

# Quantification of diet variability in a stream amphipod: implications for ecosystem functioning

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With 6 figures and 3 tables

**Abstract:** Numerous papers associate the rate of leaf litter decomposition with the presence/abundance of gammarids. However, recent studies showed that *Gammarus* sp. may have high diet diversity (as animals, moss, algae). In this context, we quantify the diet of *Gammarus fossarum* to highlight and statistically consider what many authors affirmed rather by observation. To this end, we used a recently described multivariate analysis, called %PCA, which allows investigating data dealing with diet composition. Body size and microhabitat type were revealed highly significant variables governing several parameters of the diet. In particular, our results show that food item size and predatory behaviour increased with body size, whilst the type and abundance of food consumed was related to microhabitat type. Furthermore, body-size had a significant effect on specialisation whatever the microhabitat type. Niche overlap also decreased as pairwise differences in body-size increased, allowing the aggregation of individuals from different instars. We conclude that *G. fossarum* exhibit an opportunistic behaviour, which makes necessary to reconsider the importance of gammarid “shredding” activity to accurately assess stream functioning and flux/redistribution of energy and matter (leaf litter breakdown). We discuss the functional feeding group membership of *G. fossarum* at the individual and population level.

**Key words:** *Gammarus fossarum*, opportunistic behaviour, gut content analysis, FFG, PCA

## Introduction

The functional role of species in ecosystems has received considerable attention in the past decade in both terrestrial and aquatic ecosystems (Grime 1997, Purvis & Hector 2000, Jonsson et al. 2002, Covich et al. 2004). A key issue in understanding how species richness affects ecosystem functioning involves the evaluation of whether communities have a high level

of functional redundancy (Wardle 2002). Identifying functional traits of organisms is therefore crucial for understanding how diversity affects ecosystem functioning (Naeem & Wright 2003). In this context, many studies have suggested that ecosystem functioning is mainly driven by specific traits of species (species identity) rather than by their abundance (Hooper & Vitousek 1997, Tilman et al. 1997, Wardle et al. 1997). This debate has therefore renewed considerable inter-

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est on basic knowledge of the role of species within ecosystems, and on both individual and environmental factors that can affect this role.

In aquatic systems, the function of species is generally defined by their position within a particular food web (Eggers & Jones 2000). As typical ecosystems contain countless biological species, most studies dealing with the role played by animals, particularly in aquatic systems, have generally black-boxed species into trophic categories (Yodzis & Winemiller 1999) such as the functional feeding groups (FFG) established for benthic invertebrates (Cummins 1973, Cummins & Klug 1979). These groups have been intensively used during the last decades to infer and model complex ecosystem processes (such as leaf litter breakdown), yet the link between species and process remains unclear (Crowl et al. 2001). Omnivorous taxa (e.g. amphipods) are particularly difficult to handle in diversity-function studies as they can be involved in different ecosystem functions, such as grazing of primary production, shredding of dead organic matter or predation. It is therefore of particular importance to use relevant statistical tools to quantify the trophic status variability of organisms in order to evaluate its potential functional consequences.

Quantitative methods to study the feeding role of aquatic organisms have for a long time been developed by ecologists but have mainly been restricted to fish (Strauss 1979, Hyslop 1980, Mohan & Sankaran 1988, Costello 1990, Tokeshi 1991, Cortes 1997). Owing to the considerable challenge in quantifying their food items (generally unquantifiable or semi-quantifiable; e.g. leaf, wood or animal fraction), benthic invertebrates have received less attention than fish, and therefore require specific statistical tools, such as principal component analysis in percent (%PCA) to specifically handle proportion data. Furthermore, published studies have mainly assessed feeding habits of species at a population level instead of individual level (Bridcut & Giller 1995, De Crespín de Billy et al. 2000), thereby overlooking information contained in inter-individual diet variations (i.e., the variation in the use of resource by each individual). The amphipod *Gammarus fossarum* is an interesting species to tackle this issue as it consumes a broad range of food items, which makes it problematic to clearly establish its functional role. Ecologically important parameters, such as ontogenic development, habitat and season can influence feeding habits of non-specialist species, by modifying availability and accessibility of food sources in the stream (Fuller & Mackay 1980, Harding 1997).

In a first step, our objectives were i) to define *G. fossarum*'s diet in the studied stream and ii) to assess size and microhabitat effects on diet composition. In a second step, we completed our survey by carrying out analyses on specialisation and discussed the possible implications of our findings for ecosystem functioning understanding.

## Material and methods

### Site description

The study was conducted in a first-order stream in the Vosges Mountains (North Eastern France) – la Maix (48°29'34"N, 7°03'36"E). The study stretch was 30 m long with a wetted width of 2 m. The average channel width was 2 m and the water depth ranged from 0.1 m to 0.8 m. The streambed was dominated by bryophyte-covered bedrock (50 % of study site), sand (18.5 %), and cobbles (20.9 %). Marginal microhabitats were made of submersed root mats of riparian trees (5.8 %) and pools of decomposing beech (*Fagus sylvatica*) and alder (*Alnus glutinosa*) leaves (4.8 %; Felten 2003). *G. fossarum* were very abundant in the stream, especially in microhabitats offering high quantities of organic matter. In general, more than 93 % of all gammarids were found in only three habitats: bryophyte covered bedrock, root mats and detrital pools (Dangles 2001).

### Benthic samples

April the 16<sup>th</sup> 2002, one quantitative sample of macroinvertebrates in each substrate type was taken using a 0.072 m<sup>2</sup>, 0.28-mm mesh Surber sampler net: 1) bryophytes-covered bedrock, 2) submersed roots, 3) detrital pools, 4) sand, 5) cobbles and 6) boulder. Samples were preserved in 5 % formaldehyde and sorted, identified and counted in the laboratory. *G. fossarum* were sex-determined and enumerated into 0.5-mm size classes (from 1.5 to 11 mm) of total body length defined as the distance between the base of the first antenna and the distal end of the telson (Pöckl 1992). Individuals smaller than 5 mm were considered juveniles (Pöckl 1992, Felten 2003). Males were identified by the presence of genital papillae and female by the presence of oostegites (Clemens 1950, Haley 1997). At the end of the analysis, for each size class, four replicates of *G. fossarum* were weighed (ash-free dry weight;  $\pm 0.1 \mu\text{g}$ ).

### Diet analysis

The diet composition of *G. fossarum* was determined by gut content analyses using a technique modified by Shapas & Hilsenhoff (1976) and Dangles (2002). The three first microhabitats (see above: 1 to 3) were considered for the gut content analysis since sufficient numbers of gammarids were collected to allow the assessment. For each microhabitat selected, ten individuals of each size class (2, 4, 6 and 8 mm,  $\pm 0.25$  mm) were selected. Foregut contents were placed into a drop of water on a microscope slide. Particular attention was paid to homogenise well the gut content and to slightly press the slide permitting to avoid bias due to thickness of items. Ten fields were chosen randomly at 100 $\times$  magnification, then viewed at different magnifications from 100 $\times$  to 400 $\times$ . Six food items were identified: (i) animal matter, (ii) fine amorphous detritus, (iii) diatoms, (iv)

filamentous algae, (v) coarse leaf detritus-woody debris, and (vi) particles derived from bryophytes. Fine amorphous detritus was distinguished from other items by its lack of well-defined cellular structure. Coarse leaf detritus was identified by the presence of brownish cells and palisade cell layers. Complementary studies of the gut contents of several gammarids fed with leaves, bryophytes, animals, FPOM (Fine Particles of Organic Matter, < 1000 µm) under laboratory conditions helped to recognize each kind of food material. Previous gut content analysis of gammarids sampled in La Maix stream allowed us to add a “mineral” item as these particles were found in several foreguts. The approximate percentage by area of the seven items was recorded in each field of the slide for each individual. Previous study also considered the percentage of use of various food-stuffs in gammarid guts (Dick et al. 2005). Animal items found in the foreguts of *G. fossarum* were identified to the lowest practicable taxonomic level (e.g. Chironomidae, *Baetis* sp., *Leuctra* sp.).

## Statistical analyses

To investigate spatial and ontogenic diet variability, gut contents were analysed according to microhabitat type and body size. A multivariate analysis derived from principal component analysis (further abbreviated as %PCA) was performed on percentages of each item. Because the use of proportion removes the unequal weight among individuals, semi quantitative investigations are more suitable for analyses at the individual level. Borrowing from fish literature, Principal Component Analysis in percent (% PCA) can be used to quantify the variability of feeding habits (and therefore functional roles) of benthic invertebrates in aquatic ecosystems (De Crespín de Billy et al. 2000). According to De Crespín de Billy et al. (2000), %PCA is specifically adapted to investigating diet composition data for numerous reasons. This method (1) can be performed on a proportion table (each row's sum is equal to 1), (2) is established at the individual level, (3) can test for diet variation at the population or higher level (for more details see Aitchison 1983) and (4) permit to test the significance of diet differences among groups. The statistical significance of the gammarid size and microhabitat type effects were tested by random permutation tests performed on interclass (10 000 runs: Manly 1991, Thioulouse et al. 1997).

We further quantified the level of omnivory and degree of the specialisation of *G. fossarum* feeding habits. Three parameters were selected in order to appraise the level of omnivory: 1) the number of items found in the gut (*S*), 2) the Simpson's diversity index of food items (*D*, Simpson 1949, equation (1); *i*: 1 to 10), and 3) the Levins' niche breadth index *B* (Levins 1968; equation 2).

$$D_i = 1 - \sum_{k=1}^n p_{k/i}^2 \quad (1)$$

where  $p_{k/i}$  is the proportion of the  $k^{\text{th}}$  food type in the  $i^{\text{th}}$  stomach

$$\sum_{k=1}^n p_{k/i} = 1$$

$$B = \frac{1}{\sum_{k=1}^n p_k} \quad (2)$$

where  $p_k$  is the proportion of the  $k^{\text{th}}$  food item in the diet. *B* ranges from 1 (specialisation, i.e., only one food item occurs

in the gut content) to *n* (generalisation), where *n* is the total number of food items (*n* = 6). Levin's index was calculated on average diet per ontogenic stage.

The diet specialisation was estimated using the Schoener's overlap index *O<sub>s</sub>* (Schoener 1968), measuring the similarity between food item distributions in diet contents:

$$O_s = 1 - 0.5 \sum_{k=1}^n |p_{k/h} - p_{k/j}| \quad (3)$$

where  $p_{k/h}$  and  $p_{k/j}$  are the frequencies of food item *k* in *G. fossarum*'s size *h* and *j*, respectively. Schoener's *PS* ranges from 0 when no food items are common between diets, to 1 when all items are found equally frequent. Linear regression significance was estimated using Pearson correlation coefficient test. Statistical investigations were made through t-test to assess the effects of microhabitat and individual size on omnivory and specialisation. All statistical analyses were performed using ADE-4.0 (Thioulouse et al. 1997) and Statistica v. 5.5 (StatSoft, Inc., Tulsa, Okla.).

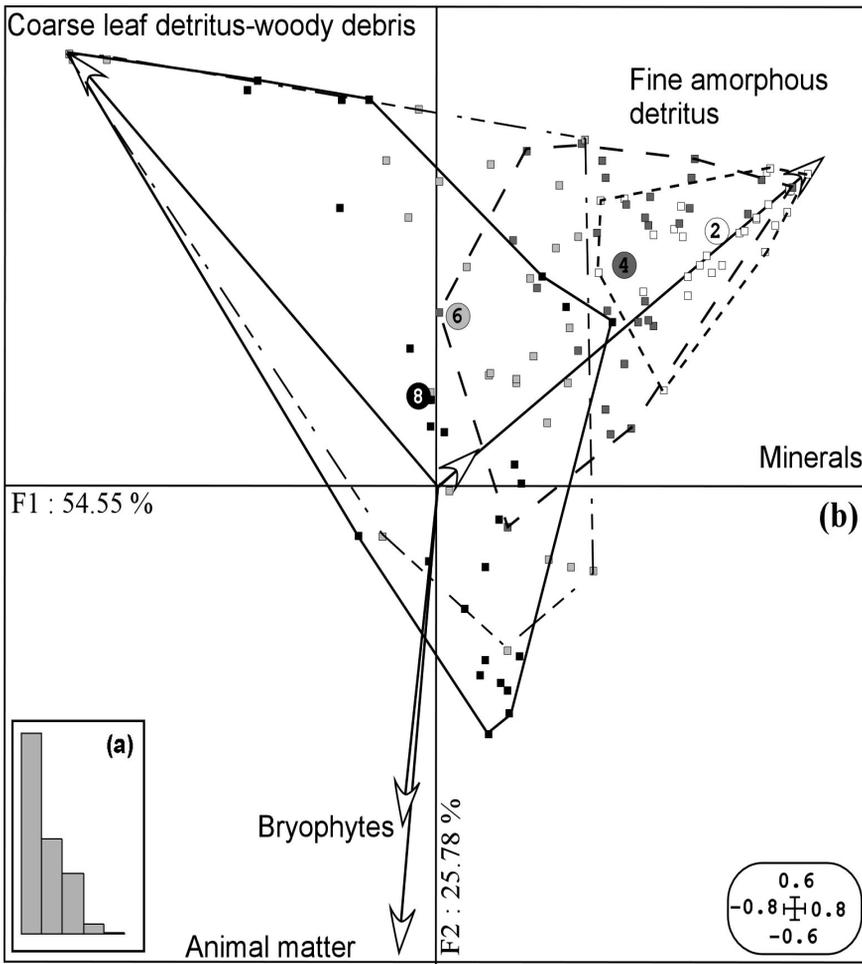
## Results

### Variability in diet composition

According to eigenvalues (Fig. 1a), the first two axes of the % PCA (respectively 54.55 % and 25.78 % of the total variation) are sufficient to illustrate the main structure of the diet composition of gammarids. However, to better explore differences in the composition of diet in relation to gammarid size and microhabitat type, the third axis is also considered (16.45 % of the total variation). Four items, i.e., coarse leaf detritus-woody debris, fine amorphous detritus, animal matter, particles derived from bryophytes out of 7, dominated the gut content (Fig. 1b). From the right-hand side towards the left, the first axis (F1) describes an increasing gradient of food item sizes ranging from fine amorphous detritus to coarse leaf detritus-woody debris whereas the second axis (F2) separates the two former items from animal matter and particles derived from bryophytes. Finally the third axis (F3, not shown) allows us to split the two latter (animal matter and particles derived from bryophytes).

**Table 1.** Within-group variance, Simpson index and number of consumed “food” item per individual amphipod (Mean ± SD) in relation with *G. fossarum* size (*n* = 30). Different letters indicate significantly different values (Student T-test, *P* < 0.05, *n* = 7).

<i>G. fossarum</i> size	Within variance	Simpson index	Number of consumed “food” item
2 mm	339.48	0.37 ± 0.15 <sup>a</sup>	3.70 ± 0.99 <sup>c</sup>
4 mm	499.07	0.50 ± 0.12 <sup>b</sup>	3.63 ± 0.96 <sup>c</sup>
6 mm	1401.8	0.57 ± 0.19 <sup>b</sup>	3.63 ± 0.96 <sup>c</sup>
8 mm	1912.8	0.56 ± 0.18 <sup>b</sup>	3.57 ± 0.94 <sup>c</sup>

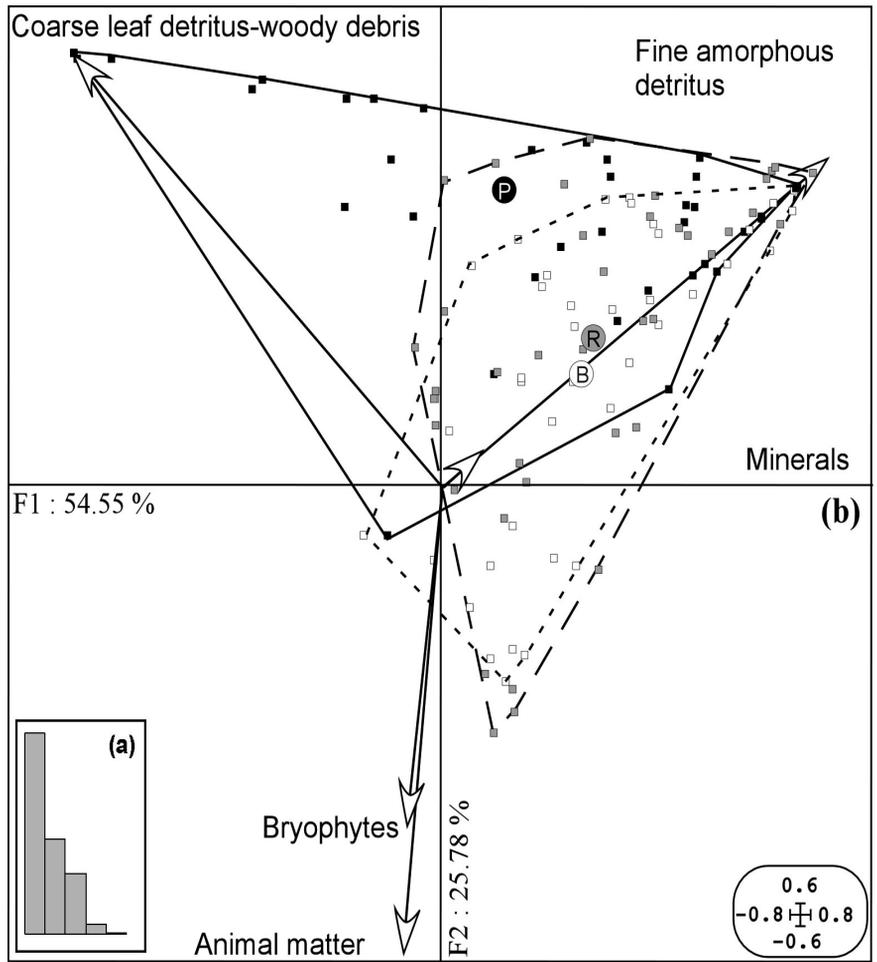


**Fig. 1.** Effect of individual size on the diet of *Gammarus fossarum*. (a) Histogram of eigenvalues (%). (b) Biplot of “food” items and *G. fossarum* gut contents obtained from a %PCA. Distribution of individual gut contents (squares) on the first factorial plane according to their “food” items (arrows). “Food” items representing <5 % of the total gut content were omitted. Specimens measuring 2 mm (2), 4 mm (4), 6 mm (6) or 8 mm (8) were labelled using open, closed dark-grey, light-grey or black squares, respectively. Convex hulls were used to label groups according to size (short dashed: 2 mm; long dashed: 4 mm; short-long dashed: 6 mm; solid: 8 mm). Medium distributions (gravity centres) of gut contents were pooled in relation with individual size (circles). (c) Proportion (mean ± SD) of the 5 main food items in relation to *G. fossarum* size.

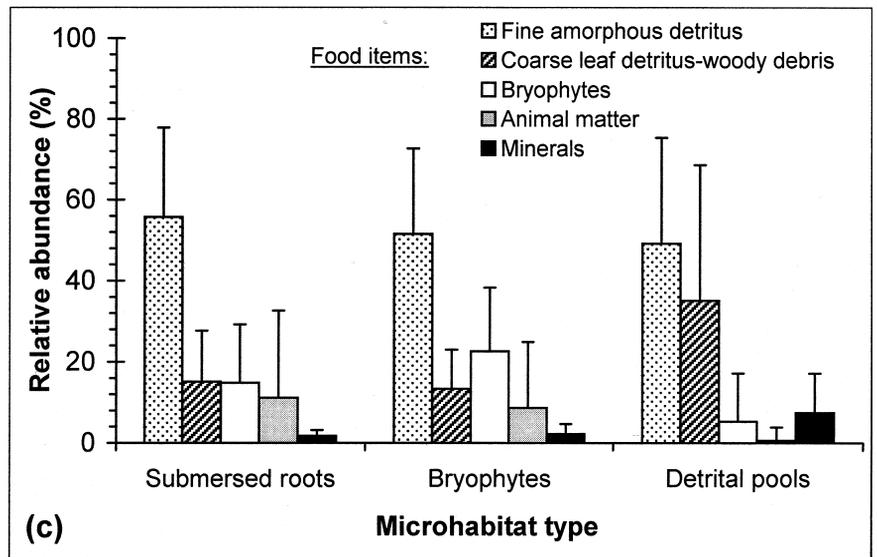
**Individual size effect**

The position of individual gut contents on the factorial plane was related to gammarid size shown by gravity centres and convex hulls (the minimal envelop sets

containing all points) in Fig. 1b. Along F1, as gammarid body size increased, the size of the food items consumed increased, shifting from diatoms and fine amorphous detritus (by relative abundance, Fig. 1c)



**Fig 2.** Effect of microhabitat on the diet of *Gammarus fossarum*. (a) Histogram of eigenvalues (%). (b) Biplot of “food” items and *G. fossarum* gut contents obtained from a %PCA. Distribution of gut contents (squares) on the first factorial plane according to their “food” items (arrows). “Food” items representing < 5 % of the total gut content were omitted. Gut contents (squares) were grouped by microhabitat type: individuals caught in bryophyte-covered bedrock (B), submersed roots mats of riparian tress (R) or detrital pools (P) were labelled using open, closed grey or black squares, respectively. Convex hulls were used to label groups according to microhabitat type (short dashed: bryophyte-covered bedrock; long dashed: submersed roots; solid: detrital pools). Medium distributions (gravity centres) of gut contents were pooled with microhabitat type (circles). (c) Proportions (mean ± SD) of the 5 main food items in relation to the type of microhabitat.



towards larger animal fractions (*Chironomidae*, *Baetis* sp. and *Leuctra* sp.), coarse leaf detritus-woody debris, and bryophytes (by relative abundance, occurrence for the first two items, Fig. 1b). No animal matter was no-

ticed in 2 mm-gammarid gut contents (and only 3 out of 30 in 4mm-gammarids fed on animal matter, Fig. 1c). The variance component explained by gammarid size accounted for 36.2 % of the total variability and

was highly significant ( $p < 0.001$ , random permutation test).

Figure 1b also shows a rise in diet variability with gammarid size (see convex hulls). Indeed, gut contents of 2 mm-individuals are grouped at the tip of the fine amorphous detritus arrow whereas other size classes are much more distributed on F1, F2 and F3 (within-group variance, Table 1). Although the number of

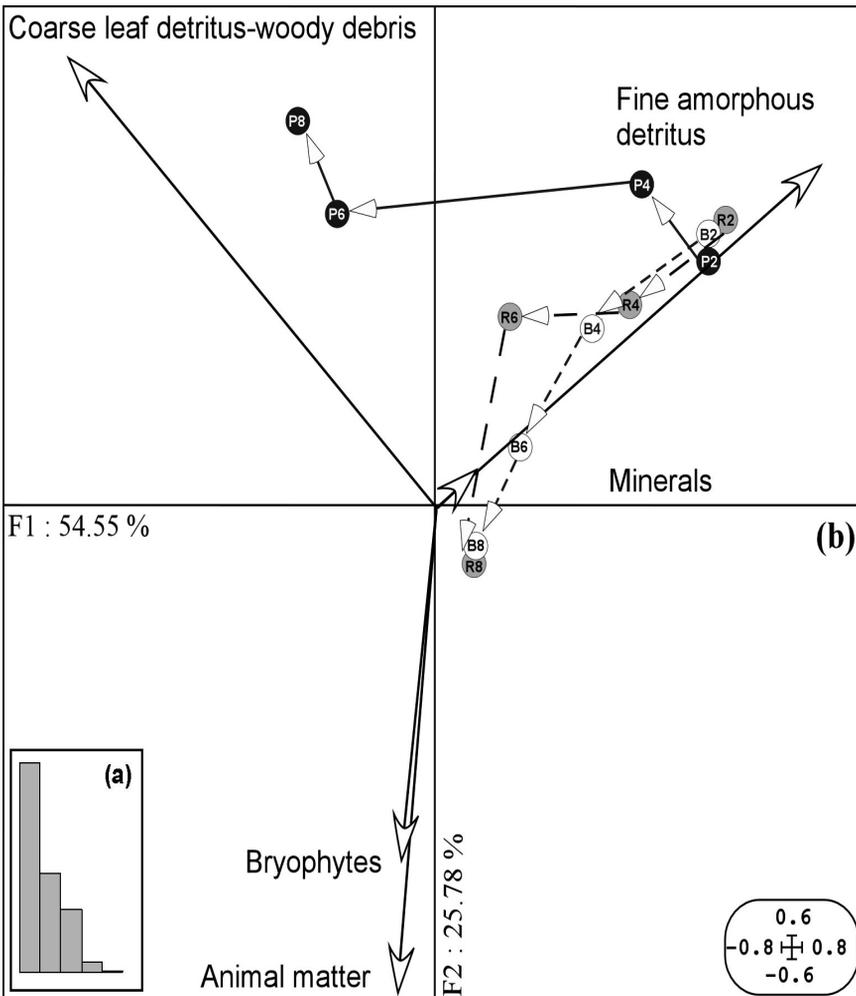
**Table 2.** Within-group variance, Simpson index and number of consumed “food” item per individual amphipod (Mean  $\pm$  SD) in relation with microhabitat type (n = 40). Different letters indicate significantly different values (Student T-test,  $P < 0.05$ , n = 7).

Microhabitat type	Within variance	Simpson index	Number of consumed “food” item
Detrital pool	2014.05	0.43 $\pm$ 0.19 <sup>a</sup>	3.18 $\pm$ 1.28 <sup>c</sup>
Submersed roots	1286.75	0.51 $\pm$ 0.17 <sup>b</sup>	3.60 $\pm$ 0.78 <sup>c</sup>
Bryophytes	1033.95	0.56 $\pm$ 0.15 <sup>b</sup>	3.95 $\pm$ 0.68 <sup>d</sup>

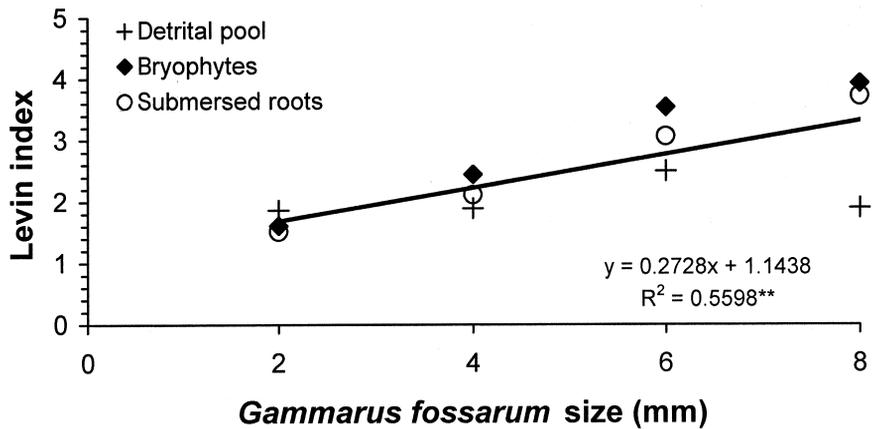
items in the guts was similar irrespective of size, the Simpson index for the 2 mm-individuals was significantly lower than the remaining size groups, showing that the small individuals have a diet based on fine amorphous detritus (Table 1).

**Microhabitat effect**

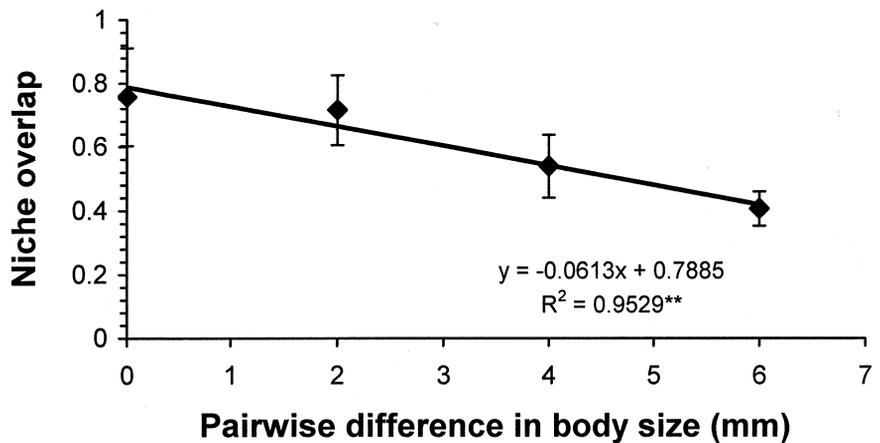
The position of individual gut contents on the factorial plane is a function of the microhabitat type (shown by gravity centre and convex hulls in Fig. 2b). The specimens of *G. fossarum* sampled in detrital pools were clearly separated and especially distributed on the superior part of the factorial plane (F1–F2). The two other microhabitats are located mainly to the right on the diagram (Fig. 2b). A grouping of individual gut contents by microhabitat type reveals that the diet of gammarids sampled in detrital pools was based on fine amorphous detritus and coarse leaf detritus-woody debris whereas specimens from other microhabitats although still feeding on coarse leaf detritus-woody de-



**Fig. 3.** Effect of individual size and microhabitat on the diet of *Gammarus fossarum*. (a) Histogram of eigenvalues (%). (b) Biplot of “food” items and *G. fossarum* gut contents obtained from a %PCA. Medium distributions (gravity centres) of gut contents (circles) on the first factorial plane according to their “food” items (arrows) pooled in relation with individual size and microhabitat. “Food” items representing < 5 % of the total gut content were omitted. Pooled individuals caught in bryophyte-covered bedrock (B), submersed roots (R) or detrital pools (P) were labelled using open, closed grey or black circles, respectively. Pooled specimens measuring 2 mm, 4 mm, 6 mm or 8 mm (8) were labelled 2, 4, 6, 8 respectively. R2: medium distribution of 2 mm-organisms sampled in submersed roots.



**Fig. 4.** Relationship between average individual niche breadth (Levin's index) and size-classes of *G. fossarum* in considering the three microhabitats studied. Significance of the regression is indicated by asterisks (Pearson test, \*\*  $p < 0.01$ ).



**Fig. 5.** Pairwise differences in body-size against niche overlap among size-classes of *Gammarus fossarum*. Significance of the regression is indicated by asterisks (Pearson test, \*\*  $p < 0.01$ ).

bris, added more animal matter and particles derived from bryophytes in their diet (Fig. 2b–c). The variance component explained by microhabitat type accounts for 11.2 % of the total variability and is highly significant ( $p < 0.001$ , random permutation test).

Figure 2b and Table 2 (within-group variance) show that the diet variability (see convex hulls) depends on microhabitat type. Thus, not only the number of items but also the Simpson index is lower in detrital pools than in submersed roots and bryophyte-covered bedrock (Table 2).

#### Individual size and microhabitat effect

The variance component explained by gammarid size and microhabitat type accounts for 59.8 % of the total variability and is highly significant ( $p < 0.001$ , random permutation test). Figure 3b clearly shows that whatever the microhabitat type, (1) 2 mm-gammarid diet was very similar and based on fine amorphous detritus, and (2) the size of ingested particles increased with individual size. However, diets in each micro-

habitat are increasingly different with size: organisms sampled in detrital pools, bryophyte-covered bedrock and submersed roots consumed more and more coarse leaf detritus-woody debris, particles derived from bryophytes and animal matter, respectively. These results show that the evolution of diet regarding size strongly depends on the type of microhabitat considered, highlighting an opportunistic behaviour of larger gammarids since each of these food items are highly represented in the associated microhabitats.

#### Specialisation of *G. fossarum*

The Levin's index increased significantly with gammarid size (Fig. 4), highlighting a generalisation of diet with size, becoming more diverse and variable regardless of the microhabitat type. However, this general trend was weak in detrital pools. Dietary overlap decreased as the size disparity increased (Fig. 5). The correlations between niche overlap values and pairwise differences among size-classes is significant ( $p < 0.01$ ).

## Discussion

In controlled conditions, *G. fossarum* are able to survive, to grow, and to reproduce while feeding on leaves (Pöckl 1995). Here we show that *G. fossarum* uses other types of food resources in streams such as animal matter, fine amorphous detritus, diatoms, filamentous algae, coarse leaf detritus-woody debris, and particles derived from bryophytes.

Cummins & Klug (1979) suggested that the occurrence of animal fragments in the guts of freshwater invertebrate “shredders” could result from scavenging or accidental ingestion. However, the recent study of Kelly et al. (2002b) showed that *G. pulex* leaf-shredding-activity was significantly lower when potential prey *Baetis rhodani* was present as compared to absent prey. According to the authors, this suggests that decaying leaf material alone does not fully satisfy the nutritional requirements of the amphipod and that, indeed, prey may be favoured over leaf material. However, the shredding of leaves even in the presence of potential prey suggests that *Gammarus* sp. are truly omnivorous or polyphagous, such as many stream-dwelling invertebrates (Warren 1995), using a wide variety of foodstuff to maximize fitness (Cruz-Rivera & Hay 2000).

### Exploring the possible reasons of variability

Size has a significant effect on *G. fossarum* diet composition since larger-sized food items become more and more important in the later stages. This pattern has been shown for several macroinvertebrate taxa (e.g., Trichoptera: Fuller & Mackay 1980, Basaguren et al. 2002; Ephemeroptera: Fuller & Desmond 1997;

Plecoptera: MacNeil et al. 1997) and linked to morphological constraints and to feeding energetic patterns (Keeley & Grant 1997). Similarly, changes observed in the diet diversity correlated with size (Table 1, within-group variance) can be associated with the increase in the size of the mouth parts, allowing to eat larger and more diverse food items. Food item dominance tends to decrease with size showing a generalization of larger *G. fossarum* diet (Table 1, Simpson index) as smaller animals fed mainly on fine amorphous detritus whereas larger individuals exhibit diets composed of more and more animal matter and coarse leaf detritus.

The significant effect of microhabitat on *G. fossarum* diet (11.2 % of total variability) supports the hypothesis that abundance of various food resources is the main factor driving the diet within a substrate (Graça et al. 2001). Even more interesting is the highly significant joint effects of individual size and microhabitat on the feeding traits of gammarids (Fig. 3). Whereas small-size individuals had similar digestive contents whatever the microhabitat, larger ones specialized according to the type of microhabitat. The diversity of habitat could then be a surrogate of the functional diversity of traits displayed by a species. In turn, habitat diversity may play an important role in facilitating the coexistence between highly abundant yet potentially strongly interacting species. Furthermore, the great mobility of gammarids might enhance, rather than reduce, selective feeding, because a large foraging range facilitates location of suitable food patches (Bärlocher 1985, Arsuffi & Suberkropp 1989, Friberg & Jacobsen 1994).

We showed that dietary overlap significantly decreases as the size disparity increases (Fig. 5), a find-

**Table 3.** Equation used to calculate Functional Feeding Group Membership (FFGM) of *G. fossarum* population. N, Number of individual (Predator: animal matter; Scraper: diatoms + filamentous algae; Shredder: coarse leaf detritus-woody debris + particles derived from bryophytes ; Collector: mineral + fine amorphous detritus).

	Equation used for the calculation of Functional Feeding Group Membership (FFGM) (%)	Population FFGM (%)	
		Without gut volume integration	With gut volume integration
		$FFGM = \frac{\sum_{size=1.5}^{10} FFGM_{size} \times N_{size}}{N_{total}}$	$FFGM = \frac{\sum_{size=1.5}^{10} FFGM_{size} \times N_{size} \times Size^3}{N_{total}}$
<b>Predator</b>	$FFGM_{size} = 0.6833 \text{ size}^2 - 3.5833 \text{ size} + 4.2167$ $R^2 = 0.9961$	2.2	8.3
<b>Scraper</b>	$FFGM_{size} = 0.0625 \text{ size}^2 - 1.0917 \text{ size} + 5.3667$ $R^2 = 0.9952$	2.4	1.3
<b>Shredder</b>	$FFGM_{size} = -1.3375 \text{ size}^2 + 20.182 \text{ size} - 25.317$ $R^2 = 0.9798$	25.9	42.6
<b>Collector</b>	$FFGM_{size} = 0.5938 \text{ size}^2 - 15.526 \text{ size} + 115.76$ $R^2 = 0.9844$	69.5	47.8

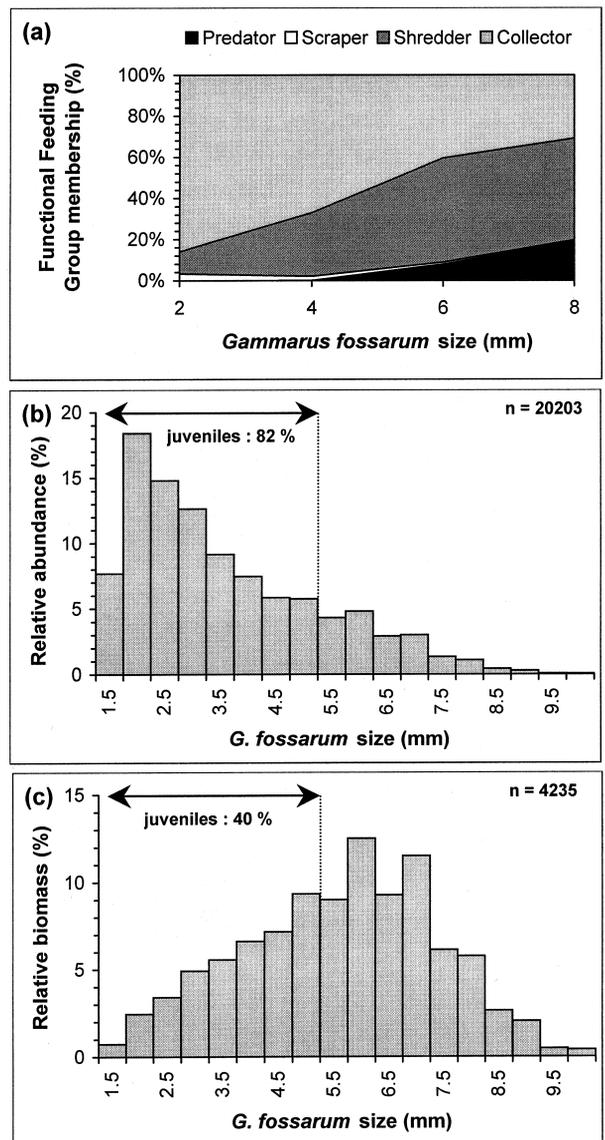
ing already reported by Woodward & Hildrew (2002) for several macroinvertebrate species. This result may partly explain why *G. fossarum* was found strongly aggregated in the studied microhabitats regardless size (Felten 2003) as intra-specific competition would be reduced.

Not only intra-population and physical factors can influence the functional traits of species but also their interactions with other species. For instance, animal matter in *G. fossarum* gut content was identified as *Baetis* sp., *Chironomidae* and *Leuctra* sp., which also feed on FPOM and CPOM. This predation could be partly a response to such competition. Thus, morphological constraints, feeding energetic and competition could be identified as important determinants of *G. fossarum* diet.

### Evaluating the bias of the FFG approach for an omnivorous species

Body-size constraints clearly play an important role in determining both niche overlap and trophic status (Woodward & Hildrew 2002). More and more studies have attempted to divide species into size categories to improve food web models (Woodward & Hildrew 2002). Gee (1988), Hildrew et al. (1980) and Dobson & Hildrew (1992) have arbitrarily divided *Leuctra* spp. and *G. pulex* samples into “large” (i.e., shredders) and “small” (i.e., collectors) to reduce bias when considering FFG categories.

Because of the significant ontogenic shift in the diet composition of gammarids, it appears paramount to combine population structure data with functional group allocation to fully appreciate the role of a species in ecosystems functioning. We used data on *G. fossarum* population composition (6 surber samples  $\times$  10 dates,  $N = 20203$  ind., La Maix, Fig 6b; Felten 2003) to integrate diets using the FFG membership results (based on *G. fossarum* diets obtained in the present study). Thus, in the first-order stream studied, *G. fossarum* population behaviour can be considered as 69.5 % collector, 25.9 % shredder, 2.2 % predator and 2.4 % scraper (Table 3). However, as gut volume differs with size, we integrated this parameter by using a balancing (cube of body size, Table 3). The *G. fossarum* population could then be considered as 47.8 % collector, 42.6 % shredder, 8.3 % predator and 1.3 % scraper. As a consequence, our results lead to a reconsideration of the shredding activity of species which we assume to be often overestimated in natural conditions, such as *G. fossarum*, since: 1) the first stages are collectors and represent a considerable proportion of



**Fig. 6.** *Gammarus fossarum* Functional Feeding Group membership in relation to size (a), and *Gammarus fossarum* total population structure in the La Maix stream (Vosges Mountains, 6 surber samples  $\times$  10 dates, 2001–2002; Felten, 2003): (b) abundance distribution, (c) biomass distribution.

the *G. fossarum* population (in our study, more than 82 % of the population were represented by individual less than 5 mm, accounting for 40 % of the total biomass, Fig. 6b-c), 2) larger gammarids can allow time to consume substantial amount of animal matter instead of shredding on leaves (Kelly et al. 2002a), 3) gammarids eat more bryophyte than previously expected., 4) *G. fossarum* exhibits an opportunistic behaviour.

This is all the more interesting since we investigated *G. fossarum* diet in a forested headwater stream in which energy flow is supported mainly by alloch-

thonous organic matter (such as leaves, Cummins et al. 1966, Wallace et al. 1999, Webster et al. 1999). In this context, the shredder potential of *G. fossarum* should have been maximized in previous studies. These results stress the need to better quantify functional traits of organisms and their source of variation in order to understand the functional role of benthic diversity in headwater streams.

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