



Spatial and temporal niche overlap of two mayfly species (Ephemeroptera): the role of substratum roughness and body size

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Abstract

Intra- and interspecific niche overlap for two mayfly species with similar life cycle timing, *Rhithrogena semicolorata* and *Ecdyonurus* sp. gr. *venosus*, were investigated. The nymphs were classified into 5 classes according to size and spatial overlaps are measured along a substratum roughness gradient. Substratum roughness selection was investigated by defining utilisation curves, optimum and tolerance values of the nymphs in relation to larval growth. Differences between species and size classes within each species were observed. *Ecdyonurus* sp. gr. *venosus* dominated on rough substrates, whereas *R. semicolorata* was most abundant on smooth substrates. An intermediate value of total interspecific substratum roughness overlap (0.49) was found. Higher intraspecific than interspecific overlap values suggested a spatial niche segregation between the two species. The results suggested that the spatial niches measured, were closer to the 'fundamental niches' than could be expected if competition was acting on the two studied populations.

Introduction

Among the physical factors influencing invertebrate distribution in lotic environments, substratum properties (such as roughness, texture, particle size, surface area, interstitial spaces or how tightly stones are packed together) play a controversial role. This is probably justified by the tendency of these properties to interact with physical and chemical variables so that in most field studies it is difficult to separate their specific effects on the aquatic fauna from the bulk of environmental variables. Although some authors have pointed out that in some cases substratum features are less important than other hydraulic characteristics, for example, boundary Reynolds number, in affecting invertebrate distribution (Statzner et al., 1988; Quinn & Hickey, 1994), many studies have revealed that the substratum can influence habitat utilisation not only at species level (Cummins & Lauff, 1969; Reice, 1980; Flecker & Allan, 1984; Ward,

1992) but also between the different life stages of stream invertebrates (Hildrew et al., 1980).

More generally, while it is unwise to claim that the substratum alone accounts for observed distributions of organisms, there is experimental evidence that benthic macroinvertebrates might be affected by specific physical attributes of the substratum. Moreover, in spite of the fact that near-bed hydraulic conditions are considered one primary template governing the distribution of benthic organisms, substrate composition is the habitat characteristic most subject to manipulation (Gore & Hamilton, 1996). Exhaustive reviews of organism–substratum relationships can be found in Cummins (1962), Hynes (1970), Minshall (1984) and Sheldon (1984).

With respect to substratum roughness, a measure of the relative position and 'protrusion' of substratum particles into the water flow, some authors have revealed an interaction between this river bed feature and the structure of aquatic invertebrate communities.

For example, Gore (1978) pointed out optimum values of substratum roughness for some species of benthic macroinvertebrates. Mainly, substratum roughness can influence the habitat selections of invertebrates by affecting the near-bed hydraulic variables. Morris (1955) identified three types of flow occurring over surfaces with differences in relative roughness, while Statzner et al. (1988) and Dittrich & Schmedtje (1995) pointed out the effects of this parameter on complex hydraulic key characteristics like boundary Reynolds number and shear stress. Moreover, Hildrew & Townsend (1977) and Ward (1992) showed that different roughness substrata provide selective refuge from predators and high flow velocity and may present different spatial constraints to the movements of benthic fauna, as well as influencing the amount of detritus trapped within crevices for foraging invertebrates.

Many authors have called for improving basic research on spatial variation in the distribution of stream organisms to aid decisions on river management. Analysis of population changes in substratum selection over the course of a life cycle will increase the reliability of habitat suitability criteria in predicting suitable physical conditions for benthic communities. In fact, it is well known that habitat selection in aquatic insects can be stage and/or size dependent (e.g. Sheldon, 1969). Moreover, competition for space can be very important in determining the structure of benthic communities (Hart, 1983; Hemphill & Cooper, 1983), leading to resource partitioning (Schoener, 1974) and different overlap patterns between species or stages (Osborne & Herricks, 1987). Species coexistence may depend upon their spatial and/or temporal specialisation in resource use, thus reducing interspecific competition (e.g. MacArthur & Levins, 1967). In addition, because macroinvertebrate larval stages rapidly grow, migrate or die, thus determining a change in the relative abundance of different sized nymphs of different species, the temporal scale should be considered when studying patterns of resource utilisation (e.g. Rader & Ward, 1987).

In an analysis of similar data to those presented here, Buffagni et al. (1995) demonstrated a spatial niche shift in the habitat selection of the nymphs of *Rhithrogena semicolorata* and *Ecdyonurus* gr. *venosus*, (called Rs and Ev, respectively). This shift was then correlated to the following physical variables and parameters: bed roughness, photoperiod, temperature, flow velocity, depth, Froude number and substratum composition evaluated as dimensional classes of inorganic particles. The results suggested

that photoperiod and bed roughness accounted for the highest fraction of variance in the nymph niche shift. Photoperiod is intrinsically linked to the body size changes of nymphs of two species, and not surprisingly it accounted for the highest amount of variance. Nevertheless, the presence of a quantitatively modest but biologically relevant temporal shift among nymphs of similar size of two species should be carefully considered (Vannote & Sweeney, 1980).

The present study aims to: (i) estimate spatial and temporal resource overlap both between these two species (Rs and Ev) as well as within each species following larval growth; (ii) define species-level and size-related substratum roughness optima and tolerance values by means of utilisation curves; (iii) suggest the potential contribution of this information to the ecological basis of stream monitoring programs.

We expected that the demonstrated spatial niche shift (Buffagni et al., 1995) would lead to the calculation of different optimum and tolerance values of substratum roughness for the different sized nymphs studied. Furthermore, we expected that the overlap values between the nymphs of the same size, or belonging to adjacent size classes, could be higher than those between nymphs with less size similarity. It is known, in fact, that *R. semicolorata* and *E. gr. venosus* nymphs tend to penetrate into substratum crevices, which are more abundant in rougher substrates (Hildrew & Townsend, 1977), as far as their body size permits (Butz, 1979).

Material and methods

The data analysed in this study were collected in the lotic reach of two lowland springs, named Fontanile Borretta and Fontanile Grande, located in the north-western part of the river Po valley about 15 km west of Milan (Cotta-Ramusino et al., 1991). The two springs have very similar ecological features (Buffagni et al., 1995). Average annual discharge is about 30 l s^{-1} with flow velocities ranging from 0 to 80 cm s^{-1} . Bottom material consists of coarse sand and gravels, with cobble in some marginal or fast flowing areas.

The mayfly fauna were sampled, from January to December 1989, with a Surber net (mesh size 0.45 mm; area 0.05 m^2) in a total of 62 areas. Numbers of samples are as follow: January = 9, March = 3, April = 12, June = 4, July = 7, September = 9, November = 13, December = 5. Among all the mayfly species collected, *Rhithrogena semicolorata* (Curtis,

1834) and *Ecdyonurus* sp. gr. *venosus* were chosen for the study because of their very high densities, up to 4700 nymphs m^{-2} for *R. semicolorata* and up to 2400 nymphs m^{-2} for *E. gr. venosus* (Buffagni, 1994).

At the same time as the biological samples were taken, bed roughness and other physical-chemical parameters were measured for all the sampled areas (Buffagni et al., 1995).

The studied source streams are characterised by the presence of a lentic and a lotic zone (where samples were collected) and by a relatively constant thermal regime (see Buffagni & Gomba, 1996). Instantaneous water temperatures, recorded for each sampling occasion, varied between 10.1 °C and 19.4 °C. As a more general trend for the two streams, the lowest temperature values usually occur between January and April and the highest ones between July and September. The Fontanile Borretta exhibited a slightly wider temperature range than Fontanile Grande, mainly due to a lesser riparian vegetation cover. Nevertheless, the overall yearly temperature trend is similar in the two springs, with values mainly fluctuating between 10 °C and 17 °C.

Bed roughness was calculated as the standard deviation of the heights of 36 graduated rods placed according to the bottom (Gore, 1978; Statzner et al., 1988). Although in this paper we use the term bed 'roughness', with reference to the ecological literature, it has to be noted that the methodology applied more precisely provides a measure of the bed 'meso-profile'. In order to collect biological data for a wide roughness range, all obviously different substratum habitats were sampled.

Specific determination of the *Ecdyonurus* specimens is not possible because of the very complex taxonomy of the Italian species of the *Ecdyonurus venosus* group (Buffagni & Belfiore, 1994). *R. semicolorata* and *E. sp. gr. venosus* nymphs were counted and body lengths measured to the nearest 0.25 mm. Nymphs were grouped in 4 (*R. semicolorata*) or 5 (*E. gr. venosus*) length classes, respectively: <2.5, 2.5–4.5, 4.5–6.5, 6.5–10.5, >10.5 mm (classes I–V).

Interspecific and intraspecific measures of niche overlap in bed roughness colonised by the nymphs of the two mayfly species were determined by using Morisita's original index of similarity [1], which gives the most accurate results in estimating unbiased niche overlap (Morisita, 1959; Smith & Zaret, 1982).

$$C = \frac{2 \sum P_{ij}P_{ik}}{\sum_n P_{ij}[(n_{ij} - 1)/(N_j - 1)] + \sum_n P_{ik}[(n_{ik} - 1)/(N_k - 1)]} \quad (1)$$

where C is the Morisita's index of niche overlap between species j and k , p_{ij} is the Proportion resources i is of the total resources used by species j , p_{ik} is the Proportion resources i is of the total resources used by species k , n_{ij} is the Number of individuals of species j that use resource category i , n_{ik} is the Number of individuals of species k that use resource category i , N_j , N_k is the Total number of individuals of each species in sample.

As the roughness measures were continuous, 0.3 standard deviation categories were used as the discrete variable. We hypothesised competition between the two species or microhabitat preference to be potentially important in controlling resource use because of the relatively uniform substrate that characterise the lowland springs.

For the statistical comparison of the overlap measures, the nonparametric Sign Test in its Exact form (Helsel & Hirsh, 1992) was used.

The Friedman test on ranks was applied to compare the normalised abundance of the size classes of the two species in different months. To reduce chance effect while comparing size classes, Tukey's Honest Significant Difference test (HSDs) was used for *post hoc* comparisons between abundances observed each month (Alpha level for critical ranges 0.05).

Microhabitat-use models were determined by fitting Gaussian response curves to the logarithm of species abundance with respect to bed roughness (Gauch & Wittaker, 1972): $\log y = a - 0.5(x-u)^2/t^2$; where u is the species optimum, t its tolerance, a measure of response breadth, and a is a coefficient related to the height of the peak (Ter Braak & Looman, 1986; Ter Braak & Prentice, 1988). STATISTICA (1997) and CANOCO for Windows v. 4.02 (Ter Braak & Smilauer, 1997) provided the software used in calculations.

Results

The average densities of the nymphs of the two species classified with respect to body size and sampling date are shown in Figure 1. The youngest nymphs (class I and II) of the two species, whose presence indicate the beginning of the life cycles, are temporarily present in the streams between November and

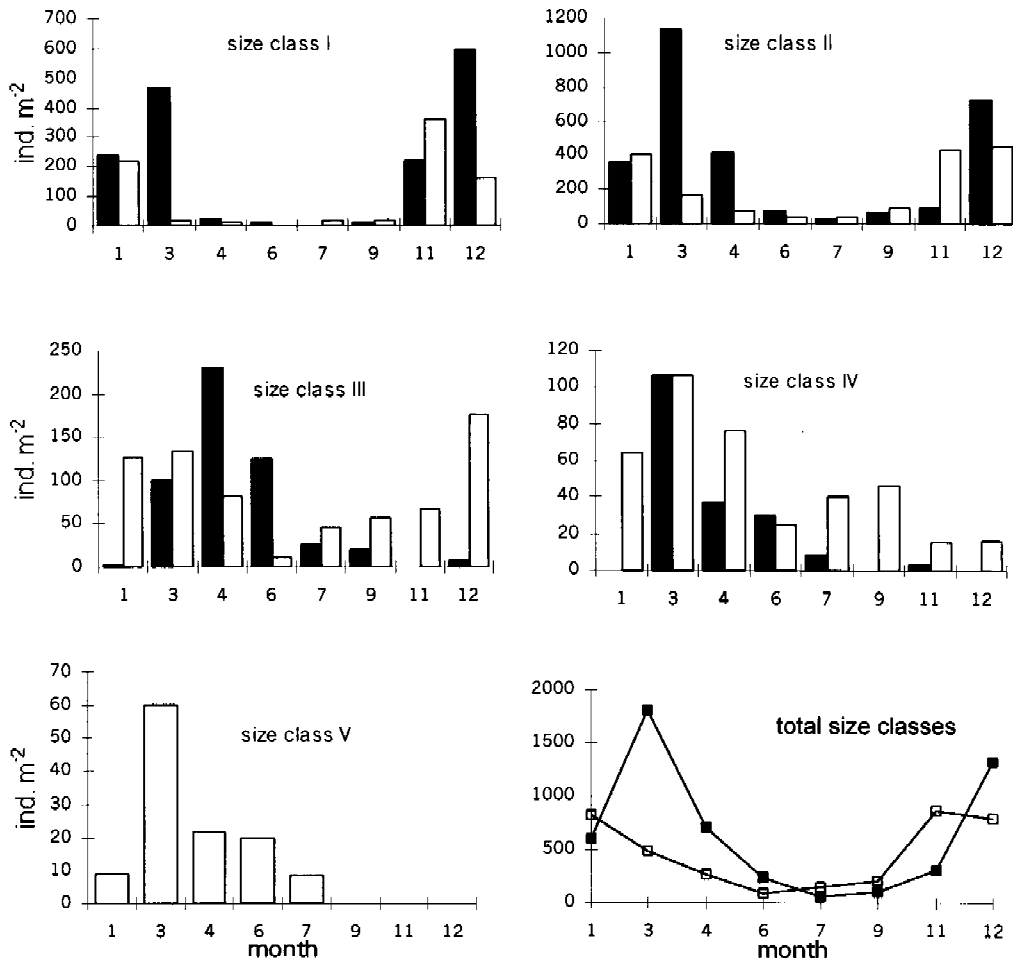


Figure 1. Mean density of the nymphs classified with respect to the body size and sampling month. Black bars and squares = *R. semicolorata* and white bars and squares = *E. sp. gr. venosus*.

March/April, and are the most abundant. The illustrated data show a synchronous initial development and a low abundance of *E. gr. venosus* nymphs classified in IV and V class. In the Fontanile Borretta and Grande, *R. semicolorata* is univoltine, with adults flying from the beginning of May until September, while *E. gr. venosus* showed a complex life cycle, with the evidence of three main development cohorts (Buffagni, unpublished data).

The results of the statistical comparison of the densities of the different-sized nymphs (normalised for each species and month) are reported in Table 1. The non-parametric Friedman test found significant differences ($p < 0.001$) in all months but March ($p = 0.7$), June ($p = 0.07$) and July ($p = 0.3$). For the remaining months, the Tukey test detected few differences among

the size classes of the two species during the year (Table 1).

Groups of size classes whose probabilities for *post hoc* tests are equal or larger than 0.5 (similar abundance observed: homogeneous groups), are indicated as group a, b, etc in Table 1

In January, *E. gr. venosus* nymphs of class II do not belong to any homogeneous group with class III and IV nymphs of *R. semicolorata*. In April, *Rs* class I show less similarity with *R. semicolorata* III, this being somewhat separated from *Ev* I and III. In September, *R. semicolorata* I and *Ev* V showed dissimilarity with *Ev* IV. As regards November and December data, the test highlighted four and three homogeneous groups, respectively. In November, the primary division was between *R. semicolorata* class I and *Ev* I and II from the other size classes, while in Decem-

Table 1. Statistical comparison of the nymphs densities grouped according to their body size and sampling month (Tukey's test). The letters (a–d) classify 4 homogenous groups within which no significant differences occur among nymph densities

Species	Length classes	Homogeneous groups							
		J	M	A	J	J	S	N	D
<i>R. semicolorata</i>	I	ab	a	a	a	a	a	bcd	c
	II	ab	a	ab	a	a	ab	ab	bc
	III	a	a	b	a	a	ab	a	a
	IV	a	a	ab	a	a	ab	ab	a
<i>E. gr. venosus</i>	I	ab	a	a	a	a	ab	d	abc
	II	b	a	a	a	a	ab	cd	abc
	III	ab	a	ab	a	a	ab	abc	abc
	IV	ab	a	ab	a	a	b	ab	ab
	V	ab	a	ab	a	a	a	a	ab

Table 2. Index of inter- and intraspecific microhabitat roughness overlap for each size class of the two mayfly species

	Size class (mm)									Total overlap
<i>R. semicolorata</i>	<2.5	–								0.49
	2.5– 4.5	0.983	–							
	4.5– 6.5	0.740	0.677	–						
	6.5–10.5	0.465	0.413	0.993	–					
<i>E. gr. venosus</i>	<2.5	0.580	0.372	0.584	0.648	–				
	2.5– 4.5	0.605	0.412	0.686	0.659	0.991	–			
	4.5– 6.5	0.385	0.284	0.593	0.465	0.733	0.905	–		
	6.5–10.5	0.150	0.126	0.450	0.561	0.525	0.695	0.985	–	
	>10.5	0.037	0.021	0.052	0.169	0.100	0.084	0.054	0.380	–
		<2.5	2.5–4.5	4.5–6.5	6.5–10.5	<2.5	2.5–4.5	4.5–6.5	6.5–10.5	>10.5
		<i>R. semicolorata</i>				<i>E. gr. venosus</i>				

ber, the main separation was between *Rs* classes I and II, apart from *Rs* III and IV.

Tables 2 and 3 show inter- and intraspecific microhabitat roughness overlap for each size class of the two mayfly species studied; an intermediate value (0.49) of total interspecific overlap, relative to substratum roughness, was found.

No significant differences between intraspecific overlap values of the two species could be identified (Table 3: a–b groups, $p > 0.05$). This means that the different size classes overlap in the same way within each of the two species. Furthermore, intraspecific overlap between adjacent length classes (I and II, II and III, III and IV: up to over 0.99) was higher, for both species, than between classes with less size similarity

(I and III, I and IV, II and IV; Table 3, $p < 0.05$). This is also true for *E. gr. venosus* nymphs longer than 10.5 mm (length class V, excluded by the statistical comparison because it is not present in *R. semicolorata*), that displayed the highest overlap value (0.38) with nymphs of class IV.

Regarding interspecific overlap, the results showed that *R. semicolorata* nymphs overlapped significantly more with small nymphs (<4.5 mm) of *E. gr. venosus* (Table 3: e/f vs g/h, $p < 0.05$) than with larger ones; on the other hand, *E. gr. venosus* nymphs overlap significantly more with larger (>4.5 mm) nymphs of *R. semicolorata* (Table 3: e/g vs f/h, $p < 0.01$). The comparison between the interspecific overlap values (sector c vs d) relative to the same size ratio between

Table 3. (a) Sectors in Table 2 defined for statistical comparison; (b) Results of comparison of overlap measures between species and length class groups as defined in Table 3a by the Exact Form of the Sign test

(a)				
	a		d	
	c		f	b
e			h	
g				
(b)				
Sector in Table 3a	n	p-value	Sign test	Comparison
a vs b	6	0.344	NS	Intraspecific overlap between species
c vs d	6	0.109	NS	Interspecific overlap between species
a&b vs c&d	12	0.0032	**	Intra- versus interspecific overlap between species (both species)
e&g vs f&h	8	0.004	**	Small Rs versus large Rs with all sizes of Ev
e&f vs g&h	8	0.035	*	Small Ev versus large Ev with all sizes of Rs
adj vs not-adj	6	0.016	*	Adjacent sizes versus not-adjacent (both species; class V excluded)

the two species (i.e. *Ev* 4.5–6.5 mm/*Rs* 2.5–4.5 mm overlap versus *Rs* 4.5–6.5 mm/*Ev* 2.5–4.5 mm overlap), did not result in significant differences. The overlap values of larger sizes of *R. semicolorata* with smaller sizes of *E. gr. venosus* were in all cases but one (*Ev* 2.5–4.5 mm/*Rs* <2.5 mm vs *Rs* 2.5–4.5 mm/*Ev* < 2.5 mm) higher than the ones of larger *E. gr. venosus* with smaller *R. semicolorata*. The overlap values of nymphs of the same size were, in three cases out of four, higher than the total interspecific overlap value (0.49). In this case, because a single value for each length class was obtained, no statistical comparison could be made.

When combining the values of the two species in order to compare intra- versus interspecific overlaps, significantly different results were obtained: Table 3: a/b vs c/d, $p < 0.01$ (intraspecific overlap values higher than interspecific ones).

Figure 2 shows optimum values and tolerance ranges predicted for different size classes by the Gaussian model fit to the log-transformed abundance of the two mayfly species as a function of bed roughness.

For all classes but III (4.5–6.5 mm) of *R. semicolorata*, significant ($p < 0.05$) Gaussian response curves were found; for the latter an indication of the optimum value of bed roughness was approximated by the average value of the bed roughness weighted by individual nymphal abundance.

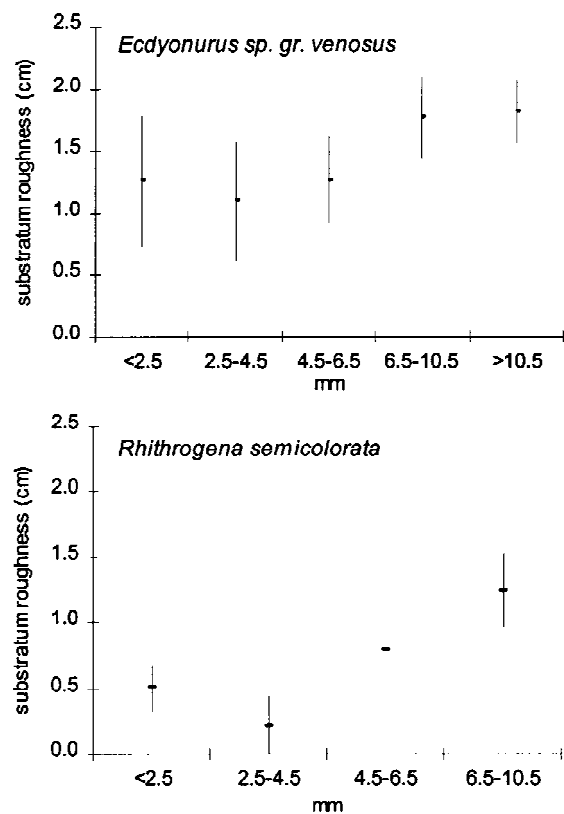


Figure 2. Optimum values and tolerance ranges predicted for the different length classes of the two mayfly species.

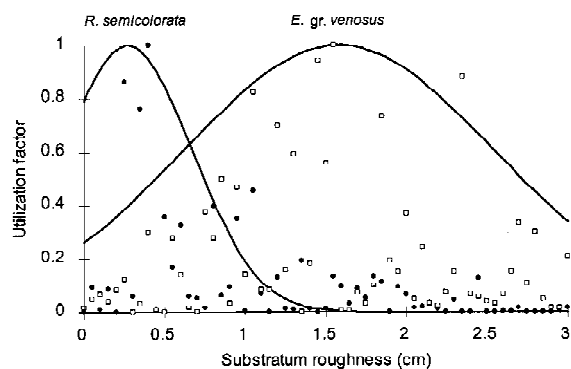


Figure 3. Gaussian utilization curves for the substratum roughness calculated for the total number of individuals of *R. semicolorata* (Rs) and *E. sp. gr. venosus* (Ev). Normalized abundance values for *R. semicolorata* (■) and *E. sp. gr. venosus* (□) are shown.

Size specific utilisation of substratum roughness classes was observed both at intraspecific and interspecific levels. In the first case larger nymphs (>6.5 mm) of both species were more abundant on rougher substratum. At the interspecific level, all size classes of *R. semicolorata* were more abundant on less rough substrata than the comparable size classes of *E. gr. venosus*.

Gaussian curves for the two mayfly species, fitted to all the individuals irrespective of their length, were plotted yielding two different curves (Fig. 3); *R. semicolorata* showing a lower optimum value (0.27 cm) and a narrow tolerance (0.40 cm) compared to *E. gr. venosus*, which showed the optimum condition of bed roughness at 1.58 cm with a tolerance of 0.96 cm.

When the proportions of the sampled individuals of the two species were grouped into different roughness classes, the smoother substratum was dominated by *R. semicolorata* nymphs and the rougher one by *E. gr. venosus* nymphs.

Discussion

The smallest nymphs of *E. gr. venosus* and *R. semicolorata* have their highest densities, and thus the contemporaneous beginning of their life cycles, during November/December. Notwithstanding different development patterns, the nymphs of size classes I–IV of the two species are consistently present in the studied streams in the same time period and corroborate the effectiveness of the observed spatial niche shift.

The data are consistent with the results of Buffagni et al. (1995) in that *R. semicolorata* and *E. gr. venosus* nymphs have low interspecific overlap with respect to

bed roughness. Intraspecific overlap values are much higher than interspecific ones. This confirms the presence of a partial spatial niche segregation between these two species.

When considering intraspecific overlap, the two species show a similar pattern. For both species, overlap between similar length classes is higher than between dissimilar sizes. Although Hearnden & Pearson (1991) found no separation by different size classes of mayfly species and different types of substratum, our results suggest the presence of a size-related shift in habitat use, as identified in many other studies (i.e. Pringle, 1982; Williams & Moore, 1986; Osborne & Herricks, 1987). This shift also appears in the different optimum values calculated for the 9 size groups (Fig. 2).

Although the importance of competition for space in benthic communities is more generally accepted for sedentary species (e.g. Hart, 1983; Hemphill & Cooper, 1983), the measured interspecific spatial shift could be attributed to competition for trophic resources and/or for microhabitat with suitable physical conditions. These results are not intended provide evidence for these causal factors; even so, we are more inclined to consider the reasons for both intra- and inter-specific spatial shifts in the different species and body-length related preferences for the physical features (and to the trophic resources related) of the colonised microhabitat. We believe that the colonised and measured spatial niches are closer to 'fundamental niches' than could be expected if competition was acting on the two studied populations.

As stated, this is a non-corroborated hypothesis, but it can be supported by considering that no substantial differences in interspecific niche overlap can be demonstrated for similar size-classes following larval growth; this, in spite of the reduced density due to emigration or mortality. As a consequence, it can be suggested that population densities do not reach the carrying capacity of the sampled areas.

Significant Gaussian functions were found between substratum roughness and abundance of nymphs for both species, as well as within the species following individual growth. This finding supports other authors' results that have demonstrated that substratum features influence invertebrate species distribution patterns, and corroborates the evidence that the alteration of the structural characteristics of the river bottom can affect the benthic community composition (e.g. Petts et al., 1985). For example, Beisel et al. (1998) indicated that substrate may be a primary determinant

of invertebrate community organisation, while current velocity and water depth emerged as secondary factors. The incorporation of the substratum roughness measure in the multiple regression models describing invertebrate distribution is, therefore, likely to improve their predictive power. The specific role of bed roughness in determining mayfly nymph distribution has been discussed elsewhere and it is worth while to recall here that the demonstrated association of a particular size class with a given substrate roughness may reflect near bed hydraulic preferenda, requirement for shelter, respiratory needs, or food habits, rather than provide an affinity for a specific bottom roughness (Ward, 1992; Buffagni et al., 1995).

Furthermore, our findings suggest that even the simple measure of the species nymphs proportions with different substratum preferences, will result in more accurate monitoring programs of river bottom modifications and more accurate predictions of alterations in ecosystem functions and/or succession. So, a simple comparison between substratum characteristics and the proportion of two mayfly species nymphs could offer an abiotic/biotic 'functional describer' that reflects ecosystem functional alterations (Bournaud & Amoros, 1984; Castella & Amoros, 1988; Copp et al., 1991; Bournaud et al., 1992).

Finally, the results confirm the possibility and usefulness of developing the utilisation functions not only at species level but also for different life stages within the species. In this respect, the development of habitat suitability criteria or preference functions *sensu* Gore & Judy (1981), to be used in methodologies for the assessment of the instream flow requirements of aquatic species like PHABSIM (Bovee et al., 1988), should take into account the seasonal change of habitat utilisation due to organism growth. In fact, such time-dependent habitat preference functions, which reflect habitat shift during development, will result in more accurate predictions of age-structured population densities.

In addition, the functions describing overall species optima and tolerance values, irrespective of nymph size class, should be developed using data carefully collected over the period of a life cycle to avoid size-weighted preference functions.

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