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Changes in distribution and behaviour of two congeneric mayflies in a boreal river and its seasonal tributaries

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Abstract

Both *Parameletus chelifer* and *P. minor* had univoltine life-cycles. For a period of 6–10 months almost no nymphs of either species were found. The first nymphs appeared near midstream in winter and later in spring when the ice had broken up, they were found in great numbers close to the bank of the main river. During spring, nymphs of *P. chelifer* colonized the newly flooded littoral faster, and a seasonal stream in an alluvial meadow in greater numbers, than did nymphs of *P. minor*. Both species also colonized 10 seasonal tributaries which showed that the springtime upstream colonization was a common behaviour. During the colonization of the seasonal stream in the alluvial meadow, the diel activity pattern changed in nymphs of both species. In the main river small nymphs showed a nocturnal activity, while large nymphs were active during day-time. In the seasonal stream, both small and large nymphs showed a diurnal activity. However, when the stream was flooded, small nymphs of both species showed nocturnal activity again. In both species, diurnal activity of mature nymphs continued during emergence. Reasons for shifts in diel activity are discussed.

Introduction

Many aquatic invertebrates follow normal water level fluctuations by moving towards or away from the shore (Moon, 1935, 1940; Olsson, 1983). Shoreward movements during spring and summer have been shown for stonefly nymphs prior to emergence (Lillehammer, 1965). Mayfly nymphs (Harker, 1953; Gibbs, 1979; Olsson, 1983) and freshwater snails (Clampitt, 1974; Horst & Costa, 1975; Boag & Bentz, 1980) are also known to move towards the shore. These movements have been explained in different ways. Organisms may escape unfavourable abiotic conditions (Hayden & Clifford, 1974; Olsson & Söderström, 1978), or they may search for habitats suitable for growth (Bishop & Hynes, 1969; Olsson & Söderström, 1978) or pupation/emergence (Hultin *et al.*, 1969; Otto, 1971).

In spring, upon snow melt, when the water levels are rising, unregulated boreal northern rivers offer unexploited habitats. Not only the uppermost littoral but also seasonal tributaries are colonized by many mayfly species (Neave, 1930; Hayden & Clifford, 1974; Olsson & Söderström, 1978; Olsson, 1983). For *Parameletus chelifer* Bengtsson and *Parameletus minor* (Bengtsson) nymphs, this springtime migration not only entails a habitat shift, but also seems to include a shift from night activity to day activity (Olsson & Söderström, 1978). For two main reasons little is known about *P. chelifer* and *P. minor*. Firstly, both species have a northern distribution in Fennoscandia and the USSR and secondly, the nymphs are difficult to separate (Saaristo & Savolainen, 1980). Recently, Söderström & Nilsson (1986) presented a full redescription of the two species but the study by Olsson & Söderström (1978) on *Parameletus chelifer* unfortunately includes both *P. chelifer* and *P. minor.*

The purpose of the present investigation was to examine the changes in seasonal distribution, and the diel activity patterns of the mayflies *P. chelifer* and *P. minor* in a northern river.

Study area

Vindelälven, a river in North Sweden, rises from the Scandian mountain chain close to the Norwegian border. The area investigated (Fig. 1) is situated in a slow flowing part of the river, in the boreal coniferous zone, near Sirapsbacken (64° 22′ N, 19° 28′ E). Here the width of the river varies between 160 and 230 m. The seasonal fluctuations in discharge are very great. The mean minimum and mean maximum flows (daily mean) in this area between 1971–1985 were 30 and 960 m^3s^{-1}, respectively (data from the Swedish Meteorological and Hydrological Institute). Normally, the river is ice-covered from the middle of November to the first half of May. The fall of the water level during winter after the ice-cover has formed causes the substrate within the littoral zones to freeze. In 1979 the frozen zone extended up to a distance of 53 m out into the river from a high-water level marker fixed on the river bank (Fig. 2). The ice broke up on 13, 11 and 8 May in 1979, 1981 and 1986, respectively.

The marginal vegetation of the northern bank of this part of the river is dominated by a dense belt of *Carex acuta* L. and in some places also by

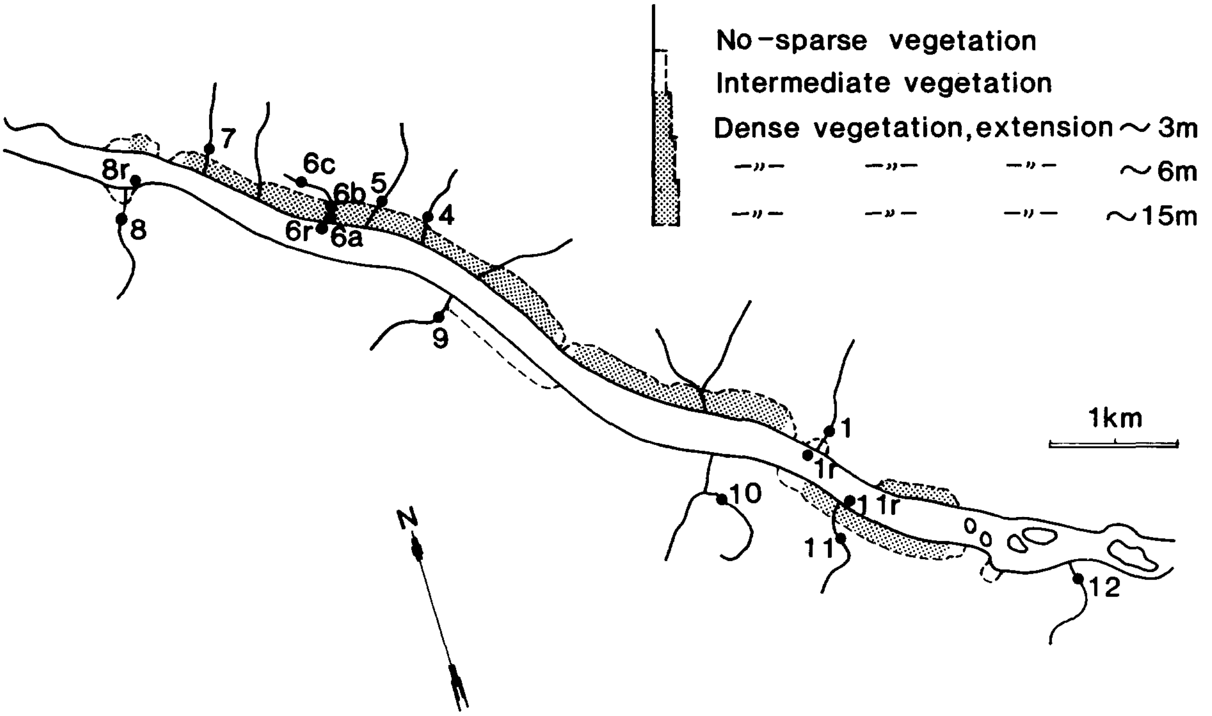

Fig. 1. Position of the sampling sites and distribution and density of the vegetation belt in the uppermost littoral of the area investigated. The vegetation belt was classified into three different classes according to the density of the dominating vegetation (*Carex acuta* and *Equisetum fluviatile*). The class with the highest density is also separated into three categories according to the extension of the vegetation belt. Site 1r, 6r, 8r and 11r were all in the main river. All the other sites were in seasonal tributaries.

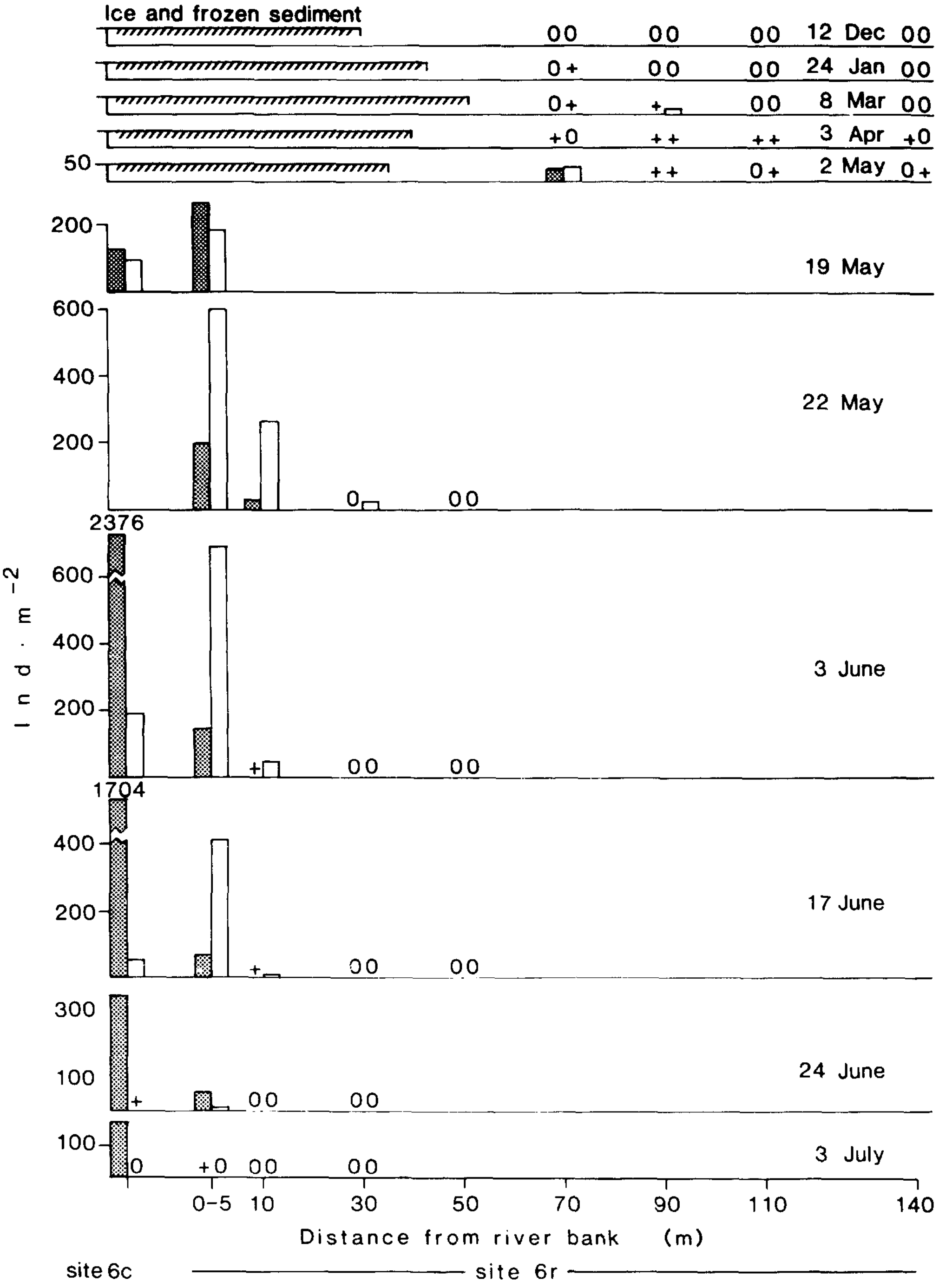

Fig. 2. Lateral distribution of *Parameletus chelifer* and *P. minor* at different times of the year at site 6c and at eight points along a transect from a high water level mark on the river bank at site 6r. Shaded bars indicate nymphs of *P. chelifer*, unshaded *P. minor*. 0, no nymphs: +, <10 nymphs m^{-2}. At each point a handnet sample was taken. The extension of ice and frozen sediment is given from 12 December 1980 to 2 May 1981.

Equisetum fluviatile L. On the southern bank of the river the marginal vegetation belt is much less dense or even absent (Fig. 1). A total of 13 tributaries enter the study area (Fig. 1). Some of them dry out during summer and all freeze into the substrate during the winter.

The small seasonal stream most thoroughly investigated (site 6a–c) has a total length of about 300 m and a width of 0.5–1 m. The stream drains an alluvial meadow, which is partially flooded every year at the time of the spring flood. The meadow and the stream usually dry out in the middle of July.

Materials and methods

The lateral distribution of nymphs of *P. chelifer* and *P. minor* was in 1980–1981 studied by using a handnet along a transect to a distance of 140 m from a high water level mark on the river bank at site 6r. Samples were also taken at site 6c in a seasonal stream. At four sites along the transect (at 70, 90, 110 and 140 m out in the river) one handnet sample, covering about 2.25 m^2, was taken at each occasion during the winter. During the spring and summer one handnet sample was taken at site 6c and four samples along the transect on site 6r (at 0–5, 10, 30 and 50 m out in the river) on each occasion. The approximate area covered by each sample varied between 0.25 and 2.0 m^2. During winter, two types of handnets (mesh size 0.5 and 0.09 mm) were used, whilst only the handnet with the coarser mesh was used during the spring and summer. The handnet samplings were performed in a standardized manner but as the area sampled differed between sites and occasions the abundance was converted to numbers m^{-2}. Sampling was performed at intervals of about 36 days during winter, and during spring and summer at intervals of about 10 days.

Mayfly nymphs colonizing different seasonal tributaries were sampled by a handnet twice in the spring of 1986. A total of 10 tributaries were investigated. The approximate area covered by each sample varied between 0.05 and 2.0 m^2 on each sampling occasion. Water samples were also collected and analysed for content of dissolved organic matter (DOM, according to Swedish Standard, 1973) and pH (Gallenkamp pH stick, PHK-120-B).

The diel activity pattern of upstream migrating nymphs was studied by a steel-sided trap (slightly modified from Olsson & Söderström, 1978). Alteratively, a glass-sided trap similar to that described by Werner (1968) and modified slightly after Olsson & Söderström (1978) was used. The traps near the bank in the main river (site 6r) operated for 3 days (5–6 May, 20–21 and 27–28 June) in 1979. The traps in the seasonal stream (site 6a–c) operated for 8 days (9–12, 13–15 and 16–17 May and 20–21 and 27–28 June) in 1979. They were emptied every second hour throughout each 24 hour period (exception 27–28 June when they were emptied every four hours). At the same time, water temperature was measured in the main river (site 6r) and in the seasonal stream (site 6c). All individuals have been counted and identified to the generic level. To estimate the number of *P. chelifer* and *P. minor* in each catch, all individuals or alternatively a subsample of up to 400 individuals were identified to the specific level. No subsampling was performed in the catches from June. The diel activity pattern of emerging subimagines of both species was studied in emergence traps (0.5x0.5x0.5 m with net-sides) both near the bank in the main river (site 6r) and in the seasonal stream (site 6c). The traps were emptied every four hours during 20–21 and 27–28 June in 1979. To test the diel activity pattern for a uniform diel activity, a conventional test of proportions was employed (Wonnacott & Wonnacott 1972):

$$|z| = (p - \hat{p})/\sqrt{\hat{p}(1 - \hat{p})/n}$$

Here, p = the hypothetical uniform proportion, $\hat{p}$ = the corresponding observed proportion of nymphs' activity during day-time hours, and n = total numbers of nymphs captured during the 24 hour period. Day-time hours were selected from 6 a.m. to 6 p.m. Thus, the activity during the lightest hours was tested against the activity during the darkest hours of each diel catch. The hypothesis of equal proportions during light vs.

dark hours was rejected at $P < 0.001$ if the z-test statistic ($|z|) > 3.29$.

To separate nymphs with respect to their physiological maturity, colour of wing-buds and appearance of mouthparts and wing-buds were noted. Length of wing-buds and wing-pads was measured under a binocular microscope fitted with a micrometer. The most mature nymphs (class 1), had dark, folded wing-buds and the mouthparts were reduced. Somewhat less mature nymphs (class 2) had yellowish-white, folded wing-buds, and the mouthparts were not reduced. Next class of nymphs (3) had transparent, unfolded wing-buds and the mouthparts were not reduced; wing-pads being $\geqslant 2.19$ mm (*P. chelifer*), $\geqslant 1.84$ mm (*P. minor*) (Fig. 3). This class could be further divided into two, class 3a and 3b. Nymphs in class 3a, were rather more mature than those in class 3b. In class 3a the difference between the length of wing-pads and wing-buds was $\leqslant 0.08$ mm, whilst the corresponding difference in class 3b was $\geqslant 0.11$ mm (Fig. 3). The least mature nymphs (class 4) had transparent, unfolded wing-buds and non-reduced mouthparts; the wing-pads being $\leqslant 2.11$ mm (*P. chelifer*), $\leqslant 1.69$ mm (*P. minor*) (Fig. 3).

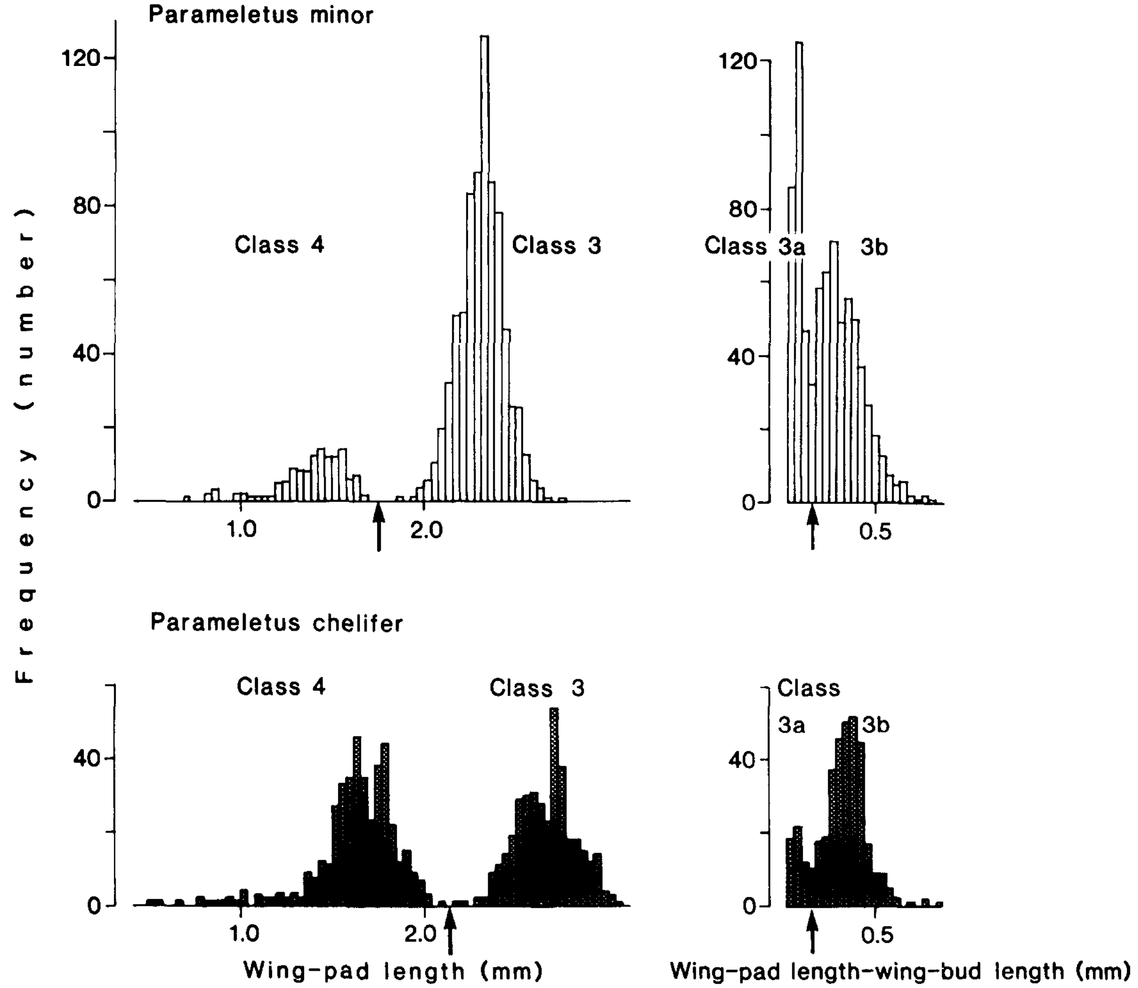

Fig. 3. Frequency distribution of wing-pad length and wing-pad length minus wing-bud length of nymphs of *Parameletus chelifer* (shaded bars) and *P. minor* (unshaded bars). Arrows mark the chosen limits between class 3 and 4 and between class 3a and 3b, respectively.

Results

Distribution

The first small nymphs of *P. minor* appeared 70 m out in the river on 24 January, and of *P. chelifer* at 90 m on 8 March (Fig. 2). Up to the 2 May, nymphs of both species were present in low numbers. Nymphs of both species became more abundant after the ice had broken up on 11 May (1981), when they started to colonize the river bank and the seasonal stream (site 6c, Fig. 2). A heavy ice transport between 11 May and 22 May, made sampling in the river impossible (except close to the bank). Samples taken during this period in 1975 showed that *Parameletus* spp could be found at a distance of at least 40 m but not 70 m from the river bank (Olsson, 1983).

On 19 May nymphs of *P. chelifer* were abundant both at the river margin and in the seasonal stream (site 6c). From 3 June nymphs of *P. chelifer* were most abundant in the seasonal stream (site 6c). Nymphs of *P. minor* were most abundant in the river from 22 May (Fig. 2). In the river, from 3 June onwards no nymphs could be found outside the 10 m point. The decrease in the number of *P. minor* from 3 June in the seasonal stream (site 6c) and 17 June in the river could be related to the emergence period. The same applied to *P. chelifer* from 17 June in the seasonal stream (site 6c). Thus, the first emerging specimens of *P. minor* were collected on 8 June in the seasonal stream (site 6c) and on 16 June in the main river in 1981. The corresponding figures for *P. chelifer* were 14 June and 30 June, respectively. From 12 July onwards no emerging specimens of either species were found.

The analyses of the water samples showed that all tributaries were more acid and had a higher concentration of DOM as compared to the main river on 1 June (Mann-Whitney U-test, $P < 0.05$) (Tab. 1). In all tributaries nymphs of both *P. chelifer* and *P. minor* were found (Tab. 1). On 1 June the tributaries on the north side of the river yielded significantly more individuals of both species than the tributaries at the south side (Mann-Whitney U-test, $P < 0.05$). At this time

Table 1. Dissolved organic material (DOM), pH and abundance of nymphs of *Parameletus chelifer* and *P. minor* in seasonal tributaries and river sites on two dates in 1986. An r indicates sampling sites in the river (cf. Fig. 1).

		pH		DOM mg $KMnO_4$ l^{-1}		P. chelifer numbers m^{-2}		P. minor numbers m^{-2}	
		13 May	1 June	13 May	1 June	13 May	1 June	13 May	1 June
Tributary	1	6.1	6.3	70.5	56.8	6	18	188	60
	4	5.8	5.8	69.8	50.6	56	4	44	236
	5	5.4	5.7	111.6	89.0	8	12	41	113
	6	5.5	6.7	96.6	30.8	224	605	168	190
	7	5.6	6.0	120.3	114.4	29	–	149	–
	8	5.2	5.8	125.9	105.8	0.5	1	17	50
	9	5.8	6.1	51.2	36.4	1	0	74	17
	10	5.5	5.5	88.5	83.5	1	3	67	56
	11	5.7	5.8	69.2	55.0	7	1	53	28
	12	5.6	5.6	74.8	62.4	22	4	43	10
Main river	1r	–	6.8	–	25.2	–	112	–	71
site	6r	6.2	7.0	42.5	25.2	406	40	188	460
	8r	–	6.9	–	25.2	–	13	–	27
	11r	6.1	6.7	47.3	28.3	36	37	221	157

nymphs of *P. chelifer* were more common in the main river compared to the tributaries on the south side (Mann-Whitney U-test, $P < 0.05$).

Diel activity

In the seasonal stream (site 6c) the daily amplitude in water temperature was much more pronounced than in the main river throughout the whole investigation period (Fig. 4). Also, the daily maximum water temperature was higher in the seasonal stream compared to the main river (except on 27–28 June).

During the upstream migration the diel activity pattern of nymphs of *P. chelifer* and *P. minor* was modified. On 5–6 May the few nymphs of *P. chelifer* that were trapped in the river seemed to be most active during the night (Fig. 5). This this diel activity could not be separated from a uniform diel activity. Nor could it be distinguished from that at site 6a, on 14–15 May, and site 6b, on 16–17 May (X^2-test, $P > 0.05$). From 9 May to 17 May, the nymphs of *P. chelifer* and *P. minor* in the seasonal stream changed from being crepuscular to being active at noon (Figs. 5 and 6). At site 6a, however, on 14–15 May, and site 6b, on 16–17 May, nymphs of both species turned nocturnal (z-test, $P < 0.001$ in both cases). On these dates the rising water level of the river had reached site 6a and 6b, respectively (see arrows in Fig. 5 and 6). With the exception of these two latter diel catches, for both species, all other diel catched from 9 May to 17 May showed a significantly higher activity during day-time (z-test, $P < 0.001$ in all cases).

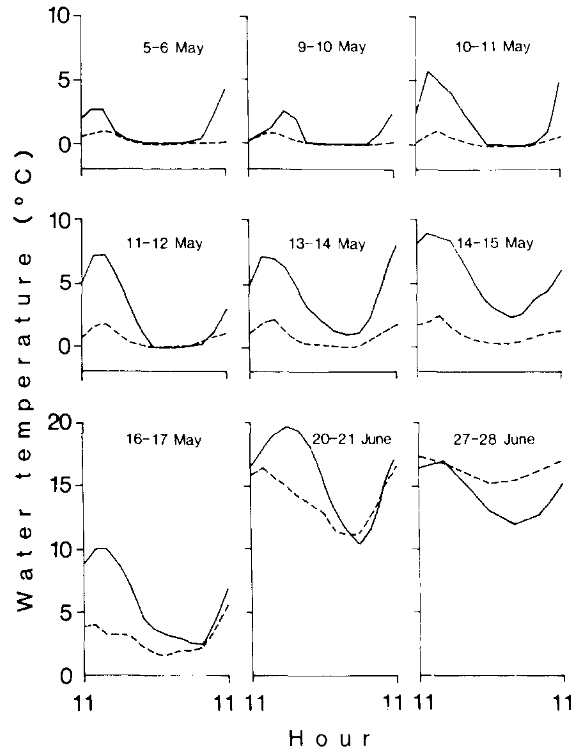

Fig. 4. The daily amplitude in water temperature in the seasonal stream in the alluvial meadow, site 6c, (solid curve) and in the main river, site 6r, (dashed curve) during 9 days in 1979. Measurements were made every second hour during each day except on 27–28 June when the intervals were 4 hours.

Nymphs of *P. chelifer* were most active around noon in the seasonal stream (site 6c) on 20–21 June and 27–28 June (z-test, $P < 0.001$, Fig. 7a). In nymphs of *P. minor* a mid-day activity was observed in the seasonal stream on 20–21 June (z-test, $P < 0.001$) and in the river on 27–28 June (z-test, $P < 0.001$, Fig. 7a). Contrary to this, nymphs of both species showed three peaks in their activity in the river (site 6r) on 20–21 June (Fig.7a). These activities were significantly different from that at site 6c on the same date (X^2-test, $P < 0.001$). Most of these individuals belonged to class 3 and 4. In *P. minor* nymphs, the two day-time peaks were mainly caused by the more physiologically mature specimens belonging to class 3a. The night-time peak was dominated by the less mature specimens of class 3b (Figs. 3 and 7b). The activity pattern of class 3a and 3b were significantly different (X^2-test, $P < 0.001$). Although very few nymphs of *P. chelifer* were caught on 20–21 June in the river, the same basic pattern of the three activity peaks as seen in *P. minor* was also apparent (Fig. 7b). The only difference was that nymphs of class 3a and 3b were more active at day-time and nymphs of class 4 during night-time (Fig. 3). As there was no difference between the sexes in this classification (X^2-test, $P > 0.05$ for both species) both sexes are treated together. The diel activity pattern of emerging individuals of both species was restricted to the middle of the day (z-test, $P < 0.001$, Fig. 7c).

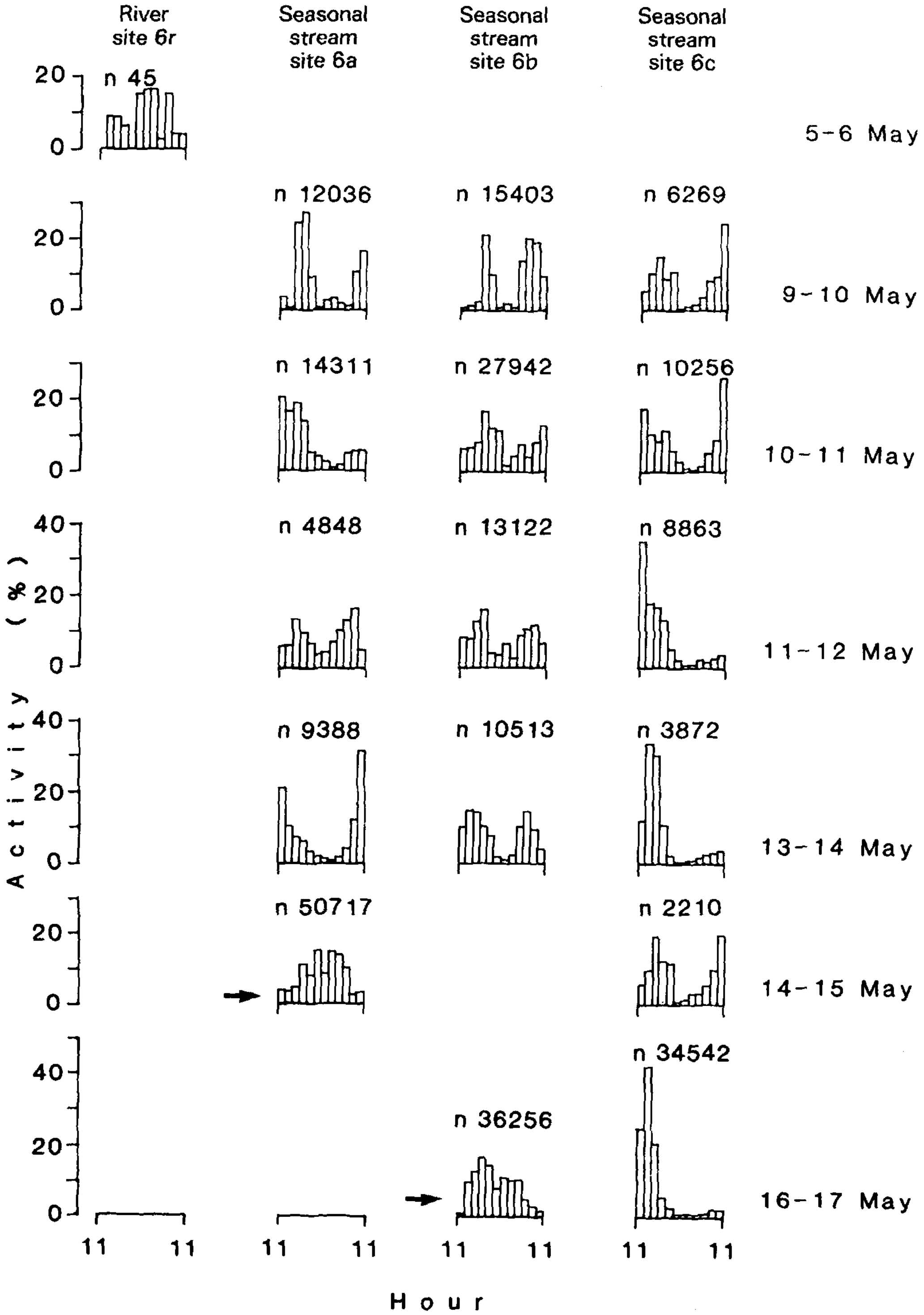

Fig. 5. Activity of upstream migrating nymphs of *Parameletus chelifer* trapped at 2-h intervals throughout seven 24-h periods during spring 1979. Activity during each 2-h interval is expressed as the percentage of the total catch during each 24-h period. Total number of nymphs caught during each 24-h period at each site is denoted by n. Arrows denote submergence due to flooding.

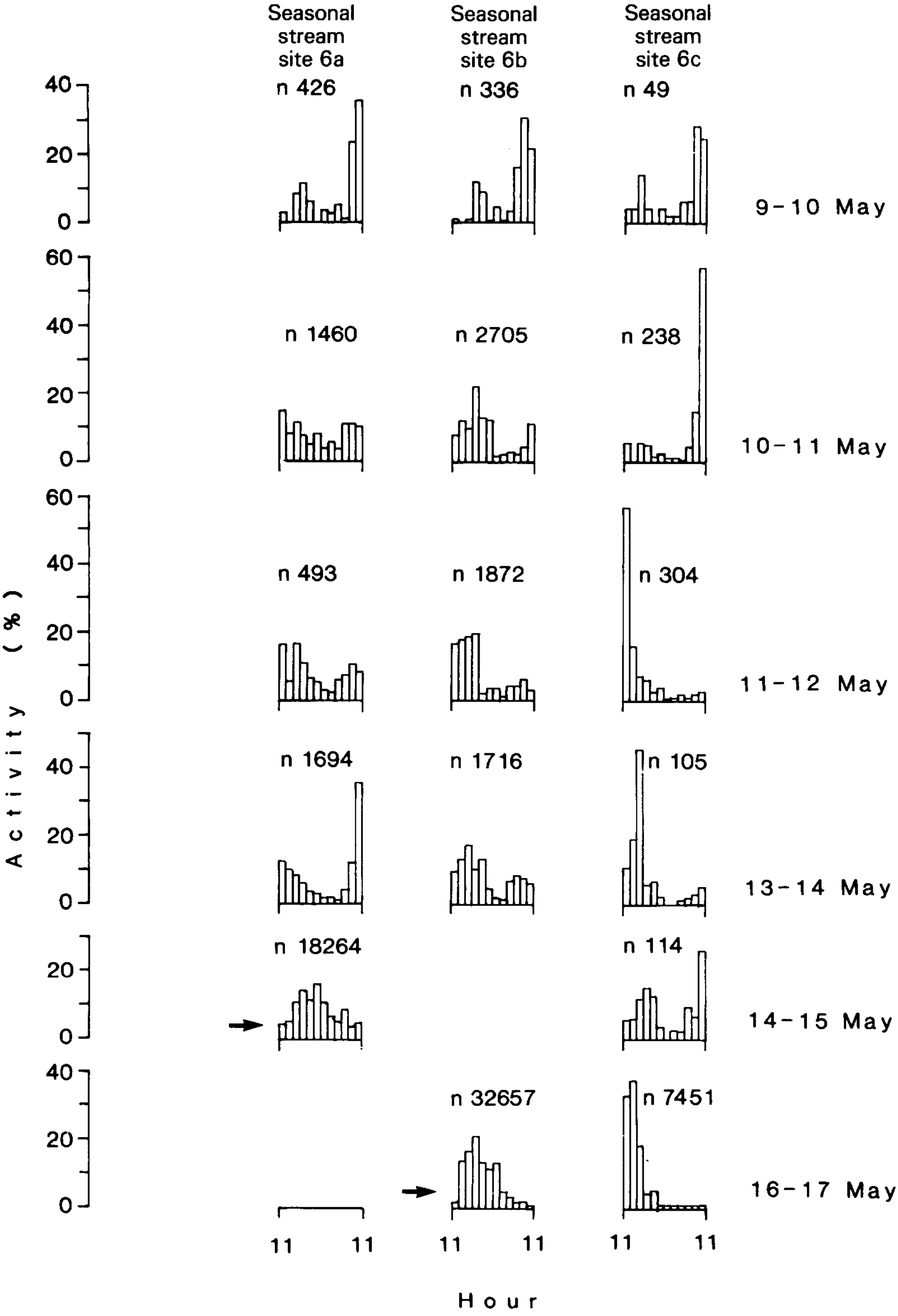

Fig. 6. Activity of upstream migrating nymphs of *Parameletus minor* trapped at 2-h intervals throughout six 24-h periods during spring 1979. Activity during each 2-h interval is expressed as the percentage of total catch during each 24-h period. Total number of nymphs caught during each 24-h period at each site is denoted by n. Arrows denote submergence due to flooding.

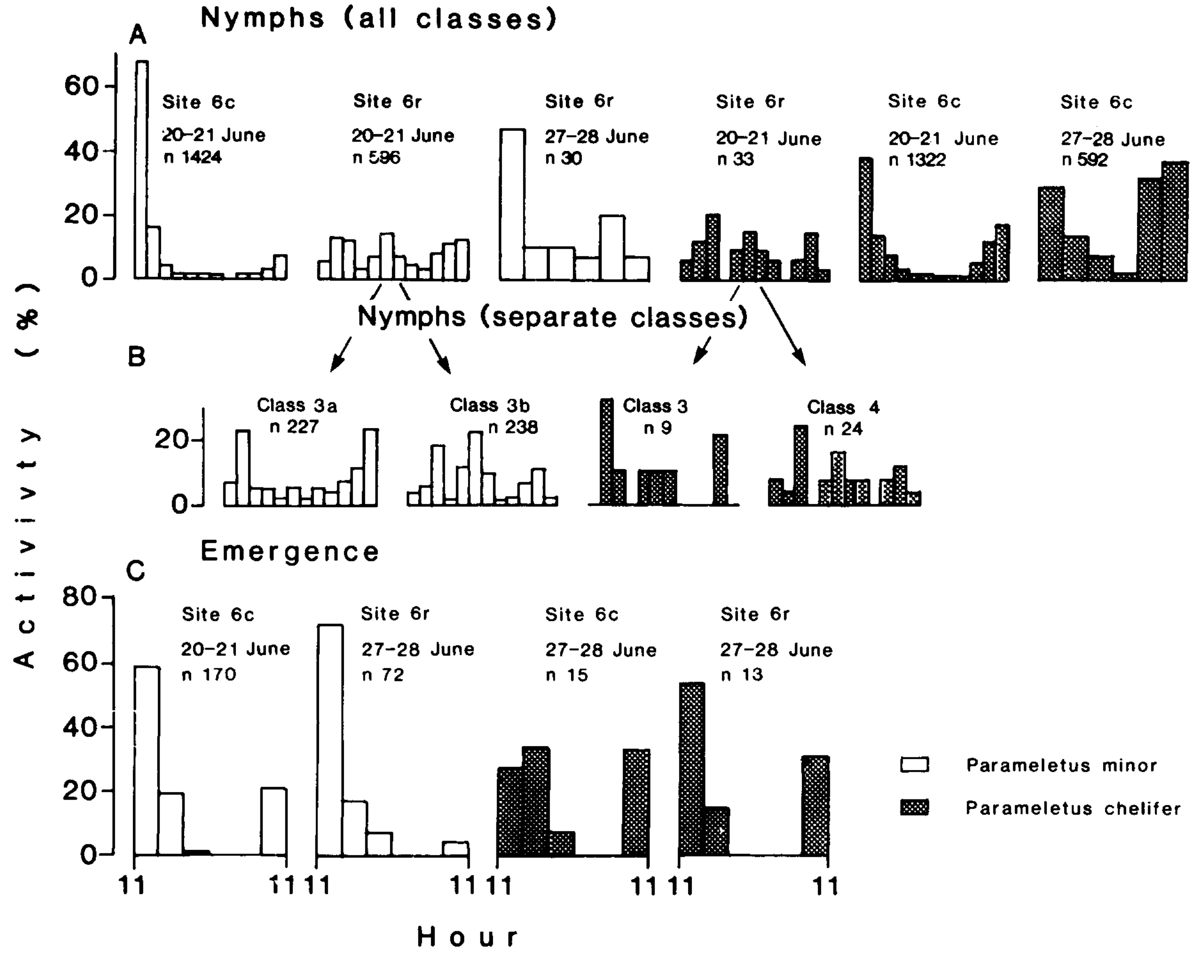

Fig. 7. Activity patterns of nymphs (A and B) and emerging subimagines (C) of *Parameletus chelifer* (shaded bars) and *P. minor* (unshaded bars) during two different 24-h periods during June 1979. Activity during each 2–4 h period is expressed as the percentage of the total catch of the 24-h period. n expresses the total number of individuals caught during each 24-h period. A = all physiological/morphological classes included, B = activity of the dominating physiological/morphological classes at site 6r on 20–21 June. Class no. 4 was the most premature one.

Discussion

Distribution

Very few nymphs of *P. chelifer* and *P. minor* could be found in the winter of 1981. Not until the ice broke up they became more abundant. Thus, a period of 6–10 months has passed since the eggs had been laid. Egg dormancy, although very likely, has not been proven in these species. Results by Edmunds *et al.* (1976) and Clifford (1982) indicate that also the eggs of the North American *Parameletus* species pass through a dormant stage. In both *P. chelifer* and *P. minor* growth, emergence and reproduction take place during a relatively short time in the summer. Egg dormancy would imply that both species have univoltine life-cycles and should be classified as summer species (Clifford, 1969).

Nymphs of both *P. chelifer* and *P. minor* rapidly colonized the littoral and the seasonal stream (site 6c) during spring. Such a behaviour has been shown for several other, mainly lentic, mayfly species (Olsson, 1983). By this behaviour the rapid current in the mid-river during the spring flood is avoided (Hayden & Clifford, 1974; Olsson & Söderström, 1978). However, other factors may also govern this behaviour. The highest abundance of *P. chelifer* and *P. minor* nymphs were found in the uppermost littoral with high vegetation density (cf. Fig. 1 and Tab. 2). Apart from a low current regime (< 5 cm per second) this habitat offers good protection from fish predators. Olsson (1983) has pointed out that the utilization of detritus, which is abundant here, as food in the uppermost littoral may be an important factor to the shore-ward movements of many mayfly species during spring. Nymphs of *P. chelifer* and *P. minor* have olfactory and/or gustatory receptors which help the nymphs to find habitats rich in food supply (Söderström, 1988). Neave (1930) showed that the upstream movement of *Leptophlebia cupida* Say was suppressed if the nymphs were kept with an adequate food supply throughout the winter.

Although both species were present in approximately equal proportion in the main river during early spring, nymphs of *P. chelifer* were more abundant in the seasonal stream (site 6c) than were *P. minor* nymphs in all three years. An explanation for this may be that by colonizing this seasonal stream, nymphs of *P. chelifer* gain more in terms of survival and/or growth, compared to nymphs of *P. minor* (Söderström & Nilsson, 1987; Söderström & Johansson, unpubl.).

The differences in abundance of both species between the different sides of the main river were probably related to the density and extension of the vegetation belt in the uppermost littoral and its resulting difference in velocity. A dense vegetation belt seems to be a habitat preferred by nymphs of *P. chelifer* and *P. minor*. A common feature of all tributaries was that they were more acid (except site 1 on 13 May) and had a higher loading of DOM than the main river. Söderström (1988) has shown that nymphs of *P. chelifer* can use a gradient of pH and nymphs of *P. minor* can use a gradient of DOM as cues in their orientation. The reactions to either pH or DOM serve to orient the nymphs to their food supply (Söderström, 1988). This would explain how nymphs of both species were able to find their way into each tributary. This implies that the upstream colonization of seasonal tributaries is a common behaviour in nymphs of *P. chelifer* and *P. minor*.

Diel activity

The diel activity patterns of premature nymphs of *P. chelifer* and *P. minor* were linked to water quality. Thus, exposure to river water or water from the seasonal stream (site 6a–c) seemed to be of profound importance. As soon as the premature nymphs of *P. chelifer* and *P. minor* entered the seasonal stream at the beginning of May they changed from crepuscular to pure noon activity. These nymphs colonized a habitat that during this time was devoid of fish predators. During upstream movements in small streams a diurnal activity has also been shown for *Leptophlebia cupida* (Hayden & Clifford, 1974) and *Parameletus* spp (Olsson & Söderström, 1978).

As the river water level rose, sites 6a and 6b became flooded on 14–15 May and 16–17 May, respectively. The activity patterns of nymphs of both species at this time were reversed to nocturnal and corresponded to that prevailing in the river. All these nymphs were premature belonging to class 4 and they were of equal length as the nymphs with the diurnal activity at site 6c (not flooded) at the same dates (Mann-Whitney U-test, $P > 0.05$). Nocturnal activity patterns have also been shown for several other aquatic invertebrates performing different activities such as drift (e.g. Waters, 1962; Müller, 1963; Madsen, 1966; Bailey, 1981; Goedmakers & Pinkster, 1981), shoreward movements (Moon, 1935), and upstream movements (Elliott, 1971).

On 20–21 June and 27–28 June, nymphs of both species in the seasonal stream had a pure noon activity. This activity pattern agreed very well with the emergence pattern. Diurnal emergence has also been shown for other mayfly species by Boerger & Clifford (1975), Friesen *et al.* (1980) and Harper *et al.* (1983). A diurnal emergence activity can be advantageous in temperate regions because of more suitable air temperature at daytime (Edmunds & Edmunds, 1980).

The physiologically most mature nymphs

trapped in the main river on 20–21 June also showed an activity pattern which may be linked to the emergence activity. However, the less mature nymphs from the river (*P. chelifer* class 4, and *P. minor* class 3b) on the same date still showed a nocturnal activity.

Vannote & Sweeney (1980) proposed that mayfly nymphs start to produce adult tissues as soon as they are exposed to a certain critical water temperature. If *P. chelifer* and *P. minor* nymphs were exposed to that temperature soon after they have reached the seasonal stream, then a shift to an activity during day-time as found in the imagines seems logical. If this was the case, then the nocturnal activity at sites 6a and 6b on 14–15 May and 16–17 May, respectively, was performed by nymphs that had not yet been exposed to that temperature. The temperature data as well as the different activity patterns of nymphs of different physiological status on 20–21 June in the main river do not, however, support this idea. It is unlikely that even the photoperiod could govern the shift in diel activity since the shift occurred at different sites on the same day. Instead, premature nymphs of *P. chelifer* and *P. minor* in the seasonal stream may have adopted a diurnal activity to increase food conversion efficiencies at day-time when water temperature is high (Vannote & Sweeney, 1980). In the seasonal stream water temperature in day-time was higher compared to the main river throughout the investigation period (except 27–28 June). Thus, energy transformation in terms of net assimilation efficiency may be favourable during day-time in the seasonal stream.

An explanation of the shift in activity pattern from night-active in the river to day-active in the seasonal stream should include the following. Many species of fish such as small pike *Esox lucius* L., roach *Rutilus rutilus* L., ten-spined stickleback *Pungitius pungitius* L., and minnow *Phoxinus phoxinus* L. hunt for invertebrates in the littoral of the main river (Söderström & Nilsson, 1987). Premature nymphs of *P. chelifer* and *P. minor* may have adopted a nocturnal activity to escape visually hunting predators. Especially in *P. chelifer* nymphs this is obvious as they were consumed by minnow and ten-spined stickleback in a higher proportion than expected (Söderström & Nilsson, 1987). Nocturnal activity has been interpreted as an antipredator adaption, i.e. prey are less active during the day when visually-hunting predators, such as fish hunt more efficiently (Thorne, 1969; Townsend, 1980). This implies that nymphs of *P. chelifer* and *P. minor* must be able to adjust their activity depending on the presence/absence of fish. The fish species that hunt for invertebrates in the littoral on the main river also use the seasonal stream as a hunting area but only when it is flooded (Söderström & Nilsson, 1987). At that time diel activity of nymphs of *P. chelifer* and *P. minor* changed from being diurnal to nocturnal. Thus, in the seasonal stream, when fish are absent, the premature nymphs can 'afford to' be active in the day-time. Nymphs of *P. chelifer* and *P. minor* are known to use chemoreception (Söderström, 1988). Peckarsky (1980) showed that nymphs of four mayfly species were able to avoid stonefly predators by chemical stimuli. *Gammarus pulex* L. (Andersson *et al.*, 1986) and *Gammarus pseudolimnaeus* Bousfield (Williams & Moore, 1982; 1985) can also detect fish predators, via olfactory means. Mature nymphs both in the seasonal stream and in the river adopted an activity pattern which corresponded to the diurnal emergence activity observed. This observation indicates that the advantages of a diurnal activity shortly before emergence must be greater than the disadvantages even in the presence of fish predators.

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