Ann. Zool. Fennici 31:245–255 ISSN 0003-455X
Helsinki 15 July 1994

Preimaginal blackflies (Diptera: Simuliidae) and their predators in a central Scandinavian lake outlet stream

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Received 13 December 1993, accepted 22 March 1994

In this study I describe the seasonal patterns of the occurrence of the blackfly species inhabiting a boreal Swedish lake outlet. Ten species were present, and the numerically dominant species were *Cnephia lapponica*, *Simulium rostratum/truncatum*, and *S. ornatum*. Densities were very high reaching maximally >120 cm^{-2} in *C. lapponica*, and >140 cm^{-2} in mixed aggregations. Along with the description of the simuliid community that of their predators was investigated. The larvae of eleven insect species of four orders were found predating on simuliid larvae. The predators with the highest average simuliid consumption were the trichopterans *Halesus* sp.and *Hydropsyche siltalai*, and the perlodid plecopterans *Isoperla grammatica*, and *Diura nanseni*. Due to differences between predator and prey phenologies, predators were variously important to different prey species. Thus, *Diura nanseni* primarily ingested *S. ornatum*, whereas *Halesus* sp. preyed heavily on larvae and pupae of *Cnephia lapponica* and *Simulium rostratum/truncatum*. Since *Hydropsyche siltalai* and *Isoperla grammatica* were common and present nearly at all times they had the greatest influence and affected all blackfly species. Presented data suggest that the impact from predators is greatest in the summer (July–August), after the main peak of blackfly larvae and pupae.

1. Introduction

Blackfly larvae are important components of stream communities. Two significant functions are their influence on particle dynamics and their value as a prey resource to predators. In some systems where blackflies are very abundant; e.g. in temperate and subarctic lake outlets, they constitute a tremendous food resource reaching astounding densities. For example, Wotton (1987a) reported larval densities reaching 120 larvae cm^{-2} in *Simulium noelleri* (complex) in a British lake outlet. The important relationships between blackfly larvae and their predators have not received due attention and comparatively little is found in the literature. However, a few recent studies have addressed how blackfly larvae react to the risk of predation in terms of changed behaviour and microhabitat selection.

The evidence of defensive behaviour in blackfly larvae is equivocal in that Ciborowski & Craig (1991) found none such by *Simulium vittatum* to the predator *Claasenia sabulosa* (Plecoptera: Perlidae), whereas Allan et al. (1987) reported successful anti-predator behaviour in large *Prosimulium onychodactylum* (complex), which repelled small nymphs of the perlodid stonefly *Hesperoperla pacifica* by biting. Dislodging and entering the drift upon contact by a predator is a further efficient avoidance behaviour (Wiley & Kohler 1981). On another level, larval simuliids may select microhabitats where they are sheltered from predators, for example in fast current refuge. Allan et al. (1987) suggested that prey preference of perlodid stonefly predators was much influenced by encounter rates. Although mayfly prey were more often encountered and attacked than blackfly larvae, the capture success was so much greater when attacking simuliids that a clear preference for blackfly prey emerged in their study. Similarly, Hansen et al. (1991) demonstrated reduced encounter and predation rates by a flatworm predator on simuliid larvae with increasing current velocity. This was due to predator and prey overlapping spatially at slow velocities mainly, and, at high velocities, the predator being less efficient, in terms of captures per attack.

For predators, it would be reasonable to expect that if blackfly larvae make up an important part of their diet, they should also show other than behavioural adaptations. Since the presence of blackfly larvae often is markedly seasonal, such adaptations could include adjusted phenologies. Only a few studies have addressed this hypothesis so far. Muotka (1993) found life cycle adjustments in a population of *Rhyacophila obliterata* to that of their simuliid prey, mainly *Simulium sublacustre* Davies (= *Simulium rostratum*, Zwick 1987), and Merritt & Wotton (1988) reported overlap between the life cycles of the muscid *Limnophora riparia* and its blackfly prey, *Simulium noelleri*. Although extensive lists of predators on blackflies exist (e.g. Davies 1981), it is poorly known which are the quantitatively important predators and in what ways their life cycles match those of their prey.

The blackfly fauna of Fennoscandia is only partly well-known and has been described by Petersen (1924), Carlsson (1962), Ussova (1964), Rubtsov & Carlsson (1965), Kuusela (1971), Raastad (1979), and Jensen (1984). Studies of the boreal part of central Sweden are scanty, and developments in Scandinavian blackfly taxonomy are wanting (Crosskey pers. comm.).

In this paper, I describe the blackfly species present in a central Scandinavian lake-outlet stream during the ice-free period between early May and the end of October and their population dynamics on two types of artificial substrates: (i) trailing pieces of wire in the water column, mimicking plants, and (ii) tiles placed on the streambed. In addition, I report on blackfly predation by a variety of benthic insect predators, evaluate their quantitative impact on the principal blackfly species, and discuss the relative importance of different predator species in different seasons.

2. Material and methods

The study was conducted in the outlet stream of Lake Bjänsjön (63°46′N, 20°02′E) in central Sweden, 15 km W Umeå. This stream is 4–5 m wide, 0.1–0.5 m deep, and has a mean discharge of approx. 1 m^3s^{-1}. Between early May and the end of October the temperature ranges between 4 and 20°C. A more detailed description of the stream and its benthic fauna has been reported elsewhere (Malmqvist 1993).

On 30 April 1990 a set of five bricks, each with 10 artificial leaves made of green garden wire (attached in a row perpendicular to the water current and trailing downstream), and another set of ten unglazed ceramic tiles, were placed in a section of the stream some 50 m downstream of the point where the water starts to flow rapidly. This was some 500 m downstream from the lake, after a section where flow is slow and smooth. Earlier observations had demonstrated high densities of blackfly larvae in this fast-flowing section. The garden wire was cylindrical in transverse section (diameter 1.5 mm), plastic-coated and 25 cm long. Five cm from the attachment point (a hole drilled in the brick), a rubber ring was positioned allowing simple and complete "stripping" of colonized larvae and pupae (Reidelbach 1991 and pers. comm.). On each sampling occasion, one garden wire unit from each brick and five tiles were taken out of the water and all larvae and pupae transferred to vials with 70% alcohol. Only the upper surface of the tiles was sampled. After the removal of animals, the sampling units were returned to the stream. On consequtive sampling occasions care was taken not to sample the same units that had been used in the previous one or two weeks (positions noted). Observations indicated that colonization was rapid, and it was not possible to visually separate colonization units that had been cleared a week earlier. The surface area of the distal 20 cm of the garden wire was 9.4 cm^2 and that of the quadratic tile 100 cm^2. In total, sampling was performed on fifteen occasions between May 7 and 26 October. In the interval between June 11 and July 25 no samples were taken. Indirect evidence and non-quantitative observations in other years suggest that blackfly abundances were low during this interval.

All larvae, or about 200 specimens when population densities were very high, and all pupae were identified to species when possible.

On nine occasions between April 2 and 2 October 2, potential predators were collected by "kick"-sampling in the vicinity of the colonization devices, care being taken not to disturb the latter. The potential predators were preserved in 70% alcohol. In the laboratory, their abdomens were opened, the guts removed, and the foregut contents teased out in a Petri dish. Configurations of microtrichia of the cephalic fans and markings on the cephalic apotome were used to identify blackfly species in the guts. The pupae and 22% of the larvae were not possible to identify.

In an attempt to quantify the impact of the predators, I assumed that simuliid densities on tiles corresponded to natural densities on the streambed, and that predator gut evacuation time was close to one day (cf. Allan 1982). Predator densities were estimated using a Surber sampler (0.1 m^2, mesh 0.25 mm). Ten samples were taken monthly from April through October.

3. Results

3.1. Blackfly colonization

Some 34000 larvae and pupae of ten species of blackflies were collected on the colonization devices at the study site in the outlet stream of Lake Bjänsjön. They belonged to the following species: *Cnephia lapponica* (Enderlein), *Prosimulium hirtipes* (Fries) (complex), *Simulium aureum* Fries, *S. cryophilum* (Rubtsov), *S. vernum* Macquart (complex), *S. noelleri* Friederichs, *S. ornatum* Meigen (complex), *Simulium* sp. near *S. morsitans* Edwards (a chromosomally distinct species, Peter Adler pers. comm.), *S. rostratum* Lundstr., and *S. truncatum* Lundstr. The latter two were not possible to reliably separate morphologically (however chromosomally distinct, Peter Adler pers. comm.), and therefore had to be considered together as *Simulium rostratum/truncatum*.

There was a clear seasonal pattern in the appearance of the different species (Fig. 1). At the beginning of the observations, the early spring peak of *S. ornatum* had just ended, and soon also that of *P. hirtipes*. The species most significant by numbers followed thereafter: *C. lapponica* and *S. rostratum/truncatum* peaking in mid-May. Whereas *C. lapponica* clearly was univoltine, *S. rostratum/truncatum* reappeared in the summer suggesting at least one more generation per year. At distinctly lower abundances, *S. cryophilum*, *S. noelleri*, and *Simulium* sp. were present in late May, obviously with only one generation annually. *S. vernum* was found in small numbers throughout the study period with a clear peak in July. *S. aureum*, a rare species in the stream was found in highest numbers in August. Finally, *S. ornatum* reappeared after the peaks of *C. lapponica* and *S. rostratum/truncatum* with several generations in the summer and autumn, and then reaching high larval abundances. From larval size data (Malmqvist, unpubl.) it was obvious that *S. ornatum* passed the winter in the larval stage. Except for this species and *Prosimulium hirtipes* all the species hibernated as eggs.

Mean densities on garden wire were almost always higher than those on tiles (Table 1). In *S. aureum*, however, all larvae were found on tiles in June and July. In *S. noelleri* and *Simulium* sp. a relatively large proportion was found on tiles at the end of May. The overall quotient between densities on wire and on tiles ranged between infinity (*P. hirtipes*) and 3.70 (*S. aureum*) (Table 1).

Abundances of larval *S. ornatum*, *C. lapponica* and *S. rostratum/truncatum* were high, and peak densities in individual samples were, expressed as numbers per square centimetre, 70.9, 127.2 and 103.6, respectively. Pupal densities were more modest and reached only 2.3, 1.3, and 11.5 cm^{-2}, respectively. Different species co-occurred,

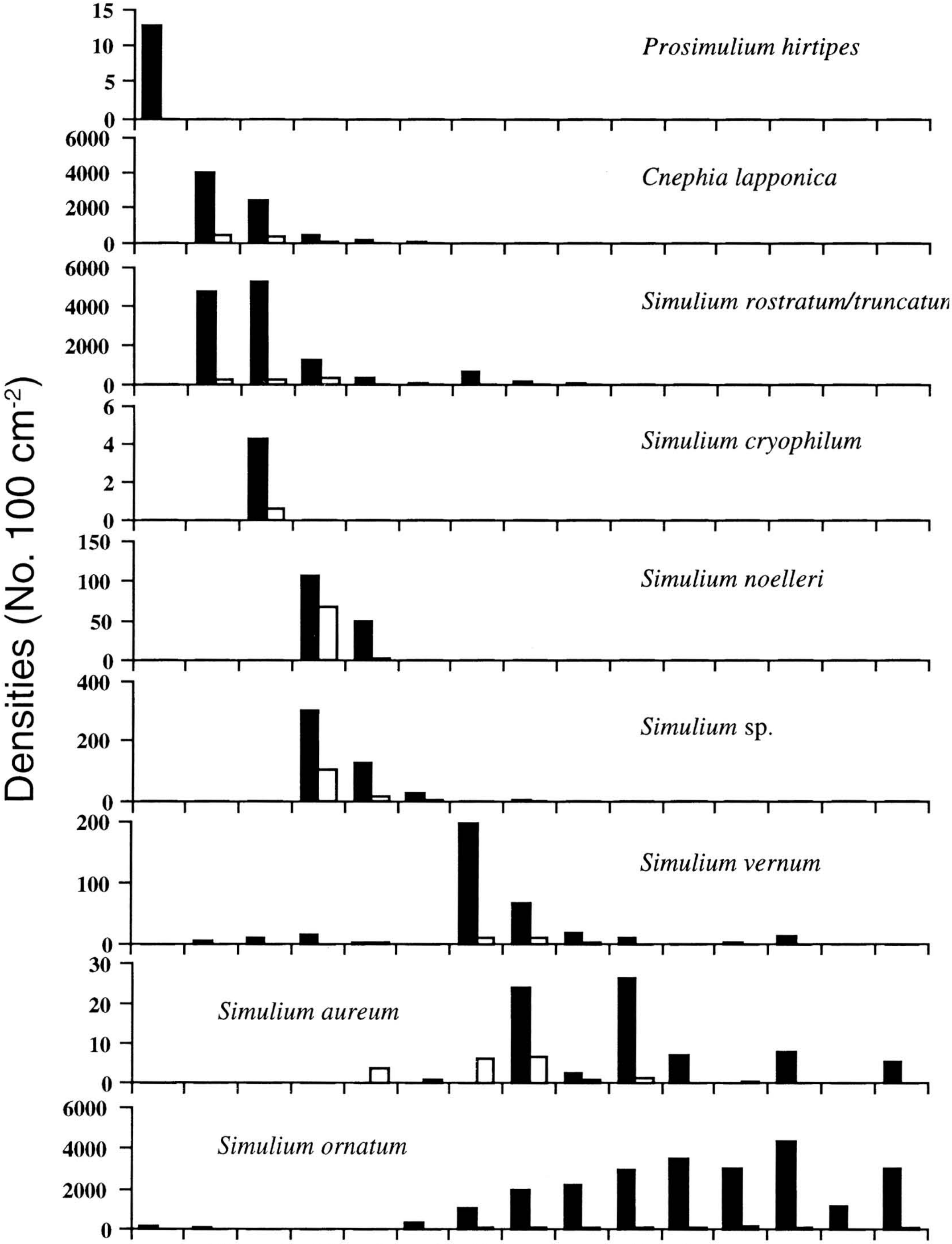

Fig. 1. The seasonal dynamics of nine blackfly species in the outlet stream of Lake Bjänsjön. The graph shows densities on artificial vegetation. Black bars denote larvae and white bars pupae.

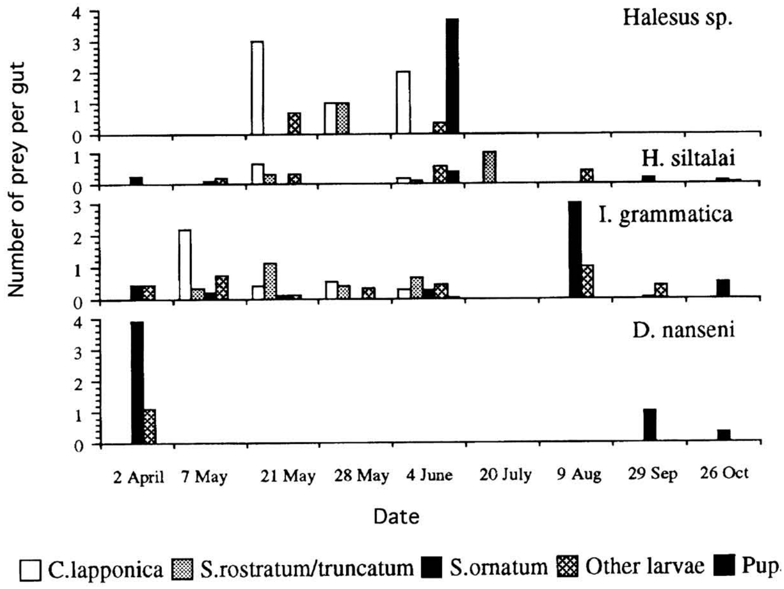

Fig. 2. The seasonal dynamics of the consumption (number of prey per gut) by four studied predators of blackfly larvae (dominant species, other species combined, and pupae).

and the highest combined density of larvae plus pupae on a single sampling unit (wire) was estimated as 148.2 cm^{-2} (pupae < 0 .1%).

Larvae were generally more common than pupae reflecting the demographic consequence of mortality throughout life, but probably more so the fact that the artificial habitats were less preferred for pupation. The first pupae, which were of *S. ornatum*, were found on May 7. This species pupated for a long period ending on September 30. Between May 28 and July 25, however, no pupae of this species were found. Pupae of *S. rostratum/ truncatum* were present from May 28 until the end of August, whereas pupae of *C. lapponica,* and *Simulium* sp. were present for a considerably shorter time.

Table. 1. The relative densities of of blackfly larvae expressed as the quotient of densities on two artificia substrates (garden wire and ceramic tiles). Since flow rate over wire always exceeded that on tiles the relative densities indicate a species' flow "preference".

Species	Relative density (wire/tile)	Flow "preference" characteristics
P. hirtipes	∞	fast
S. ornatum	63.40	^
C. lapponica	34.35	^
S. rostratum/truncatum	19.96	^
Simulium sp.	15.24	^
S. vernum	14.68	^
S. noelleri	11.87	^
unidentified	9.73	^
S. cryophilum	7.07	^
S. aureum	3.70	slow

Distributional patterns on each substrate unit were not observed directly, but the association patterns comparing entire units demonstrated a significant positive relationship between *C. lapponica* and *S. rostratum/truncatum*, whereas the relationship between *S. ornatum* and *S. rostratum/truncatum* was negative on wire (Table 2).

3.2. Predators and their gut contents

Larvae from at least eleven insect species of four orders were found predating on blackfly larvae or pupae. These were Plecoptera: *Isoperla grammatica*, *Diura nanseni*, Trichoptera: *Halesus ?radiatus*, *Hydropsyche siltalai*, *Rhyacophila nubila*, *Polycentropus flavomaculatus*, *P. irroratus*, *Chaetopteryx villosa*, *Potamophylax cingulatus*, Odonata: *Cordulegaster boltoni*, and Megaloptera: *Sialis fuliginosa*. Most important predators were *Halesus* sp., *H. siltalai*, *I. grammatica*, and *D. nanseni*. Their consumption of the numerically dominant blackflies is depicted in Fig. 2. While all species fed on larval blackflies, pupae were more rarely found in the guts. In *Halesus* sp., however, on average nearly four pupae per gut were found. Whereas *Rhyacophila nubila* contained blackfly larvae, the greatly fragmented gut contents (cf. Martin & Mackay 1982, Malmqvist & Sjöström 1984) rendered them impossible to classify, either qualitatively or quantitatively.

Due to the phenology of both predator and prey, they were asymmetrically important to each other. Thus, larvae of *C. lapponica* and *S. rostratum/truncatum*, although never those of *S. ornatum*, were important prey to larvae of *Halesus* sp. which were present in early summer. *S. ornatum* was the main blackfly prey of *D. nanseni*. Since *H. siltalai* and *I. grammatica* were present over large parts of the year they contained larvae of all these three blackfly species. Late instar larvae of *Halesus* sp. seem to specialize on blackfly prey, both larvae and pupae, which made up virtually 100% of the gut contents in late May–early June (Table 3). Also in *I. grammatica* a consistently very high proportion of the gut contents was blackfly larvae. Only in the September sample this proportion dropped below 50%. At this time of the year only small larvae of *I. grammatica* were present, and then the food consisted of about equal numbers of chironomid and simuliid prey.

A crude estimate of predator impact suggested that the total daily rate of predation of all important predators, excl. *Rhyacophila nubila*, ranged between 60 and 800 larvae per square metre (Table 4). This would imply that 0.2–10% of the present larvae were consumed per day with a minimum in May and a maximum in August. Thus the peak in May of *C. lapponica* and *S. rostratum/truncatum* effectively swamped the predators. The greatest impact was indicated to have been caused by *Hydropsyche siltalai* followed by *Isoperla grammatica*. Low densities of *Halesus* sp. limited their effect despite an apparent specialisation on blackfly prey.

4. Discussion

The densities of preimaginal blackflies in this study were extremely high reaching similar values to the highest ones recorded, exceeding 100 cm^{-2} (Wotton 1987a, b). The technique involving artificial substrates might pose problems in estimating true densities (cf. Colbo 1987, Morin 1987), although similar natural densities were no doubt present locally at this Swedish lake outlet.

The high densities *per se* pose several interesting problems, including those related to competition, or cooperation between blackflies, and relationships with predators. I deal with interactions among blackflies first. Present data suggest that high densities are tolerated by *Cnephia lapponica* and *Simulium rostratum/truncatum*. In *S. ornatum*, however, a clear negative associa-

Table 2. Associations between densities of species pairs of larvae (Pearson correlations on log-transformed data) of the dominant blackfly species on different sampling units of two different types. Non-significant relationships are indicated by "ns". Only those sampling units were included on which both species of a pair were present.

Species pair	Substrate	*n*	Association	R^2	*P*
C. lapponica vs. *S. rostratum/truncatum*	wire	26	positive	0.82	< 0.001
	tile	19	positive	0.54	< 0.001
C. lapponica vs. *S. ornatum*	wire	11	negative	0.26	ns
	tile	7	positive	0.21	ns
S. rostratum/truncatum vs. *S. ornatum*	wire	31	negative	0.25	< 0.01
	tile	32	negative	0.06	ns

tion was found with *S. rostratum/truncatum*. This suggests that *S. ornatum* may be outcompeted by the other two superabundant species in a similar manner as it was by *Simulium noelleri* in an English lake outlet (Wotton 1987a). The fact that *Simulium ornatum* was present, and abundantly so at all times of the year except for the one month's slot when *Cnephia lapponica* and *Simulium rostratum/truncatum* had their major spring peaks, suggests that *S. ornatum* was coping best in the absence of the others. *S. ornatum* is indeed considered a generalist species (Petersen 1924, Crosskey 1991), whereas the other two are more or less lake-outlet specialists, and should therefore be expected to perform better at a site like the one studied. To conclusively demonstrate that competitive effects are involved, and not merely differences in habitat preferences such as flow conditions or substrate texture, experiments are needed. These should be designed so that also the importance of scale could be evaluated. The competition hypothesis is complicated by the fact that the observed seasonal pattern may reflect competition in the past (cf. Connell 1980).

Table 3. The relative importance of blackfly larvae and pupae to their principal predators. The proportion is relative to the number of all prey individuals found in the guts. The total number of predator guts (Np) and prey items (Ni) are indicated.

Species	Date	Np	Ni	Blackflies in diet (%)
Diura nanseni	2 Apr	7	74	47.3
	29 Sep	5	14	35.7
	26 Oct	10	5	60.0
Isoperla grammatica	7 May	39	158	86.7
	21 May	19	34	97.1
	28 May	26	40	92.7
	4 Jun	27	48	95.8
	29 Sep	24	26	42.3
	17 Oct	22	39	87.2
	26 Oct	43	24	91.7
Halesus sp.	21 May	6	25	96.0
	28 May	5	11	100.0
	4 Jun	6	37	100.0
Hydropsyche siltalai	21 May	3	7	57.1
	4 Jun	25	23	95.7
	26 Oct	40	23	17.4
Polycentropus flavomaculatus	21 May	2	4	75
	4 Jun	10	16	75

Temporal segregation of species is one of several possible mechanisms to avoid direct interactions and is common in closely-related aquatic insect species (Grant & Mackay 1969), which is also found in blackflies (e.g. Ussova 1964, Wotton et al. 1979). In the outlet of Lake Bjänsjön, a clear sequence of species appeared over a relatively short time in early summer (Fig. 1).

All predators studied seemed to rely heavily on a blackfly diet, at least during parts of the season. While the larvae of *Isoperla grammatica* had a constant high proportion of simuliid larvae in their guts, those of *Hydropsyche siltalai*, although present all the year around, included blackflies in their diet predominantly in May/June when penultimate and ultimate instars dominated. The latter species still appeared to have a greater impact on blackfly larvae than the other species owing to their high densities (Table 4). *Diura nanseni* kept a high level of predation on those species present in the larval stage in the winter, and took a large proportion of the larval blackfly population especially in early spring. Predation from this species is also likely to be high in the winter.

The timing of predator life cycles with those of preimaginal blackflies is of particular interest. Since all the different predators in the study stream had their own seasonality, each species will encounter a different spectrum of blackfly species. If blackflies indeed make up a major prey of a predator one would expect adaptations to the prey species biology, including behaviour and seasonality. Firm evidence where stream-living invertebrate predators show adaptive timing with their prey is scarce, however Muotka (1993) presents a case where the life cycle of *Rhyacophila obliterata* appears especially well-tuned to the major peak in blackfly abundance in a Finnish lake outlet stream. Out of the predator species studied here, *Isoperla grammatica* and *Halesus* sp. seemed to be the ones most strongly relying on a blackfly diet. Indeed, larvae of *Halesus* sp. appeared to switch habitat in spring, migrating to stony riffles from slow-flowing areas (Malmqvist, pers. obs.), a behaviour that might well be adaptive. The life cycle of *I. grammatica* in the study stream was similar to that in South Swedish streams, where blackflies made up a much smaller proportion of their diet (Malmqvist & Sjöström 1989, Malmqvist et al. 1991). This indicates that this perlodid's life cycle may be independent of the life cycle of its blackfly prey.

Limnephilid larvae are usually classified as shredders or, in fewer instances, as collectors or scrapers (Wiggins 1984). That several species are major predators of blackflies has rarely been reported (although see Pacaud 1942, Peterson & Davies 1960, Giller & Sangpradub 1993, Otto 1993). In this study, last instar *Halesus* sp. were important predators of both blackfly larvae and pupae. It is not clear whether the consumption of animal prey by a typical detritivorous species depends on a physiological requirement, or is merely reflecting the fact that blackflies make up a nutritious and easily-harvested resource.

There are several reports on biotic relationships between blackfly larvae and hydropsychid caddis larvae underlining the general importance of the latter as predators (Jones 1949, Peterson & Davies 1960, Burton & McRae 1972, Pavlichenko 1977 in Crosskey 1990, Malmqvist et al. 1991, Moor 1991, 1992, who termed hydropsychids "exapted" simuliid specialist predators, Schorscher 1991, Englund 1993) or competitors (Hemphill 1988). Schorscher (1991), in the only quantitative report on predation by hydropsychids on blackfly larvae, reported that the daily predation rate could be as high as 40% of simuliid standing crop. In a tropical stream, she found that *Simulium* s.l. larvae were able to survive by an extremely rapid generation time of 5–6 d, although predation by hydropsychids was believed to contribute to a seasonal decline of the blackfly larvae. The impact reported here suggests that predation by hydropsychids on blackfly larvae also could be considerable in boreal lake outlet ecosystems.

Unfortunately, it was not possible to evaluate the importance of the relationship between *Rhyacophila nubila* and the simuliids. As the species is known to feed heavily on blackfly larvae when they are abundant (e.g. Muotka 1993), it is likely that this was also the case in the present study. The densities of *R. nubila* were

Table 4. Daily consumption rates per square metre by four predators, and their combined predation rate as the percentage of the available number of simuliid larvae. Mean predator densities (individuals per square metre) are given within brackets. Total predator densities also include *Polycentropus flavomaculatus* and *Rhyacophila nubila* with the overall densities of 7.6 and 5.6 individuals per square metre, respectively.

Month	Consumption (No. m^{-2}d^{-1})				Total	Total predation (% per day)
	Halesus	*H. siltalai*	*I. grammatica*	*D. nanseni*		
April	0.00	34.75	51.92	5.00	91.67	–
	(5)	(139)	(59)	(1)	(232)	
May	10.33	96.71	87.47	0.00	194.51	0.18
	(5)	(178)	(40)	(1)	(257)	
June	20.57	129.15	2.85	0.00	152.57	1.59
	(3)	(105)	(2)	(0)	(242)	
July	0.00	346.00	0.00	0.00	346.00	2.87
	(0)	(346)	(16)	(14)	(526)	
Aug	0.00	315.62	388.00	58.00	761.62	10.36
	(0)	(734)	(97)	(58)	(1169)	
Sep	0.00	83.78	27.09	30.33	141.20	2.10
	(0)	(418)	(58)	(23)	(626)	
Oct	0.00	38.70	20.40	6.30	65.40	1.64
	(0)	(258)	(40)	(21)	(496)	

< 10 m^{-2} in April and May, and ranged between 50 and 115 m^{-2} in June through October. Their impact could therefore be at least of similar importance as any of the other predators. *Polycentropus flavomaculatus* densities were between 75 and 200 m^{-2} in autumn, but guts contained blackflies virtually only in spring when the densities of this predator were low (18–24 m^{-2}). Other predators contained low amounts of blackflies and were comparatively rare.

It is possible that larval simuliids feed faster at relatively low current velocities (Ciborowski & Craig 1989). Therefore, it is surprising to find that many species dwell in microhabitats where current speeds are high. This paradox was suggested to have its explanation in an active avoidance of microhabitats where predatory stoneflies may be more successful, i.e. at lower current speeds (Allan et al. 1987). This was also one of several explanations suggested by Fuller and DeStaffan (1988) after observations of low capture success of one Megaloptera and two Plecoptera predator species in a laboratory experiment. Habitats with fast flow could serve as refuges also from predatory flatworms (Hansen et al. 1991).

Optimum current velocities for feeding in the species I studied are not known. The fact that garden wire in most cases had much higher larval densities than tiles does support the predation refuge hypothesis since the wires were positioned in faster (mainstream) flow than the tiles. Narrow plants in fast current are probably relatively safe sites for the larvae; only in very few instances was a predator, then *Rhyacophila nubila*, found on the garden wire in the present study. Other predators probably do not, or can not, use these rich food patches. Alternatively, predatory insects avoid exposing themselves to fish by dwelling on the top surfaces of tiles or on artificial plants (as well as on natural stones and plants). Rigorous experiments could help resolve whether blackfly larvae prefer high current speeds due to more efficient feeding or to predator avoidance.

The reason for simuliid presence in microhabitats with slower current velocities could be the overall very high densities where some larvae may have been excluded from the most favourable patches, or alternatively, where nearly all patches are sufficiently rewarding (cf. Muotka 1993). In habitats where current is generally weak, caddis larvae may enter submerged plants to consume blackfly larvae (Otto 1993).

If, as it seems, there is a discrepancy between patches for optimal feeding and predator avoidance, this poses interesting questions about the interrelations between pairs of different predator and prey species. For example, simuliids preferring, for whatever reason, a relative slow current speed profile, e.g. *Simulium aureum*, would be expected to be more vulnerable to invertebrate predators, whereas fast current taxa such as *Cnephia lapponica* would be less exposed to predation. On the other hand, the larvae of these simuliids probably risk encountering quite different predators, not only because they occur in different microhabitats but also due to different phenologies. If slow flow rates promote increased feeding rates, and thereby shortened development times, the overall risk of predation would not necessarily increase. In addition to flow, predation on blackflies is obviously influenced by season and probably also by the different hunting techniques exhibited by various predator species. Spill-over effects of individuals from aggregations of mass-occurring species into suboptimal habitats, in terms of predation risk, are also likely to be important.

Acknowledgements. I thank Drs Göran Englund, Timo Muotka, Christian Otto, and Roger Wotton for valuable comments on the manuscript. Dr. Peter Adler, using larval chromosomes, kindly helped with the identification of material from the study stream. Åsa Eriksson provided technical assistance. Financial support was received from the Swedish Natural Science Research Council and the Swedish Natural Protection Board.

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