Ann. Zool. Fennici 30:287–297
Helsinki 15 December 1993

ISSN 0003-455X
© 1993 Finnish Zoological Publishing Board

Microhabitat use by predaceous stream insects in relation to seasonal changes in prey availability

Timo Muotka

Muotka, T., Department of Biology, University of Jyväskylä, 40100 Jyväskylä and Oulanka Biological Station, University of Oulu, FIN-90570 Oulu, Finland

Received 1 April 1993, accepted 16 May 1993

Seasonal variation in microhabitat use of the predaceous stream insects *Diura nanseni* (Plecoptera), and *Rhyacophila nubila* and *R. obliterata* (Trichoptera) was studied in northern Finland. Samples were taken in May, August and October from a 2nd order forest stream, and in June and July from a lake outlet where *R. obliterata* was the only predatory species. Prey, especially simuliid and chironomid larvae, were aggregated on all sampling occasions at both sites. *D. nanseni* aggregated only in August, and prey availability did not affect its microhabitat use. *R. nubila* was most strongly aggregated in October and May, favouring stones with high numbers of sedentary prey which also formed the major part of its diet on all sampling occasions. *R. obliterata* aggregated where simuliids, its most important prey, were abundant. Microhabitat selection and aggressive defence by the prey, and mutual interference between the predators, are suggested as reasons for the lack of aggregative response by *D. nanseni*. In contrast, both rhyacophilid species aggregated strongly to microhabitats with temporarily high availability of semi-sessile prey.

1. Introduction

Theoretically, predators are expected to concentrate their foraging efforts in the areas of highest prey density (e.g. Hassell 1978, Stephens & Krebs 1986). This aggregative response is brought about by a change in the movement patterns (increased turning rate, reduced speed of movement) once a favourable resource patch is located ("area-restricted search"). This behaviour leads to a nonrandom spatial distribution of predators ("prey-taxis" sensu Kareiva & Odell 1987). On the other hand, antipredatory responses of mobile prey reduce the amount of habitat overlap between predator and prey. In this "behavioural response race", no clear pattern in the distributions of predator and prey is expected if the responses of both contestants are equally strong (Sih 1984).

Studies on the microdistribution of lotic insect predators and their prey have produced somewhat contradictory results. Unstable prey patches and mutual interference between predators have resulted in a lack of aggregative response in many laboratory and field experiments (Walde & Davies 1984, Peckarsky & Penton 1985, Feltmate et al. 1986, Peckarsky 1988). On the other hand, field surveys often show extensive overlap in the habitat distributions of invertebrate predators and their semi-sessile prey like black fly and midge larvae (Hildrew & Townsend 1976, 1982, Malmqvist & Sjöström 1984; but see Peckarsky 1988 and 1991a). Hildrew & Townsend (1982) suggested that overlap in microhabitat use is a real consequence of the predators' attraction to the areas of high prey density, not merely a by-product of similar microhabitat requirements.

Lotic insect predators live in an environment, where the species composition and size-structure of the prey assemblage varies seasonally. A temporarily high availability of semi-sessile prey may create potential for aggregative responses, which diminish as soon as the prey assemblage becomes dominated by more mobile prey types. The purpose of this study was to examine seasonal changes in the microhabitat distribution of three predatory stream insects, two caddisflies (*Rhyacophila nubila* (Zett.) and *R. obliterata* McL.) and one stonefly (*Diura nanseni* Klap.). Also, an attempt was made to examine the relative importance of prey characteristics and physical habitat attributes to the micro-habitat use by these invertebrate predators at different times of the year.

2. Material and methods

2.1. Study streams

Invertebrates in two streams in the Oulanka National Park, northeastern Finland (66°22′N, 29°20′E) were studied. The main study site, stream Putaanoja, is a 2nd order forest stream with high pH (7.3–7.9) and conductivity (8.9–29.9 mS/m). At the study site, Putaanoja is 4–5 m wide with a dense riparian canopy (birch, *Betula* spp., and alder, *Alnus incana*, as the major species). Current velocity varies from 30–80 cm/s, and stream substrate is composed mainly of flat boulders or cobbles.

Samples were collected also from the outlet of a small (ca. 4 ha) oligotrophic lake (stream Rytipuro). This is a narrow (ca. 1 m), shallow stream with slow to moderate flow (20–60 cm/s). pH (7.4–7.9) and conductivity (9.6–14.6 mS/m) are rather high. The riparian zone consists mainly of coniferous trees (mostly *Pinus sylvestris*), and is not nearly as dense as at Putaanoja. Stream bottom is primarily cobbles, and moss growth on the stones is negligible. This site was described in more detail by Muotka (1990).

Putaanoja harbours an abundant fish fauna (sculpin *Cottus poecilopus*, 0.6 ind./m^2, and minnow *Phoxinus phoxinus*, 0.3 ind./m^2), whereas the only fish species occasionally found in the upper reaches of Rytipuro is the ten-spined stickleback *Pungitius pungitius*.

2.2. Field and laboratory methods

Benthic samples were collected on three occasions in Putaanoja (6–8 August and 14–16 October 1990, and 8–10 May 1991). *D. nanseni* and *R. nubila* were obtained in high numbers, whereas *R. obliterata* was too rare to be included in the analyses. Accordingly, samples were collected also from the outlet of Lake Rytilampi, where *R. obliterata* is the major invertebrate predator. Other predaceous insects at this site, although in much lower densities, are *Isoperla grammatica* Poda and *Diura bicaudata* L. In Rytipuro, samples were obtained on only two occasions, 17–18 June and 3–4 July 1991. These samples allowed examination of the microdistribution of *R. obliterata* in relation to the availability of a seasonally abundant prey, black fly larvae. Black flies (mostly *Simulium sublacustre* Davies) form dense larval aggregations in this outlet from early June onwards. Larval development is very rapid, giving rise to adults in 2–3 weeks. By early July the stream is already nearly devoid of black flies (Muotka, unpubl.)

Natural, cobble-sized stream stones were used as sampling units, with the number of samples being 50 (May) or 60 (August and October) in Putaanoja, and 30 in Rytipuro. Samples were obtained by stratified random sampling: a 30–40 m long stream reach was divided into regularly spaced transects across the channel, and 1–2 samples were taken from random positions along each transect. I collected the samples by placing a frame with a net (mesh size 0.25 mm) downstream of a stone, then removing the stone into the net. Invertebrates dislodged from the stone and trapped by the net were included in the sample. Depth of water (cm), current velocity (cm/s, Novar streamflo-probe 403), and stone surface area (dm^2, as the product of two perpendicular dimensions; see McCreadie & Colbo 1991) were measured in the field. In Rytipuro, there was so little variation in the depth of water (range 12–20 cm) that depth was not measured separately for each stone. Moss biomass in each sample was quantified by drying mosses at 105°C overnight, then weighing. No mosses occurred on the stones in Rytipuro. Because the amount of coarse detritus associated with stones was negligible on all sampling occasions, this variable was not measured. Samples were preserved in 70% ethanol in the field, and associated invertebrates were later sorted in the laboratory. Numbers of the most abundant prey types (nymphs of *Baetis* mayflies, simuliids and chironomids) were counted for each stone. All other potential prey were lumped as "other prey", including other mayflies, non-predaceous stone-flies, caddisfly larvae and unidentified Dipterans. Species that are of minor importance as food for predatory insects were disregarded (T. Muotka, *pers. obs.*; see also Malmqvist & Sjöström 1984). This group included burrowing annelids (Oligochaeta), molluscs, aquatic mites and elminthid beetles. Also, 5th instar hydropsychid and limnephilid caddis larvae too large to be consumed by the predators were excluded from this group. Because different size groups of *Baetis* spp. and simuliids, the two prey types with largest size variation, gave qualitatively similar results, size-class specific data on prey availability were omitted from subsequent analysis. For rhyacophilids, only fourth and fifth instar larvae were used in the statistical analysis, because smaller specimens are not predominantly carnivorous (Muotka, unpubl.).

If multivariate analysis suggested an association between predator and prey distributions, gut contents of the predator were analysed to examine whether microhabitat overlap was connected to consumption of a particular prey taxon. Gut contents were mounted in polyvinol lactophenol under cover slips. Prey were identified and counted on the basis of sclerotized body parts with reference to slide mounted specimens of the taxa available in benthos. The entire slide was scanned for identifiable animal material; this method has been found the most reliable one for analysing diet composition of *Rhyacophila* larvae (Martin & Mackay 1982).

2.3. Statistical analysis

First, the dispersion patterns of predators and their prey at different times of the season were analysed. From the plethora of indices available for this purpose, Lloyd's measure of "patchiness" (= ratio of mean crowding to mean density, m^*/m; Lloyd 1967) was chosen, for two reasons: 1) it is biologically interpretable, measuring "how many times as 'crowded' an individual is, on the average, as it would be if the population had a random distribution" (Lloyd 1967); 2) for this index there is a modification for cases where the quadrat size is not constant ("adjusted mean crowding", Watanabe 1988). Values higher than one indicate clumped, lower than one regular distribution patterns, respectively. A distribution-free method (Reed 1983), based on application of the jackknife, was used to calculate 95% confidence intervals for the index. Traditionally, ecologists have been preoccupied by the variance:mean-ratio as an index of both aggregation and deviation from randomness. While showing that no index can fulfil both purposes, Hurlbert (1990) made a strong case against s^2/m as a measure of aggregation, because it, unlike the "patchiness"-index, lacks a biologically meaningful interpretation. Downing (1991) has recently criticized Lloyd's index (and many other indices of dispersion), because of its dependence on population density. Ideally, these indices should only be used for examining deviation from randomness of the population under study (e.g. Ripley 1981). Comparisons among populations from different places or sampling times must be interpreted tentatively. However, density variations of the predators studied here were so small that even comparisons between sampling occasions seem justified.

To examine the relative importance of different variables to the microhabitat use by the predators, an approach based on Principal Components Analysis (PCA), modified from Grossman & Freeman (1987) was applied. First, each variable was evaluated for its normality with normal probability plots and Shapiro-Wilks test (Zar 1984). When necessary, appropriate transformations were used to make the data in better accord with the assumptions of PCA (approximate multivariate normality, linear relationships between variables). Accordingly, depth was not transformed for any analysis, whereas log-transformations were used for velocity, stone size, moss biomass, and prey density. Next, PCA was run on the correlation matrix of environmental variables. The first component (which was usually the only one for which a plausible biological explanation could be found) was divided into four or five equally spaced intervals ("microhabitat" categories), and the distributions of the predators along the component were scored. Chi-square analysis was used to test for the goodness of fit between microhabitat availability and use, as represented by corresponding component scores. In case of a significant overall difference, a "subdivided" chi-square analysis (Zar 1984) was conducted to see which, if any, of the component categories contributed significantly to the observed discrepancy between availability and use. Finally, the average microhabitat characteristics in significantly over- or under-represented habitat categories were compared with concurrent microhabitat availability to reveal the factors most influential in microhabitat use by the species examined.

3. Results

3.1. Species densities and distribution patterns

Chironomids were the most abundant prey in Putaanoja in August, whereas 'other prey' dominated in May (mostly ephemerellid mayflies) and October (ephemerellids and cased caddis larvae of the genus *Micrasema*) (Table 1). Black flies were abundant only in August, reaching densities well over 1000 ind./m^2. *Baetis* mayflies were present throughout the sampling period, but mostly in rather low numbers. Prey densities were especially low in late spring, and this time of the season obviously represents a period of resource scarcity for the invertebrate predators.

Prey (excluding black flies) were aggregated on all sampling occasions in Putaanoja, most conspicuously so in October (Table 1). Simuliids were most aggregated in August, when individual black flies were nearly 8 times more 'crowded' than in a randomly distributed population. How-

Table 1. Densities (ind./dm^2) and index of dispersion (L, jack-knifed estimates of Lloyd's "patchiness" adjusted for stone size) for two predators and their prey in Putaanoja. Head width ± *SD* in millimetres. 95% confidence intervals in parentheses.

		6 May (*n* = 50)		10 August (*n* = 60)		16 October (*n* = 60)	
Diura nanseni	Density	0.45	(0.25)	1.28	(0.46)	0.79	(0.25)
	L	1.38	(0.60)	1.26	(0.11)	1.56	(0.70)
	Head width	2.24	(0.13)	1.23	(0.16)	1.76	(0.14)
Rhyacophila nubila	Density	0.29	(0.13)	1.14	(0.35)	1.10	(0.57)
	L	2.79	(0.43)	1.36	(0.06)	4.94	(0.39)
	Head width	1.14	(0.11)	0.83	(0.14)	1.11	(0.13)
Baetis spp.	Density	1.22	(0.71)	2.90	(0.78)	5.86	(3.00)
	L	3.86	(0.61)	1.99	(0.15)	4.32	(0.40)
Simuliidae	Density	1.09	(0.45)	11.06	(8.68)	0.42	(0.23)
	L	2.10	(1.57)	7.70	(0.96)	3.55	(0.87)
Chironomidae	Density	2.67	(0.83)	18.30	(6.19)	14.28	(6.87)
	L	1.75	(0.39)	2.41	(0.06)	5.54	(1.00)
Other prey	Density	4.75	(1.49)	16.12	(3.67)	18.30	(6.71)
	L	2.07	(0.14)	1.70	(0.05)	3.01	(0.20)

ever, because the mean density of black flies varied considerably among sampling times, this result must be interpreted cautiously.

At the Rytipuro outlet, a mass emergence of black flies took place between the two sampling occasions. Simuliid density declined accordingly, while the distribution pattern remained aggregated (Table 2). The level of aggregation was not nearly as high as in Putaanoja, possibly because even the less favourable microhabitats were densely occupied by black flies at the outlet site in June. No other prey were abundant in Rytipuro, and the overall prey density in early July was even lower than in Putaanoja in May.

Diura nanseni exhibited a synchronous nymphal development throughout the study period, with emergence taking place in early June (see also Kuusela 1984). The density of *D. nanseni* declined steadily from August 1990 to May 1991 (Table 1). For the most part, the distribution pattern of this species could not be distinguished from random. Only in August, when the nymphs were small, was there a tendency towards aggregation. All five instars of *Rhyacophila nubila* were present on every sampling occasion. In May, the population was dominated by fifth instar larvae, whereas most specimens collected in August were in their third or fourth instars. Species density was highest in August and October, with more than 100 ind./m^2 (Table 1). Interestingly, *R. nubila* showed only slight aggregation in August, when the abundance and patchiness of black flies was highest. On the other hand, *R. nubila* was highly contagiously distributed in the autumn, when other prey groups, especially chironomids, were most aggregated.

Most specimens of *Rhyacophila obliterata* in Rytipuro had already reached their final instar by June 16. Shortly after the emergence of black flies mature larvae of *R. obliterata* started to pupate, and larval densities declined abruptly (Table 2). This species was slightly aggregated in June, whereas in July the patchiness-index was less than 1, indicating a regular distribution pattern. However, because the number of individuals collected in July was very low ($n = 14$), the regularity may have been more apparent than real.

Table 2. Densities (ind./dm^2) and index of dispersion (L, jack-knifed estimates of Lloyd's "patchiness" adjusted for stone size) for *R. obliterata* and its prey in Rytipuro. Head width ± *SD* in millimetres. 95% confidence intervals in parentheses.

	16 June		3 July	
Rhyacophila obliterata				
Density	1.19	(0.56)	0.43	(0.15)
L	1.55	(0.21)	0.48	(0.13)
Head width	1.54	(0.07)	1.48	(0.09)
Baetis spp.				
Density	1.58	(0.86)	3.07	(0.95)
L	6.06	(1.21)	1.55	(0.11)
Simuliidae				
Density	157.72	(121.20)	2.84	(2.43)
L	3.58	(0.79)	2.62	(0.36)
Chironomidae				
Density	2.25	(1.17)	1.35	(0.60)
L	2.99	(0.69)	1.73	(0.21)
Other prey				
Density	2.48	(1.41)	2.08	(1.36)
L	3.89	(0.74)	5.28	(1.91)

3.2. Microhabitat use by the predators

Microhabitat use by *D. nanseni* in May could not be distinguished from random, although it seemed to be associated with comparatively large stones (Fig. 1). The fairly small nymphs present in August showed even less consistent habitat use (Fig. 1). October was the only time when *D. nanseni* selected microhabitats based on their physical characters: moss cover was high and flow rate rather low in microhabitats used by *D. nanseni* (Fig. 1, Table 3). In contrast, none of the prey variables contributed importantly to microhabitat use by this predator on any of the sampling dates.

In early spring, *R. nubila* used microhabitats in about the proportions they were available (Fig. 1). In August, it occurred disproportionately often in microhabitats with high numbers of simuliids and chironomids (Fig. 1, Table 3). Not surprisingly, these two prey items also made up the major proportion (almost 90%) of the predator's diet in August (Fig. 2). However, the percent variance explained by the first component was rather low, which suggests that *R. nubila* was responding to a complex set of microhabitat

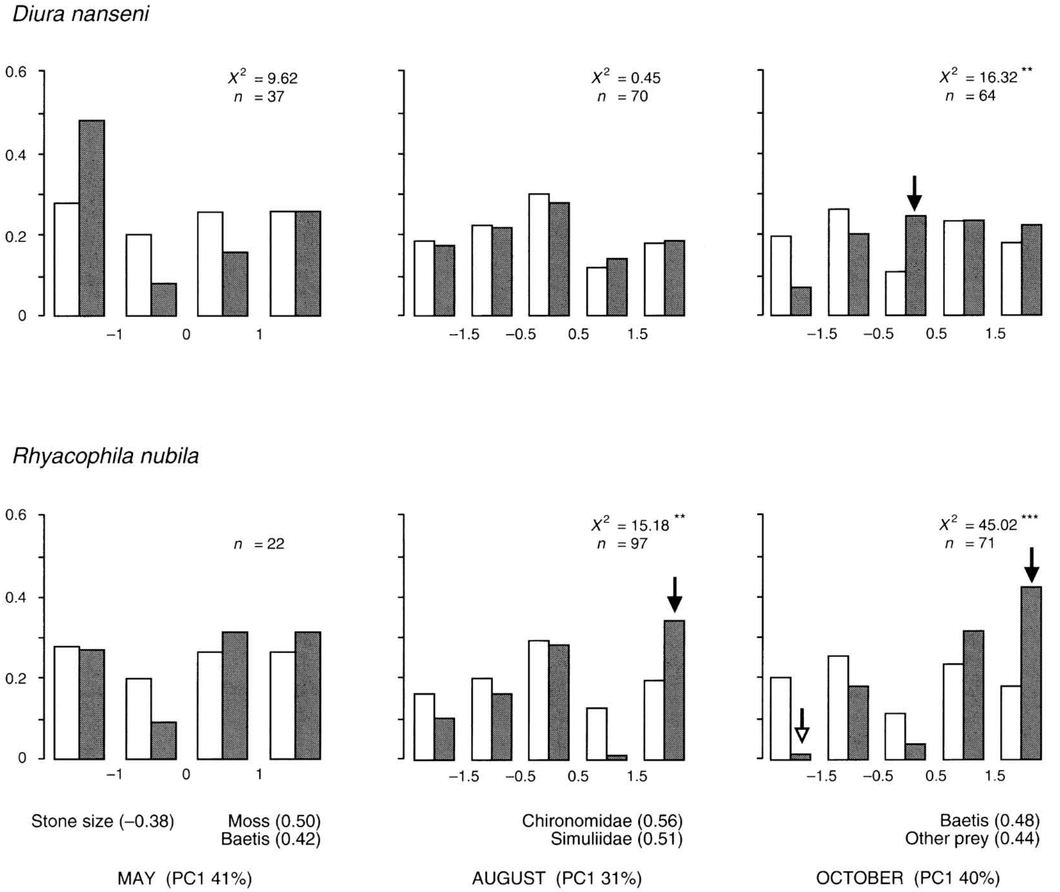

Fig. 1. Proportion of habitats available (open bars), and used (shaded bars) by *D. nanseni* and *R. nubila*, in different component categories (border values shown between bars) of the first principal component. Percent variation explained by the component is given under each axis. Categories furthest left and right pool all microhabitats with component scores less than –1.5 (or –1.0 in May) and more than 1.5 (or 1.0), respectively. Chi-square analysis tests for goodness-of-fit in the availability and use of microhabitat categories; it was not performed in May for *R. nubila* because of a small sample size. Significance: ** = $P < 0.01$, *** = $P < 0.001$, n = number of individuals. Black arrows indicate significant over-, open arrows under-representation of a given microhabitat category. Variables with highest loadings are given under the axes, with loading values in parentheses.

variables, although the availability of dipteran prey may well have been the decisive factor in microhabitat use. Finally, in October, non-random microhabitat use was again observed, and it was mostly effected by the numbers of baetids and of 'other prey' (Fig. 1, Table 3). Because these prey taxa often occurred within tufts of moss, it is not possible, without manipulative experiments, to tell apart the independent effects of these variables. Nevertheless, baetids, ephemerellid mayflies and *Micrasema*-caddisflies formed a bulk of the diet of *Rhyacophila* in October (Fig. 2). The predator still ingested simuliids surprisingly often, although this prey was rare at this time of the season.

In June, *R. obliterata* showed distinctive microhabitat selection for stones with high abundance of larval black flies (Fig. 3, Table 3). Be-

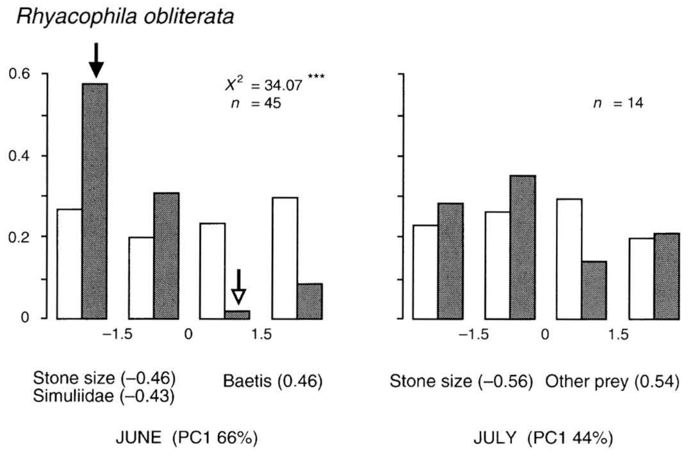
Rhyacophila obliterata

Fig. 2. Proportion of habitats available (open bars) and used (shaded bars) by *R. obliterata* in different component categories of the first principal component. For further explanations, see Fig. 1.

cause simuliid abundance and stone size were highly inter-correlated (Spearman rank correlation, $r_s = 0.723$, $P < 0.001$), it is difficult to evaluate the relative importance of these two variables. However, even after controlling for the effects of stone size, *R. obliterata* showed a positive association with black fly larvae (Kendall partial correlation, $r = 0.483$). Furthermore, in July, after the abundance of black flies had dropped, *R. obliterata* did not prefer large stones (stone size: 1.28 ± 0.17 dm^2, $n = 14$ and 1.14 ± 0.13 dm^2, $n = 16$ in microhabitats occupied vs. not occupied by *R. obliterata* in July, respectively). None of the measured microhabitat variables had an observable effect on microhabitat use by *R. obliterata* in July (Fig. 3).

Black flies were by far the most important prey item for *R. obliterata* in June, comprising 83% of all prey ingested (Fig. 2). In July, the dietary composition was much more varied. Simuliids were still the dominant prey item (Fig. 2), in spite of their much reduced availabil-

Table 3. Average microhabitats in the component categories showing significant over (+) or under (–) representation of predators. Average microhabitat availability is also given. *n* = number of samples in a respective category. See text for details.

			Depth	Flow	Moss	Stone	Prey density (ind./dm^2)			
	n		(cm)	(cm/s)	(gDM/dm^2)	size (dm^2)	*Baetis*	Chiron.	Simul.	Other
June										
R. obliterata	8	+		37.9	0.0	2.6	0.1	1.1	1214.2	0.5
	9	–		50.0	0.0	0.9	0.9	0.6	54.0	1.6
availability	30			36.8	0.0	1.0	1.6	2.0	25.8	2.1
August										
R. nubila	12	+	13.1	38.5	13.6	1.7	5.8	91.8	107.8	49.5
availability	60		19.6	29.6	3.1	1.3	10.1	10.7	2.3	261.5
October										
D. nanseni	7	+	20.7	27.4	19.8	1.3	3.3	22.7	0.0	22.7
R. nubila	11	+	20.5	44.0	35.2	1.0	19.2	56.2	0.9	65.6
	12	–	21.1	27.5	3.0	2.1	0.9	2.0	0.1	3.2
availability	60		21.4	39.9	11.8	1.6	5.8	15.0	0.4	19.5

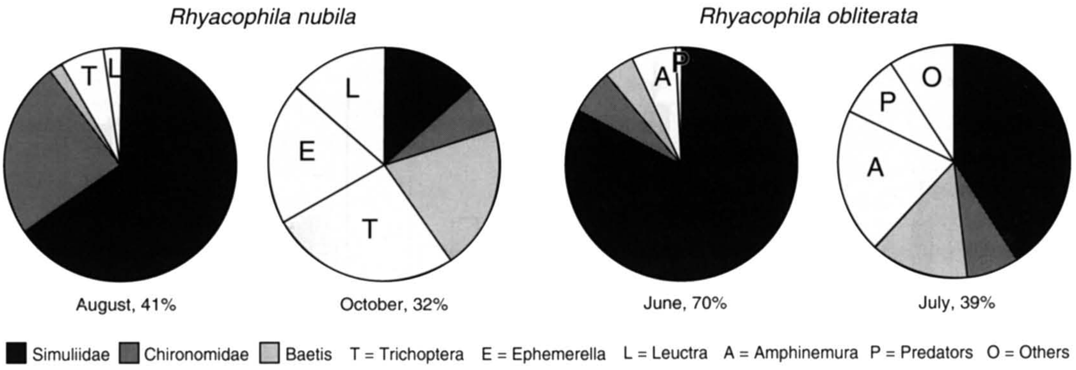

Fig. 3. Gut contents (as proportion of total number of prey ingested) of *Rhyacophila nubila* in Putaanoja, and *R. obliterata* in Rytipuro. The percentage value indicates the average gut fullness (maximum gut diameter as percent of head width; see Martin & Mackay 1982). Number of studied individuals = 25.

ity in benthos. There was also some evidence of intra-guild predation in July; 4 out of 25 specimens dissected for gut content analysis had consumed either isoperlid stoneflies or second to third instar rhyacophilid larvae.

4. Discussion

Foraging theory predicts an aggregative response of foragers to their resources, and, indeed, this pattern has been documented in numerous field and laboratory studies (for reviews, see e.g. Hassell 1978, Stephens & Krebs 1986). If a predator concentrates its foraging efforts in areas of highest prey density, this should increase its feeding rate (e.g. Hildrew & Townsend 1982, Walde & Davies 1984, Malmqvist 1991), and, ultimately, its fitness relative to other individuals in the population (Sih 1983). Many lotic insect predators, however, do not seem to meet these expectations. Predaceous stoneflies, especially, are often randomly distributed, not showing any obvious relationship to the spatial distribution of their prey (Peckarsky & Dodson 1980, Peckarsky 1988, 1991a, Walde & Davies 1984, Feltmate et al. 1986). In most of these studies, mayfly larvae, especially of the genus *Baetis*, were the major prey available. These highly mobile invertebrates may form "unstable prey patches" (Walde & Davies 1984, Peckarsky & Penton 1985), which disperse when a predator enters the patch. However, this is not an appropriate explanation for a lack of aggregative response to more sedentary prey, such as simuliid and chironomid larvae (although simuliids also often drift when contacted by a predator; Wiley & Kohler 1981, Allan & Flecker 1988). In this study, these prey groups were frequently highly aggregated, yet *D. nanseni* did not seem to concentrate its foraging efforts in patches with high numbers of these apparently vulnerable, "cost-effective" (Feminella & Stewart 1986) prey. At least three explanations may account for this. First, prey may avoid contacts with the predator by selecting microhabitats where the predator's foraging efficiency is low, or which the predator avoids. Simuliids generally favour microhabitats with high current velocities, whereas predaceous stoneflies are rarely seen on the upper surfaces of stones (Allan et al. 1986, 1987). Hansen et al. (1991) showed that black flies reduced their encounter rate with an invertebrate predator, and also had better chances of surviving attacks by the predator, by selecting high velocity microhabitats. Thus, although the preference for high currents by black flies probably originally evolved for other purposes (e.g. efficient food acquisition), it may well be an important antipredatory trait in present-day predator-prey interactions.

Second, sedentary prey may aggressively defend themselves against an attacking predator.

Although chironomids do not do this, simuliids sometimes repel small stoneflies by fiercely biting the predator to its head region (Allan & Flecker 1988, Tikkanen & Muotka, unpubl.). Although only documented in simplified laboratory conditions, this could well be a mechanism preventing stoneflies from aggregating to high-density patches of larval simuliids in the field also. This mechanism may provide a size-refuge for the prey at the time of the season when the stoneflies are still rather small, thus emphasizing the importance of size relationships in studies of lotic predator-prey interactions.

Third, intraspecific interactions might prevent stoneflies from aggregating in patches of sedentary prey. Interference competition between stoneflies is known to affect most aspects of their foraging behaviour (Walde & Davies 1984, Peckarsky & Penton 1985, Sjöström 1985, Malmqvist 1991, Peckarsky 1991b), and, ultimately, growth and fecundity (Peckarsky & Cowan 1991). Walde & Davies (1984) suggested that, because of mutual interference between predators, there is not much advantage in being able to accurately assess prey density. Thus, random distribution might actually be the optimal one for predaceous stoneflies.

Peckarsky (1991a) has recently suggested that habitat selection by predatory stoneflies has evolved more as a response to avoid predation by fish than for efficient foraging on their own prey (see also Soluk & Collins 1988, Feltmate & Williams 1989). Large stones are less susceptible to physical disturbance, thus making better refugia against fish predators (see also Feltmate et al. 1986). Feltmate & Williams (1991) demonstrated that stonefly nymphs possess an ability for spatial learning, being able to locate stones that provide the best refuge from fish. Moss cover could clearly also serve as a refuge from predators. In my study, high moss cover was the only factor affecting microhabitat use by *D. nanseni*. This microhabitat feature may be favoured because it provides refuge against fish predators, is consistently associated with high numbers of potential prey, or both. Feltmate & Williams (1991) suggested that spatial learning could also aid predaceous stoneflies in locating prey patches, but because these are continuously redistributed (Townsend & Hildrew 1976), and often not consistently associated with physical habitat variables (Peckarsky 1991a), this seems unlikely.

Most previous studies of microhabitat use by predaceous stream insects have considered only predatory stoneflies (but see Hildrew & Townsend 1976, 1982 and Malmqvist & Sjöström 1984). In my study, the caddis larva *R. nubila* showed strong aggregation in May and October, when prey were relatively scarce, whereas it was nearly randomly distributed in August, when prey, especially simuliids, were more abundant. Similar seasonal shifts in the aggregative response of lotic insect predators were attributed to seasonally varying prey levels by Townsend & Hildrew (1978; see also Hildrew & Townsend 1982). If food is not a limiting factor, no aggregative response is expected to occur (e.g. Crawley 1975). Black flies represented a major proportion of the prey items for both *Rhyacophila* species and, as soon as the numbers of simuliids decreased, rhyacophilids may have experienced food limitation. Selective consumption of black flies by a rhyacophilid (*Rhyacophila inculta*) was also recorded by Dudgeon & Richardson (1988).

According to the few records available, *Rhyacophila* larvae are often associated with large, moss covered rocks (Malmqvist & Sjöström 1984, Singh et al. 1984, Martin 1985). In this study, *R. nubila* favoured microhabitats with high numbers of sedentary prey (simuliids, chironomids and cased caddis larvae). However, because these prey types frequently occurred within tufts of moss, no unequivocal conclusions can be made about the relative importance of these intercorrelated variables, based on non-experimental data. *R. obliterata*, on the other hand, showed a remarkably strong relationship with the availability of black fly larvae. Sih (1983) suggested that feeding considerations should be especially important shortly before seasonally unfavourable periods. Individuals of *R. obliterata* not able to conclude their larval development before the emergence of black flies in late June clearly face such a period in early July. Since chironomids occurred in very low numbers in this stream, there was no alternative semi-sessile prey to switch to. Accordingly, no single prey dominated the diet of *R. obliterata* in July.

Neither predator or prey response seems to dominate in the "behavioural response race" (Sih

1984) between rhyacophilids and larval black flies. Although *R. obliterata* is clearly able to utilize the seasonal availability of black fly larvae, the risk for an individual black fly to fall prey is probably only minor. In fact, simuliids may even gain from aggregating, because prey risk per individual may be smaller in large groups ("dilution effect", e.g. Bertram 1978). Wrona & Dixon (1991) have recently documented an example of this effect in a lotic predator-prey interaction. They showed that pupae of *Rhyacophila vao* gain fitness advantages by aggregating, mainly because the dilution effect outweighs the higher predator encounter rates of larger groups.

Encounter rate is the most important behavioural component in many aquatic predator-prey interactions (Cooper et al. 1985; see also Sih & Moore 1990). In most studies of feeding preferences of lotic insect predators, no information on encounter rates with various prey types is presented (Allan et al. 1987). While overlap in microhabitat use between predator and prey may not directly translate into encounter frequencies, it should give a rough estimate of the probability of encounter in the field. In this study, microhabitat overlap was always connected to high consumption of the prey in question.

Inter-correlations between habitat variables makes interpretation of field-detected patterns often difficult. As such, correlative studies are best used for suggesting hypothesis for manipulative work (e.g. James & McCulloch 1990). Also, to better understand predator aggregation (or lack of it), one must study particular predator-prey interactions in many spatial and temporal scales. Varying the spatial scale may reveal patterns that go undetected in studies conducted at scales constrained by traditional sampling techniques. Especially, if "full pattern sampling" employing distance measures (e.g. Ripley 1981, Upton & Fingleton 1985) is logistically feasible, it may open up new potential for revealing spatial patterns in lotic predator-prey relationships.

Acknowledgements. I wrote the first draft of this manuscript during my stay at the Kellogg Biological Station, Michigan State University, spring 1992; my thanks go to all the people working at the station for creating such an inspiring atmosphere. S. Cooper thoroughly revised an earlier version of the manuscript, much to its benefit. He would probably still disagree on many statistical issues. Comments by B. Peckarsky, E. Ranta, J. Sarvala and D. D. Williams were also most helpful. A. Juntunen, E. Keinu and R. Paavola aided in the tedious process of collecting, counting and keying the invertebrates. This study was supported by grants from the Emil Aaltonen Foundation, the Heikki and Hilma Honkanen Foundation and the Academy of Finland.

References

Allan, J. D. & Flecker, A. S. 1988: Preference in stoneflies: a comparative analysis of prey vulnerability. — Oecologia 76:496–503.

Allan, J. D., Flecker, A. S. & McClintock, N. L. 1986: Diel epibenthic activity of mayfly nymphs, and its concordance with behavioral drift. — Limnol. Oceanogr. 31:1057–1065.

— 1987: Prey preference of stoneflies: sedentary vs. mobile prey. — Oikos 49:323–331.

Bertram, B. R. 1978: Living in groups: predators and prey. — In: Krebs, J. R. & Davies, N. B. (eds.), Behavioural ecology: an evolutionary approach: 64–96. Sinauer, Sunderland, Mass.

Cooper, S. D., Smith, D. W. & Bence J. R. 1985: Prey selection by freshwater predators with different foraging strategies. — Can. J. Fish. Aquat. Sci. 42:1720–1732.

Crawley, M. J. 1975: The numerical responses of insect predators to changes in prey density. — J. Anim. Ecol. 44:877–892.

Downing, J. A. 1991: Biological heterogeneity in aquatic ecosystems. — In: Kolasa, J. & Pickett, S. T. A. (eds.), Ecological heterogeneity: 160–180. Springer-Verlag, New York.

Dudgeon, D. & Richardson, J. S. 1988: Dietary variations of predaceous caddisfly larvae (Trichoptera: Rhyacophilidae, Polycentropodidae and Arctopsychidae) from British Columbian streams. — Hydrobiologia 160:33–43.

Feltmate, B. W. & Williams, D. D. 1989: Influence of rainbow trout (Oncorhynchus mykiss) on density and feeding behaviour of a perlid stonefly. — Can. J. Fish. Aquat. Sci. 46:1575–1580.

— 1991: Path and spatial learning in a stonefly nymph. — Oikos 60:64–68.

Feltmate, B. W., Baker, R. L. & Pointing, P. J. 1986: Distribution of the stonefly nymph Paragnetina media (Plecoptera: Perlidae): influence of prey, predators, current speed, and substrate composition. — Can. J. Fish. Aquat. Sci. 43:1582–1587.

Feminella, J. W. & Stewart K. W. 1986: Diet and predation by three leaf-associated stoneflies (Plecoptera) in an Arkansas mountain stream. — Freshwater Biol. 16:521–538.

Grossman, G. D. & Freeman, M. C. 1987: Microhabitat use in a stream fish assemblage. — J. Zool. 212:151–176.

Hansen, R. A., Hart, D. D. & Merz, R. A. 1991: Flow mediates predator-prey interactions between triclad flatworms and larval black flies. — Oikos 60:187–196.

Hassell, M. P. 1978: The dynamics of arthropod predator-prey systems. — Princeton University Press, Princeton, N.J.

Hildrew, A. G. & Townsend, C. R. 1976: The distribution of two predators and their prey in an iron-rich stream. — J. Animal Ecol. 45:41–57.

— 1982: Predators and prey in a patchy environment: a freshwater study. — J. Animal Ecol. 51:797–815.

Hurlbert, S. H. 1990: Spatial distribution of the montane unicorn. — Oikos 58:257–271.

James, F. C. & McCulloch, C. E. 1990: Multivariate analysis in ecology and systematics: panacea or Pandora's box? — Ann. Rev. Ecol. Syst. 21:129–166.

Kareiva, P. & Odell, G. 1987: Swarms of predators exhibit "preytaxis" if individual predators use area-restricted search. — Amer. Nat. 130:233–270.

Kuusela, K. 1984: Emergence of Plecoptera in two lotic habitats in the Oulanka National Park, northeastern Finland. — Ann. Limnol. 20:63–68.

Lloyd, M. 1967: Mean crowding. — J. Animal Ecol. 36:1–30.

Malmqvist, B. 1991: Stonefly functional responses: influence of substrate heterogeneity and predator interaction. — Verh. Int. Ver. Limnol. 24:2895–2900.

Malmqvist, B. & Sjöström, P. 1984: The microdistribution of some lotic insect predators in relation to their prey and to abiotic factors. — Freshwater Biol. 14:649–656.

Martin, I. D. 1985: Microhabitat selection and life cycle patterns of two Rhyacophila species (Trichoptera: Rhyacophilidae) in southern Ontario streams. — Freshwater Biol. 15:1–14.

Martin, I. D. & Mackay, R. J. 1982: Interpreting the diet of Rhyacophila larvae (Trichoptera) from gut analysis: an evaluation of techniques. — Can. J. Zool. 60:783–789.

McCreadie, J. W. & Colbo, M. H. 1991: A critical examination of four methods of estimating the surface area of stone surface from streams in relation to sampling Simuliidae (Diptera). — Hydrobiologia 220:205–210.

Muotka, T. 1990: Coexistence in a guild of filter-feeding caddis larvae: do different instars act as different species? — Oecologia 85:281–292.

Peckarsky, B. L. 1988: Why predaceous stoneflies do not aggregate with their prey? — Verh. Int. Ver. Limnol. 23:2135–2140.

— 1991a: Habitat selection by stream-dwelling predatory stoneflies. — Can. J. Fish. Aquat. Sci. 48:1069–1076.

— 1991b: Mechanisms of intra- and interspecific interference between larval stoneflies. — Oecologia 85:521–529.

Peckarsky, B. L. & Cowan, C. A. 1991: Consequences of larval intraspecific competition to stonefly growth and fecundity. — Oecologia 88:277–288.

Peckarsky, B. L. & Dodson, S. I. 1980: An experimental analysis of biological factors contributing to stream community structure. — Ecology 61:1283–1290.

Peckarsky, B. L. & Penton, M. A. 1985: Is predaceous stonefly behavior affected by competition? — Ecology 66:1717–1728.

Reed, W. J. 1983: Confidence estimation of ecological aggregation indices based on counts – a robust procedure. — Biometrics 39:987–998.

Ripley, B. D. 1981. Spatial statistics. — Wiley, New York.

Sih, A. 1983: Optimal patch use: variation in selective pressure for efficient foraging. — Amer. Nat. 120:666–685.

— 1984: The behavioral response race between predator and prey. — Amer. Nat. 123:143–150.

Sih, A. & Moore, R. D. 1990: Interacting effects of predator and prey behavior in determining diets. — In: Hughes, R. N. (ed.), Behavioural mechanisms of food selection: 771–796. Springer-Verlag, Berlin.

Singh, M. P., Smith, S. M. & Harrison, A. D. 1984: Life cycles, microdistribution, and food of two species of caddisflies (Trichoptera) in a wooded stream in Southern Ontario. — Can. J. Zool. 62:2582–2588.

Sjöström, P. 1985: Territoriality in nymphs of Dinocras cephalotes (Plecoptera). — Oikos 45:353–357.

Soluk, D. A. & Collins, N. C. 1988: A mechanism for interference between stream predators: responses of the stonefly Agnetina capitata to the presence of sculpins. — Oecologia 76:630–632.

Stephens, D. W. & Krebs, J. R. 1986: Foraging theory. — Princeton University Press, Princeton, N.J.

Townsend, C. R. & Hildrew, A. G. 1976: Field experiments on the drifting, colonization and continuous redistribution of stream benthos. — J. Animal Ecol. 45:759–772.

— 1978: Predation strategy and resource utilisation by Plectrocnemia conspersa (Curtis) (Trichoptera: Polycentropodidae). — In: Crichton, I. (ed.), Proc. 2nd Int. Symp. Trichoptera: 283–291. Junk, The Hague.

Upton, G. J. G. & Fingleton, B. 1985: Spatial data analysis by example. I. Point pattern and quantitative data. — Wiley, Chichister.

Walde, S. & Davies, R. W. 1984: The effect of intraspecific interference on Kogotus nonus (Plecoptera) foraging behaviour. — Can. J. Zool. 62:2221–2226.

Watanabe, N. 1988: A new proposal for measurement of the adjusted mean crowding through consideration of size variability in habitat units. — Res. Popul. Ecol. 30:215–225.

Wiley, M. J. & Kohler, S. L. 1981: An assessment of biological interactions in an epilithic stream community using time-lapse cinematography. — Hydrobiologia 78:183–188.

Wrona, F. J. & Dixon, R. W. J. 1991: Group size and predation risk: a field analysis of encounter and dilution effects. — Amer. Nat. 137:186–201.

Zar, J. H. 1984: Biostatistical analysis. 2nd ed. — Prentice-Hall, N. J.