Culicidae L | 38.3 | 15.7 | 1702 | 3.6 | 4.1 | 159 | | | | | | |
| Culicidae P | 30.7 | 15.8 | 1365 | 3.3 | 2.4 | 146 | | | | | | |
| Empididae L | | | | | | | | | | 0.1 | 0.4 | 6 |
| Sphaeriidae | 0.7 | 1.5 | 32 | 1.7 | 2.4 | 76 | | | | | | |
| Predators | | | | | | | | | | | | |
| <i>Isoperla grammatica</i> | | | | | | | 0.1 | 0.4 | 6 | 0.9 | 1.2 | 38 |
| <i>Siphonoperla burmeisteri</i> | | | | | | | | | | 0.3 | 0.8 | 13 |
| <i>Callicorixa wollastoni</i> ad | | | | | | | 0.3 | 0.5 | 13 | | | |
| <i>Sigara falleni</i> ad | | | | | | | 0.1 | 0.4 | 6 | 0.1 | 0.4 | 6 |
| <i>Haliplus fulvus</i> ad | | | | | | | 0.6 | 0.8 | 25 | 0.9 | 0.9 | 38 |
| <i>Hydroporus brevis</i> ad | | | | 0.1 | 0.4 | 6 | | | | | | |
| <i>H. fuscipennis</i> ad | | | | 0.1 | 0.4 | 6 | | | | | | |
| <i>H. striola</i> L | | | | 0.1 | 0.4 | 6 | | | | | | |
| <i>H. striola</i> ad | 0.1 | 0.4 | 6 | 1.4 | 1.4 | 64 | | | | | | |
| <i>Agabus arcticus</i> ad | | | | | | | | | | 0.1 | 0.4 | 6 |
| <i>A. congener</i> L | 0.1 | 0.4 | 6 | | | | | | | | | |
| <i>Colymbetes paykulli</i> L | 0.4 | 0.5 | 19 | | | | | | | | | |
| <i>C. paykulli</i> ad | | | | 0.1 | 0.4 | 6 | | | | | | |
| <i>C. striatus</i> L | 0.1 | 0.4 | 6 | | | | | | | | | |
| <i>Agrypnea obsoleta</i> L | 0.3 | 0.8 | 13 | | | | 0.3 | 0.5 | 13 | | | |
| Total | 217.8 | 60.8 | 9680 | 58.1 | 18.4 | 2582 | 24.3 | 7.7 | 1080 | 15.8 | 6.7 | 704 |

in the seasonal pond until 17 June when nymphs of both *P. chelifera* and *L. vespertina* became more abundant. Chironomid larvae became abundant from 9 June on. *P. chelifera* and *P. minor* were the most abundant mayflies in the seasonal pond on 13 May. *P. chelifera* remains at the same dominance level throughout the investigation period. The pond was completely flooded by the river on 1 June. From that date, both *L. vespertina* and *H. fuscogrisea* increased in abundance. The absolute abundance of potential invertebrate prey in the pond was 9,633 and 2,500 inds m⁻² on 9 and 17 June, respectively (Table 3). This decline is significant for *P. minor*, *P. chelifera*, *H. fuscogrisea*, Culicidae and the total fauna (Mann-Whitney *U*-test, $P < 0.01$).

In the river, both *P. chelifera*, *L. vespertina* and the total fauna showed significantly lower abundancies on both 9 and 17 June relative to the seasonal pond (Mann-Whitney *U*-test, $P < 0.01$). On 9 June also *P. minor* and *H. fuscogrisea* were significantly less abundant in the river relative to the seasonal pond (Mann-Whitney *U*-test, $P < 0.01$), but not on 17 June.

Actual predators and predation rates

Fish predation. The stomach contents of minnows and ten-spined sticklebacks from both the river margin and the seasonal pond are shown in Fig. 2 together with the corresponding relative abundance of benthic invertebrates. In the river, on 9 June, minnows preyed on *P. chelifera* and *P. minor* nymphs in the same proportion as they were present. On the 17 June they consumed significantly more of *P. chelifera* nymphs than expected from the nymphs' abundance in the bottom samples ($X^2 = 27.7$, $P < 0.001$). In the river, the ten-spined sticklebacks consumed a significantly higher proportion of nymphs of *P. chelifera* than expected ($X^2 = 37.9$, $P < 0.001$) on 9 June. In total, the roaches captured in the river ($n = 5$) in 1979 had consumed only ten nymphs of *Parameletus* spp (26% of all food items), whereas the pikes had not consumed any *Parameletus* nymphs.

In the seasonal pond, minnows did not feed on *Parameletus* nymphs ($X^2 = 33.7$, $P < 0.001$) on 9 June. All 16 small roaches caught in the river lagoon on 17 June had mainly

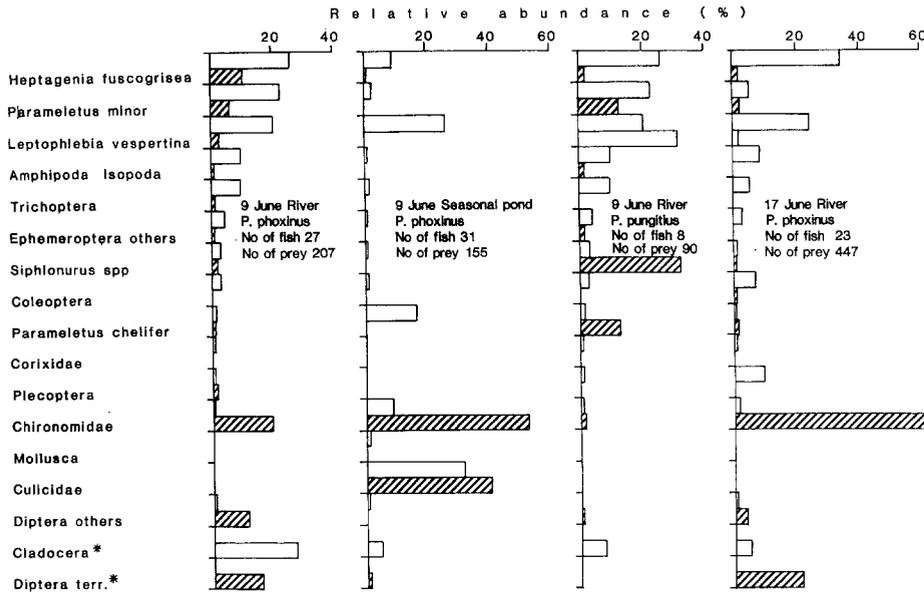


Fig. 2. Stomach contents of *Poxinus phoxinus* and *Pungitius pungitius* captured at the river margin and in the seasonal pond. The unshaded bars show the relative abundance of different prey in bottom samples, and the shaded bars show relative occurrence in stomachs. Asterisks denote taxa not counted in bottom samples and not included in the statistical tests

consumed cladocerans (87% of all food items). The ten pikes and the four larger roaches caught in gill-nets there in 1986 all had empty stomachs and were close to spawning. In contrast, pikes caught in the seasonal pond in 1979 had in total consumed 1,003 *Parameletus* nymphs (93% of all food items). The corresponding value for roach is 319 *Parameletus* nymphs (72% of all food items). Unfortunately the spawning status was not recorded in 1979.

Invertebrate predation. When invertebrate predators, common at the river margin, were offered a prey composition corresponding to that observed in the river, the adult water beetles *Agabus arcticus* (Payk.) and *Haliphus fulvus* (F.) and the caddisfly larva *Agrypnea obsoleta* (Hagen) consumed significantly more nymphs than expected of *H. fuscogrisea* and *L. vespertina*, respectively (Fig. 3). The adult predators *Rhantus exsoletus* (Forst.), *Hydroporus palustris* (L.) and *Callicorixa wollastoni* (Dgl. & Sc.) consumed prey in the same proportion as presented. Larvae of *A. obsoleta* showed the highest and adults of *H. fulvus* the lowest consumption rate of *Parameletus* nymphs (Table 4).

When adult dytiscids were offered a prey composition corresponding to that observed in the seasonal pond they consumed significantly more mosquito larvae than expected (Fig. 4). Under the same condition, adults of *C. wollastoni* consumed significantly more nymphs of *L. vespertina* than expected, while larvae of *A. obsoleta* consumed prey in the same proportion as they were offered (Fig. 4). The two latter predators may occasionally appear in the seasonal pond during flood. Larvae of *A. erichsoni* consumed significantly more mosquito larvae, while larvae of *Colymbetes paykulli/striatus* consumed prey in the same proportion as they were offered (Fig. 4). The consumption rate was markedly higher in dytiscid larvae than in adults (Table 4), and also *Agrypnea* larvae had relatively high rates.

Prey selection

In larvae of both *A. erichsoni* and *C. paykulli*, capture rates and efficiencies for mosquito larvae and *Parameletus* nymphs did not show any significant difference (Mann-Whitney *U*-test, $P > 0.05$) (Table 5). Larvae of *A. erichsoni*

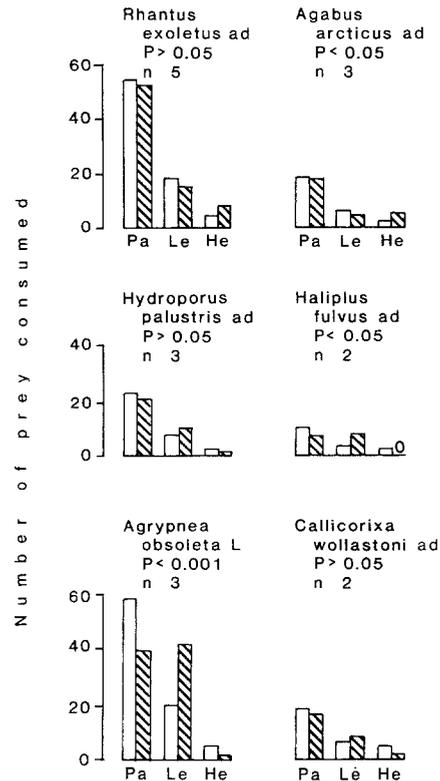


Fig. 3. Consumption by species of mayfly nymphs by six different macroinvertebrate predators (ad = adult, L = larva) occurring at the river margin. Shaded bars represent the total numbers of prey eaten. Unshaded bars represent expected number of prey that should be eaten from the prey composition offered; 72 *Parameletus* spp (Pa), 23 *Leptophlebia vespertina* (Le) and 5 *Heptagenia fuscogrisea* (He) nymphs. Number of replicates denoted (*n*). *P* values indicate if the proportion of prey consumed significantly differed from that offered (χ^2 -test)

had significantly higher encounter and attack rates with *Parameletus* nymphs than with mosquito larvae (Mann-Whitney *U*-test, $P < 0.05$) (Table 5). As this predator consumed significantly more mosquito larvae than expected (Fig. 4), it must have a preference for this type of prey.

Table 4. Consumption rate of different prey taxa by the macroinvertebrate predators used in the 24 h experiments (ad=adult, L=larva, L3=larval instar 3). Prey composition in terms of Mayflies+mosquitoes corresponds to that prevailing in the seasonal pond, while prey in terms of only mayfly nymphs, corresponds to that prevailing at the river margin

| Predator | Prey composition | No. of prey consumed per h | | |
|----------------------------------------|-----------------------|----------------------------|-------------|-------|
| | | Culicidae | Parameletus | Total |
| <i>Callicorixa wollastoni</i> ad | mayflies + mosquitoes | 0.36 | 0.39 | 1.18 |
| <i>Hydoporus striola</i> ad | mayflies + mosquitoes | 0.82 | 0.21 | 1.08 |
| <i>Agabus erichsoni/subtilis</i> ad | mayflies + mosquitoes | 0.38 | 0.07 | 0.49 |
| <i>A. erichsoni</i> L3 | mayflies + mosquitoes | 1.63 | 0.82 | 2.63 |
| <i>Colymbetes paykulli/striatus</i> L3 | mayflies + mosquitoes | 0.96 | 0.63 | 2.00 |
| <i>Agrypnea obsoleta</i> L | mayflies + mosquitoes | 1.19 | 0.60 | 2.17 |
| <i>Callicorixa wollastoni</i> ad | mayflies | | 0.33 | 0.52 |
| <i>Haliplus fulvus</i> ad | mayflies | | 0.15 | 0.29 |
| <i>Hydoporus palustris</i> ad | mayflies | | 0.29 | 0.44 |
| <i>Agabus arcticus</i> ad | mayflies | | 0.25 | 0.36 |
| <i>Rhantus exsoletus</i> ad | mayflies | | 0.44 | 0.63 |
| <i>Agrypnea obsoleta</i> L | mayflies | | 0.56 | 1.15 |

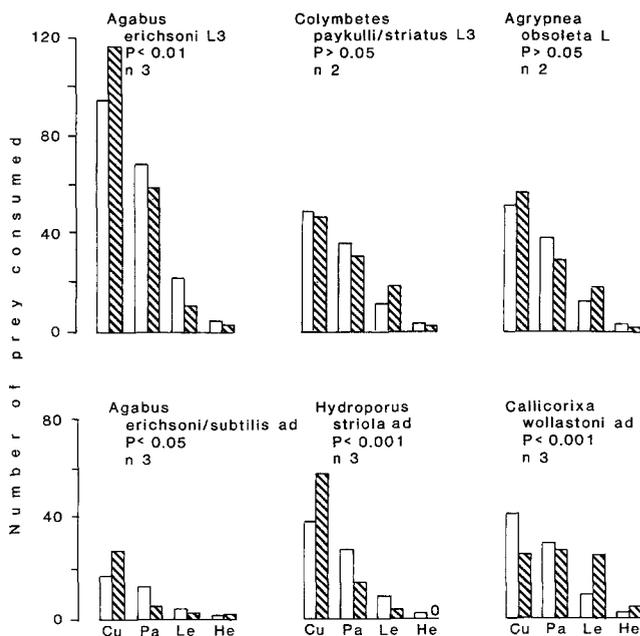


Fig. 4. Consumption by species of mayfly nymphs and mosquito larvae by six different macroinvertebrate predators (ad = adult, L = larva, L3 = larval instar 3) occurring in the seasonal pond. Shaded bars represent the total number of prey eaten. Unshaded bars represent the expected number of prey that should be eaten from the prey composition offered; 100 Culicidae (Cu), 72 *Parameletus* spp (Pa), 23 *Leptophlebia vespertina* (Le), and 5 *Heptagenia fus-grisea* (He). Number of replicates indicated by n. P values indicate if proportion of prey consumed significantly differed from that offered (χ^2 -test)

In *C. paykulli* no significant difference in encounter or attack rates was found between the two kinds of prey offered. Thus, the larvae of *C. paykulli* showed no preference for any prey type (cf. Fig. 4).

Discussion

The two very similar mayfly species *P. chelifera* and *P. minor* have partly different habitat preferences. While almost the

entire population of *P. chelifera* migrate to the seasonal pond, nymphs of *P. minor* are equally abundant in the river and in the pond (Table 3 and Söderström, unpublished work).

During times of flood the seasonal pond is visited for feeding and/or spawning by pike, roach and minnow. However, the duration of the river flood shows a pronounced interannual variation. In some years it is very short, and its initial occurrence varies within at least four weeks (mid May to mid June). Temporal variation in water temperature and flood occurrence probably result in that pike and roach will use the lagoon either for spawning or feeding in alternate years (Svärdsson 1952, June 1971). This variation could explain the large difference between 1979 and 1986 in number of prey consumed by large pike and roach.

Conclusively, the predation pressure from large fish on *Parameletus* spp could be important in some years. The predation pressure from minnow on *P. minor* and especially *P. chelifera* was much higher in the river. Minnows in the seasonal pond mainly consumed dipteran larvae. Tenspined sticklebacks were only observed in the river where they consumed a substantial proportion of nymphs of *P. chelifera*.

The data presented on fish abundance and stomach contents permit some general conclusions to be drawn. First, while fish predation is continuous at the river margin, it is restricted to short periods of time in the seasonal pond. Especially the mayfly nymphs that, like *P. chelifera*, arrive at the seasonal pond early in the spring, can avoid fish predation for a considerable period of time. Second, sticklebacks that eat a large proportion of *Parameletus* nymphs, especially *P. chelifera*, are restricted to the river margin. Minnows do not seem to eat *Parameletus* when visiting the seasonal pond during flood. In total, fish predation on *Parameletus* appears to be much more pronounced in the river than in the seasonal pond, especially on *P. chelifera*. The impact of fish predation on mayfly nymphs can be important. In a Norwegian mountain lake, trout consumed 30–40% of the total annual mayfly production (Brittain 1982).

Total macroinvertebrate densities were higher in the seasonal pond than at the river margin. In May and early

Table 5. Number of encounters, attacks and captures per hour and capture efficiency for third instar larvae of two different dytiscid species which were offered five culicid larvae and five *Parameletus* spp. nymphs with continuous replenishment. Values within brackets display S.D.

| Predator | Prey | Number per h | | | Capture efficiency |
|----------------------------|------------------------|--------------|-------------|-------------|--------------------|
| | | Encounters | Attacks | Captures | |
| <i>Agabus erichsoni</i> | Culicidae | 6.59 (4.83) | 2.26 (2.40) | 1.09 (1.28) | 0.35 (0.42) |
| | <i>Parameletus</i> spp | 16.93 (9.41) | 8.80 (3.55) | 1.87 (1.14) | 0.23 (0.16) |
| <i>Colymbetes paykulli</i> | Culicidae | 11.23 (9.06) | 5.79 (4.29) | 1.64 (1.03) | 0.50 (0.42) |
| | <i>Parameletus</i> spp | 16.37 (4.88) | 9.16 (5.29) | 2.11 (1.14) | 0.23 (0.13) |

June this difference was caused largely by the presence of a high number of mosquito larvae in the pond. *Aedes communis* (DeG.) overwinters in the egg stage, and small larvae are present in the seasonal pond soon after water from the melting snow appears. As the dominating predaceous *Agabus* species also have hibernating eggs, these larvae can use this food resource from its first time of appearance (Nilsson 1986a). The abundance of invertebrate predators was very similar in both habitats. Assuming that average feeding rates are the same in both habitats, then due to dilution each prey individual should have a higher probability of not being eaten by an invertebrate predator in the seasonal pond (cf. Wilson 1980). However, temperature difference may result in different feeding rates (Jamieson and Scudder 1977; Peckarsky 1982), and temperature was somewhat higher in the seasonal pond (Söderström, unpublished work). Thompson (1978) has also shown that the attack coefficient increased and the handling time decreased with increasing water temperature for the predatory damselfly *Ischnura elegans* (van der Linden) feeding on *Daphnia* sp. Impact of predation could be estimated from the results of the Ekman grab sampling. However, the reduction in numbers of *P. minor* between 9 and 17 June in the seasonal pond and in the river may, to a large extent, be caused by emergence. Because of a later emergence, the decrease in numbers of *P. chelifera* in both habitats must be caused chiefly by either mortality or migration. Although this decrease is not statistically significant in the river habitat, earlier investigations have shown a drastic decrease in numbers of *P. chelifera* in the river prior to the onset of emergence (Söderström, unpublished work). Values of total mortality calculated from abundance of prey and capture rates were much higher than the decrease in abundance observed in the Ekman grab samples between 9 and 17 June in both habitats. This result was probably caused by the simplified experimental conditions. Similar observations were reported by James (1964) in the dytiscid *Laccophilus maculosus* Say feeding on *Aedes atropalpus* (Coq.) in rock pools.

Nymphs of *Parameletus* spp were in most cases consumed in a lower proportion than the one offered in a predator-prey situation corresponding to that in the seasonal pond. Thus, mayfly nymphs, and especially *P. chelifera*, may here increase their survival rate because of the high abundance of alternative prey in terms of mosquito larvae. A decrease in abundance of mosquito larvae could later be compensated for by the increasing abundance of *L. vespertina*. In a river situation, predation on *Parameletus* spp was according to expectation, and consequently predation seemed more intense here.

Predators of the sit-and-wait type, such as the larvae of *A. erichsoni*, are predicted to eat more mobile prey relative to sedentary ones, due to a higher encounter rate (Cooper et al. 1985). In our experiment this predator had higher encounter and attack rates with *Parameletus* nymphs than with mosquito larvae, while capture rate and efficiency were equal for both prey types. The fact that it still consumed more culicids than the proportion offered lends strong support to a selection of this kind of prey. The highly mobile adult macroinvertebrate predators in the seasonal pond that consumed significantly more mosquito larvae also lends support to a preference for this kind of prey.

As the invertebrate predators are more speciose, with different species acting in the two habitats, their total impact on *Parameletus* is very hard to estimate. Invertebrate predator densities were subequal in both habitats, but the total consumption from these predators on *Parameletus* nymphs may differ. Probably, total consumption was higher in the seasonal pond where temperature was high and less omnivorous predators dominated. However, the higher prey densities recorded in the seasonal pond indicate a lower predation pressure on each individual. Selection of mosquito larvae by the predators also seem to favour the *Parameletus* nymphs that utilized the seasonal pond, especially those of *P. chelifera* that were very abundant. If nymphs of *P. chelifera* remained in the river they should probably be exposed to a higher predation pressure compared to that in the seasonal pond. Our general conclusion is, that the mortality of *P. chelifera* nymphs caused by predation was lowered in the seasonal pond compared to the river margin. For nymphs of *P. minor* the difference in mortality between the two habitats was seemingly not so pronounced.

Densities of macroinvertebrate predators were difficult to estimate because of their relatively low numbers and low catchability. This means that our data on their absolute and relative abundance are weak. Generally, we believe that the impact of macroinvertebrate predation peaked earlier in the seasonal pond than at the river margin. The temporary nature of the pond imposes the need for a fast development (Wiggins et al. 1980). The dominating dytiscids are, by their life cycles, primarily adapted to feed on mosquito larvae (Nilsson 1986a) – a resource that shows a rapid decrease in early June.

The more permanent nature of the river habitat indicates that invertebrate predators are not forced to achieve a fast development there, and life cycles are generally adapted to a food resource that is abundant during summer (Nilsson 1986b). This is evident in the dominating dytiscid species, such as *Hydroporus palustris*, *Agabus arcticus* and

Rhantus exsoletus, which all pass larval stages during summer in the river.

If this view is correct, the colonization of the seasonal pond would be most profitable late in the season when invertebrate predation here is relaxed (Nilsson 1986a). Thus, *P. chelifera* that emerges late in the season should be favoured. On the other hand, the early emergence of *P. minor* would decrease the relative advantage of colonizing the seasonal pond. The maximum time available for the nymphal development in the seasonal pond varies between years. Each year at least some *P. chelifera* nymphs die from desiccation, and thus a trade off seems to exist. Advantages from relaxed predation are balanced against the risk of mortality from desiccation.

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