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Ecological traits of the amphipod invader *Dikerogammarus villosus* on a mesohabitat scale.

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With 4 figures and 1 table in the text

Abstract. Since 1995, *Dikerogammarus villosus* SOWINSKI, a Ponto-Caspian amphipod species, has been invading most of Western Europe's hydrosystems. *D. villosus* geographic extension and quickly increasing population density has enabled it to become a major component of macrobenthic assemblages in recipient ecosystems. For this study, the ecological characteristics of *D. villosus* on a mesohabitat scale were investigated at a station in the Moselle River. The results show that this amphipod is able to colonize a wide range of substratum types, thus posing a threat to all freshwater ecosystems. Rivers whose dominant substratum is cobbles and which have tree roots along the banks could harbour particularly high densities of *D. villosus*. A relationship exists between substratum particle size and the length of the individuals, and spatial segregation according to length was shown. This allows the species to limit intra-specific competition between generations while facilitating reproduction. A strong association exists between *D. villosus* and other Ponto-Caspian species, such as *Dreissena polymorpha* and *Corophium curvispinum*, in keeping with Invasional Meltdown Theory. Four taxa (Coenagrionidae, *Calopteryx splendens*, *Corophium curvispinum* and *Gammarus pulex*) exhibited spatial niches that overlap significantly that of *D. villosus*. According to the predatory behaviour of the newcomer, their populations may be severely impacted.

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Introduction.

The spatio-temporal distribution of macroinvertebrates on a river bottom is the basis of biotic relationships, such as competition or predation. On a local scale, the success and impact of a non-indigenous species depend on its ability to use available habitats and on the overlapping of its spatial niche with that of other species already in place.

Dikerogammarus villosus is the latest successful invader in Western European hydrosystems. It is present since 1995 in the Rhine River (BIJ DE VAATE & KLINK 1995) and since 1999 in the Moselle River (DEVIN et al. 2001). It is expected to be the next successful invader in the North American Great Lakes, as the newest uninvited guest at the invasional meltdown party occurring there (RICCIARDI 2001). In recently colonised areas, *D. villosus* became the dominant amphipod species (DICK & PLATVOET 2000, DEVIN et al. 2001), thanks to life history traits that favoured rapid population increases (DEVIN et al. in press). In addition, *D. villosus* high reproductive capacity combined with an ability to spread rapidly makes it likely to become a cosmopolitan species with worldwide distribution in the near future. Nonetheless, *D. villosus* impact on a given recipient ecosystem community remains poorly documented. Laboratory experiments have shown that it exhibits aggressive, predatory behaviour among other gammarids (DICK & PLATVOET 2000), and preys upon all macroinvertebrate groups (DICK et al. 2002). This predatory behaviour, combined with elevated population densities, may have a severe impact on other macroinvertebrate populations and destabilise the invaded ecosystem within a short period of time. Thus it appears necessary to expand our understanding of *D. villosus* ecology and spatial distribution at a local scale in order to determine (1) which type of substratum the species is best able to

colonise and inhabit and, as a consequence, (2) which species it can be expected to interact with in the colonised ecosystem.

We sought to determine the spatial distribution of *D. villosus* among the mesohabitats constituting a river bottom, and the relationships between the newcomer and the species already in place. Results are discussed in terms of the advantages and disadvantages of biotic relationships from an eco-evolutionist point of view, focusing on the integration of a new species within a macrobenthic community.

Material and methods

Study area

The spatial distribution of *D. villosus* was studied in the Moselle River near Metz (49°12'N, 6°12'E), in Northeastern France. This station was chosen because of its accessibility and its being one of the rare non-canalised sections of the Moselle River with high diversity of mesohabitats. The river is approximately 100m wide, and macroinvertebrates can be sampled without using a boat in 70% of its width. Moreover, the presence of non-indigenous species in this station has been qualitatively followed for several years. It allows us to state that *Corbicula fluminea*, *C. fluminalis* and *Corophium curvispinum* established here in 1994 and *Hypania invalida* in 2001. *D. villosus* was first observed in 1999.

Sampling strategy

Five field campaigns were undertaken between autumn 2000 and autumn 2001, i.e. one campaign per season. Three sample collection methods were used: two types of modified Surber samplers (0.05m² and 0.1m², both with 500 µm mesh size) and a dip net (500 µm mesh size) when the water column was too high, especially in winter. Regardless of the method used, substratum was collected down to a depth of approximately five centimetres. The mean

particle size of each mineral sample was then determined at the laboratory according to CUMMINS' classification (1962). Macroinvertebrate abundances were not ascribed to a single surface unit because there was little variation in the surface sampled, but a logarithmic transformation of data was adopted, resulting in a semi-quantitative approach that minimises the variation range of abundances between samples.

During each of the five campaigns, we systematically sampled the available mesohabitats. Organic mesohabitats were sampled twice and mineral substrata three times. The number of samples varied between 16 in winter and 26 in summer, the difference being due essentially to the presence or absence of macrophytes, and of tree roots along the banks, that were spalled up during the river spate. For each of the 102 samples taken, current velocity and minimum distance to the river bank were recorded. The bivalvia *Corbicula* sp. constitutes a particular mesohabitat present in the Moselle River. In some areas, more than 90% of the river bed macroinvertebrates are this Asiatic clam, with densities of up to 4500 live individuals per square metre (unpublished data). This particular substratum, representing about 5% of the river bottom surface, was sampled three times per campaign.

The environmental variables describing each sample were coded into modalities for statistical analysis (Table 1). The approach adopted for categorising substratum modalities followed that of BOURNAUD & COGERINO (1986).

Macroinvertebrate samples were frozen (-25°C) shortly after collection in order to best preserve the colouration of *D. villosus*. After defrosting the samples, macroinvertebrates were rapidly sorted under a stereomicroscope. Most taxa were identified to genus level, with exotic species identified to species level, some autochthonous taxa recorded to family level and Oligochaeta and Nematoda recorded as such. Gammarids smaller than three mm, whose identification becomes difficult below this size, were classified as Gammaridae juveniles. Each *D. villosus* individual was measured from the tip of the rostrum to the base of the telson

using a stereomicroscope fitted with an eye-piece micrometer. This measurement was the most frequently used (KOSTALOS 1979, HYNES 1955, MUSKÓ 1993) and allows interspecific comparisons. Moreover, the telson is fragile, thus some individuals lost it before measurement. Those between three and six mm were classified as *D. villosus* juveniles. Individuals larger than six mm were sexed based on sexual dimorphism, with males showing densely setose antennae and gnathopods. Colouration was also noted: striped (hereafter referred to as Type 1), spotted (Type 2), melanic (Type 3) and melanic or amber with a dorsal stripe (Type 4). Juveniles were classified as Type 5. Individuals were assigned to one of four size classes, as detailed in Fig. 2e, males being larger than females in each class.

Statistical analysis

The Index of Dispersion $ID = \frac{s^2}{\bar{x}}$ (LUDWIG & REYNOLDS 1988), where s^2 and \bar{x} are respectively the variance and the mean of the *D. villosus* abundances over the 102 samples, was calculated and statistically tested ($d = \sqrt{2 * ID * (N - 1)} - \sqrt{2 * (N - 1) - 1}$, with N the total number of samples). If $d > 1.96$, the spatial distribution of *D. villosus* could be considered as spatially clumped. The distribution of *D. villosus* on the river bottom was then analysed according to its pattern of colouration, sex and size class. The 4311 *D. villosus* found during the five campaigns were ordinated in an array, with lines representing the 89 samples where *D. villosus* was present and columns for the 25 combinations of sex, length class and colouration pattern observed. Each box of this array contains the number of individuals collected in a given mesohabitat. Relationships between *D. villosus* distribution and substratum were investigated using a factorial correspondence analysis (FCA). Roots and/or macrophytes were not sampled at each campaign, being absent in winter and rare in autumn. Thus, the temporal effect was very high (Fig. 1), and a within-dates analysis (DOLÉDEC & CHESSEL 1989) appeared necessary to eliminate this effect.

For a second FCA of the whole faunal list, including *D. villosus*, only macroinvertebrates that were present in at least 5% of the samples (thus present in at least six samples taken within the year) were retained. This list contains 41 lines corresponding to 37 taxa and four *D. villosus* length classes, and 102 columns, corresponding to the total number of samples. The occurrence of *D. villosus* within the community, subdivided in quartiles, was studied for each season and each sample.

Niche breadth and niche overlap (LEVINS 1968) with *D. villosus* were calculated for each taxonomic unit using the following equations:

Niche breadth: $A' = \frac{e^H}{N}$, where H' is the Shannon diversity index and N the number of resource classes.

Niche overlap of species 1 with species 2: $LO_{1,2} = \frac{\sum_j^r [(p_{1j})(p_{2j})]}{\sum_j^r p_{1j}^2}$, where p_{1j} and p_{2j} are respectively the frequency of occurrence of species 1 and 2 on a given resource j .

Niche breadths and niche overlaps were calculated considering one faunal list for the whole year. The N resource classes were the nine substratum types, thus j ranged between 1 and 9 (Table I).

A cluster analysis was based on the faunal list cited above, from which taxa absent in at least two campaigns were excluded in an attempt to underscore only those relationships occurring throughout the year. An FCA was performed on this dataset, keeping a number of axes representing at least 50% of the total inertia. Species were classified on the first five FCA axes with Statistica software, using Ward's method applied to Euclidean distances. All the multivariate analyses were performed using ADE-4 software, a package for multivariate analysis and graphical display (THIOULOUSE et al. 1997).

Results

The Index of Dispersion of *D. villosus* on the river bottom was 1.75. The statistical analysis reveals that this species exhibited a clumped spatial distribution ($d=4.61$, Negative Binomial Distribution, $p<0.001$).

The multivariate analysis of *D. villosus* distribution on the river bottom showed no spatial segregation trends related to colouration pattern or sex (Figs. 2c & 2d). A Chi-square test was performed and confirmed that individual colour types and males and females showed no difference in spatial distribution ($p=0.051$ and $p=0.849$ for colour type and sex, respectively). However, distribution of size classes was clearly different (Fig. 2e, $p<0.0001$) and, notably, inertia increased with the mean length of the individuals. This result was confirmed by the niche breadth, which increased with size (0.56 for juveniles, 0.60, 0.84 and 0.81 for class A, B and C, respectively). The decomposition of the total inertia in *D. villosus* data (Fig. 1) revealed that the effect of bank distance, habitat type and current velocity were low, thus the corresponding factorial planes are not shown. Once the temporal effect was suppressed, the substratum effect became the highest, corresponding to 17.4% of the total variability.

The juveniles seemed to have a higher affinity for roots and macrophytes (substratum types 7 and 8). The largest *D. villosus* were found in a wide range of substrata, but were more present in cobble (substratum type 4). Small and medium-sized individuals were both present in other substrata, but a specific substratum preference was not defined clearly for either of these two intermediate size classes (Figs. 2e & 2f). The modality 'Sand' (substratum type 1) is not present on the factorial plane (Fig. 2f) because *D. villosus* were never found on this substratum.

The analysis of the complete faunal list confirms that current velocity and distance to the bank did not seem to play a role in the microdistribution of invertebrates at our station (Fig. 1 shows a low inertia for these two factors).

This analysis confirms that *D. villosus* exhibited highest affinity for roots, boulders and cobbles (substratum types 7, 5 and 4), but not for sand, and deposition habitat in general (habitat type 3) (Figs. 3a and 3c). A granulometric gradient appeared, with the numbers of *D. villosus* present increasing as the mineral particle size increased (substratum types 3, 4 and 5). Along axis F1, a temporal gradient appears (Fig. 3b), with the lowest abundances (winter campaign) in samples on the left of the first factorial plane and samples with the highest abundances on the right. Presenting intermediate abundances, the autumn and spring campaigns are in the centre of the factorial plane.

The cluster analysis (Fig. 4) allowed to separate the macroinvertebrate community into three groups which are marked in Fig. 3a.: the first composed of taxa associated with *Corbicula* sp. on the river bottom and the third including taxa associated with macrophytes (see Figs. 3a and 3c). The second group included all the amphipods found in the Moselle River, and showed a particular association of medium and large *D. villosus* (categories 3 and 4) with *D. polymorpha*, and a sub-group including *C. curvispinum*, juvenile and small *D. villosus* (categories 1 and 2), *G. tigrinus* and the Gammaridae juveniles.

Considering one faunal list per campaign, *D. villosus* was always among the most abundant species at our station (first quartile), but dominated the assemblages only once, in the spring. This was probably due to the high abundances of juveniles during this campaign. If we consider the rank of *D. villosus* among the 102 samples, in one third of the cases it was in the first quartile (35 times) as well as the second quartile (37 times), and it appeared 12 times in the fourth quartile, corresponding to 12 samples where the species was absent. Considering

all 102 samples, *D. villosus* was the dominant species only seven times. It ranked second twelve times and third seven times.

Finally, four taxonomic units (*Calopteryx splendens*, *Corophium curvispinum*, *Gammarus pulex*, and the Coenagrionidae family), presenting both high niche overlaps with *D. villosus* (ranging from 0.579 to 0.754) and low niche breadths (ranging from 0.257 to 0.496), were suspected to highly compete for space with it.

Discussion

The study of microdistribution allows us to define which biological factors helped *D. villosus*, directly or indirectly, to establish dense populations in the colonized ecosystem. The niche breadth of the species was 0.64, showing an ability to colonize a wide range of substratum types. This large niche breadth shows that the composition of a river's substratum mosaic may not prevent the establishment of *D. villosus*, this species being present in almost all types of substrata, except sand. Based on these mesohabitat preferences, a river with mainly cobble as a substratum and tree roots along the banks may well harbour extremely dense *D. villosus* populations. This species has an aggregated distribution, which is common in aquatic macroinvertebrates, and may be influenced by both abiotic (i.e. substratum type) and biotic (competition, predation) factors (MURPHY et al. 1998).

A segregation of each size class distribution was observed on the river bottom, with the smallest *D. villosus* individuals in particular found on roots and macrophytes and the largest individuals on cobble. Substratum particle size is a frequently studied factor governing the microdistribution of stream invertebrates. Such a correlation has already been shown for insects (CUMMINS & LAUFF 1969), as well as for several species of gammarids (PRINGLE 1982, ADAMS et al. 1987, GRAÇA et al. 1994, DAHL & GREENBERG 1996 for *G. pulex*, OLYSLAGER & WILLIAMS 1993 for *G. pseudolimnaeus*).

This separation of size classes on the river bottom gave *D. villosus* several advantages, each of which are different according to the size class considered. Firstly, large individuals lived among large particles affording protection from both high current velocity and common predators of gammarids, such as fishes (OLYSLAGER & WILLIAMS 1993, DAHL & GREENBERG 1996). Furthermore, the largest *D. villosus* were found to live together, thus the probability for a mature individual to find a mate was increased. The lack of overlap between size classes also decreased the competition of medium-sized males with larger ones. The biggest individuals were not found among boulders, this microhabitat lacking adapted crevices (REES 1972). Secondly, the smallest individuals occupied roots and macrophytes, mesohabitats that were abundant and available when the first reproduction phase occurred. This has already been found for *G. pulex* in England (GRAÇA et al. 1994). However, in some studies, the largest *G. pulex* were found in macrophytes (BOLLACHE et al. 2000) and large *G. lacustris* had a higher affinity for algae (SHANNON et al. 1994), but in these studies distribution seemed more likely to be influenced by food availability. Roots and macrophytes provide both refuge owing to their complex shapes, and a source of food for small individuals. Living plants themselves, or their specific faunal assemblages, have been identified as a food supply for *G. pulex* juveniles (SUTCLIFFE et al. 1981). Finally, the different size classes correspond to individual cohorts from various generations. Cannibalism, specifically of adults eating juveniles, is a common phenomenon in gammarids (MACNEIL et al. 1999). Thus spatial segregation reduces the overlap of different generations of *D. villosus* and limits intra-specific competition.

At this site the macroinvertebrate community could be divided into three distinct mesohabitat distribution groups. The first and third ones had no or low interactions with *D. villosus*, and were taxa assemblages of particular substratum. Achaeta, Oligochaeta, Polychaeta and Bivalvia were mainly found in the *Corbicula* substratum, constituting the first

group, while Diptera and some Pulmonata associated with macrophytes formed the third group. The second group included all gammarids. In this one, a strong sub-association of medium and large *D. villosus* with *D. polymorpha* was evident. It has already been shown that *D. polymorpha* favours the amphipod population by increasing both the habitat complexity of the colonized substratum (potential refuges) and the abundance of macroinvertebrates – potential prey for *D. villosus*– due to biodeposition exploited by deposit feeders (RICCIARDI et al. 1997, GONZALEZ & DOWNING 1999). Moreover, these two species have co-evolved over a long period of time, as they both originate from the Ponto-Caspian basin. This association fits the Invasional Meltdown Theory (SIMBERLOFF & VON HOLLE 1999), which proposes that positive interaction between species with co-evolutive pasts increases the probability of successful establishment of exotic species of the same origin. A newcomer from a given geographic area becoming established in a recipient ecosystem favours the successful introduction of a second exotic species from the same geographic area, which could then favour a third one and so on, a kind of exotic species snowball effect. In this second group were to be found the Trichoptera *Ecnomus tenellus*, which inhabited large particle sizes in low current velocity and have a predatory diet, occupying a niche that overlapped strongly that of *D. villosus*. Small and juvenile *D. villosus*, *G. tigrinus* and *C. curvispinum* were also associated. This association concerned gammarids within a similar size spectrum, which could explain similarities in their distribution. Another possibility is that *G. tigrinus* had been excluded from the other substrata by *D. villosus* through an exclusive competition process. Such a phenomenon has already been shown for the two crayfish, *Orconectes virilis* and *O. immunis*, the first and more aggressive one excluding the other from certain substrata (BOVBJERG 1970). A second association of species that have co-evolved existed between small *D. villosus* and *C. curvispinum*, but their relationship cannot be clearly defined as one of competition, predation or commensalism. In any event, even when *D. villosus* was very

abundant, we did not find any proof that the benthic community was destabilised by its presence.

We cannot affirm that niche overlaps observed one year after the establishment of *D. villosus* in the Moselle River were not influenced by previously established biotic relationships. However, the niche overlaps measured allowed us to check that four taxa, among which are two other amphipods, *G. pulex* and the invader *C. curvispinum*, and some Odonata (*Calopteryx splendens* and the Coenagrionidae) were found in the same substrata as *D. villosus*. Considering its predatory behaviour (DICK & PLATVOET 2000, DICK et al. 2002), these four populations are presumably threatened.

Abiotic factors, such as high substratum heterogeneity, which reduces intra-specific competition, may have favoured the success of *D. villosus* at this site of the Moselle River. Biotic factors, such as the presence of other species of the same origin, may also have facilitated its establishment.

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Table 1. Modalities of the five environmental variables defining each sample. The codes are those used in the multivariate analysis. In the last column, N= the number of samples corresponding to each modality.

Variable	Modality	Code	N
Date	Autumn 2000	1	20
	Winter 2001	2	16
	Spring 2001	3	20
	Summer 2001	4	26
	Autumn 2001	5	20
Habitat type	Organic	1	35
	Erosion	2	30
	Deposition	3	22
	<i>Corbicula</i> sp.	4	15
Substratum	Sand	1	9
	Gravel	2	13
	Pebble	3	15
	Cobble	4	8
	Boulder	5	7
	<i>Corbicula</i> sp.	6	15
	Roots	7	6
	Macrophytes	8	21
	Organic detritus	9	8
Current velocity (m/s)	≤0.05	1	25
]0.05-0.3]	2	56
	>0.3	3	21
Bank distance (m)	≤2	1	35
]2-5]	2	32
	> 5	3	35
<i>D. villosus</i> Colouration pattern	Striped	1	438
	Spotted	2	669
	Melanic	3	427
	Dorsal stripe	4	457
	Juveniles	5	2320
<i>D. villosus</i> sex	Juveniles	1	2320
	Males	2	834
	Females	3	1157
<i>D. villosus</i> size (mm)	< 6	1	2320
	♀ [6-9[♂ [6-10[2	1268
	♀ [9-12[♂ [10-15[3	569
	♀ ≥12 ♂ ≥15	4	154

Table 1. DEVIN S., PISCART C., BEISEL J.N. and MORETEAU J.C.

Figure 1.

Contribution of the five environmental variables measured in each sample to the total variability (=total inertia).

Figure 2.

Factorial analysis on *D. villosus* microdistribution. (a) Eigenvalues. The position of the different groups of *D. villosus* on the factorial plane F1-F2 (b) and the distribution of the colour types (c), sex (d) and length classes (e) are to be compared with the position of the substrata (f). Juveniles exhibit no colour type and were not sexed, thus there is only one combination of colour type/sex/size class, and a single dot on the factorial planes.

Figure 3.

Factorial analysis on the whole faunal list. The distribution of taxa along axes F1-F2 (a) is to be analysed according to the date (b), substratum (c), and habitat (d). The three groups were constituted on the basis of the cluster analysis presented in Fig. 4. *D. villosus* 1-4 refers to size classes defined in Fig. 2. Groups on Fig. 3a are constituted on the basis of the cluster analysis and the ellipses encompass 95% confidence limits for each group.

Figure 4.

Cluster analysis of the whole faunal list. According to the aggregation distance histogram, a separation into three groups was made at a distance of 4.4.

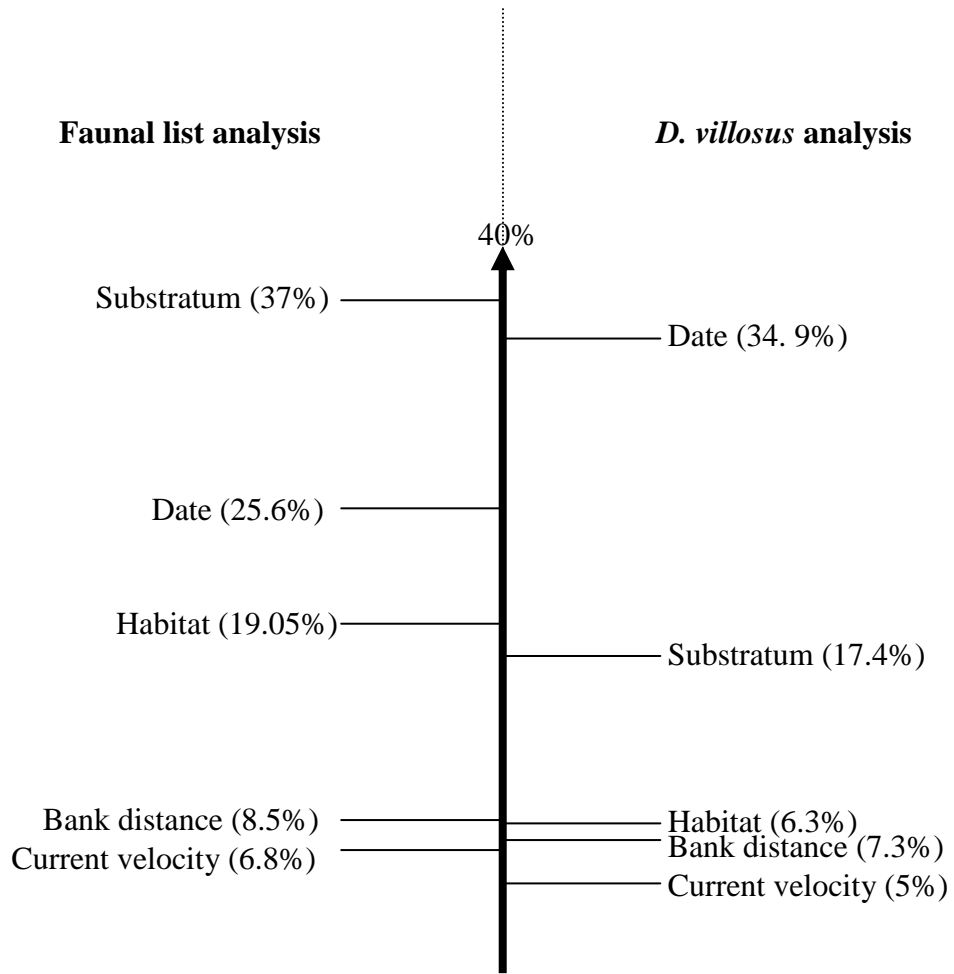


Figure 1. DEVIN S., PISCART C., BEISEL J.N. and MORETEAU J.C.

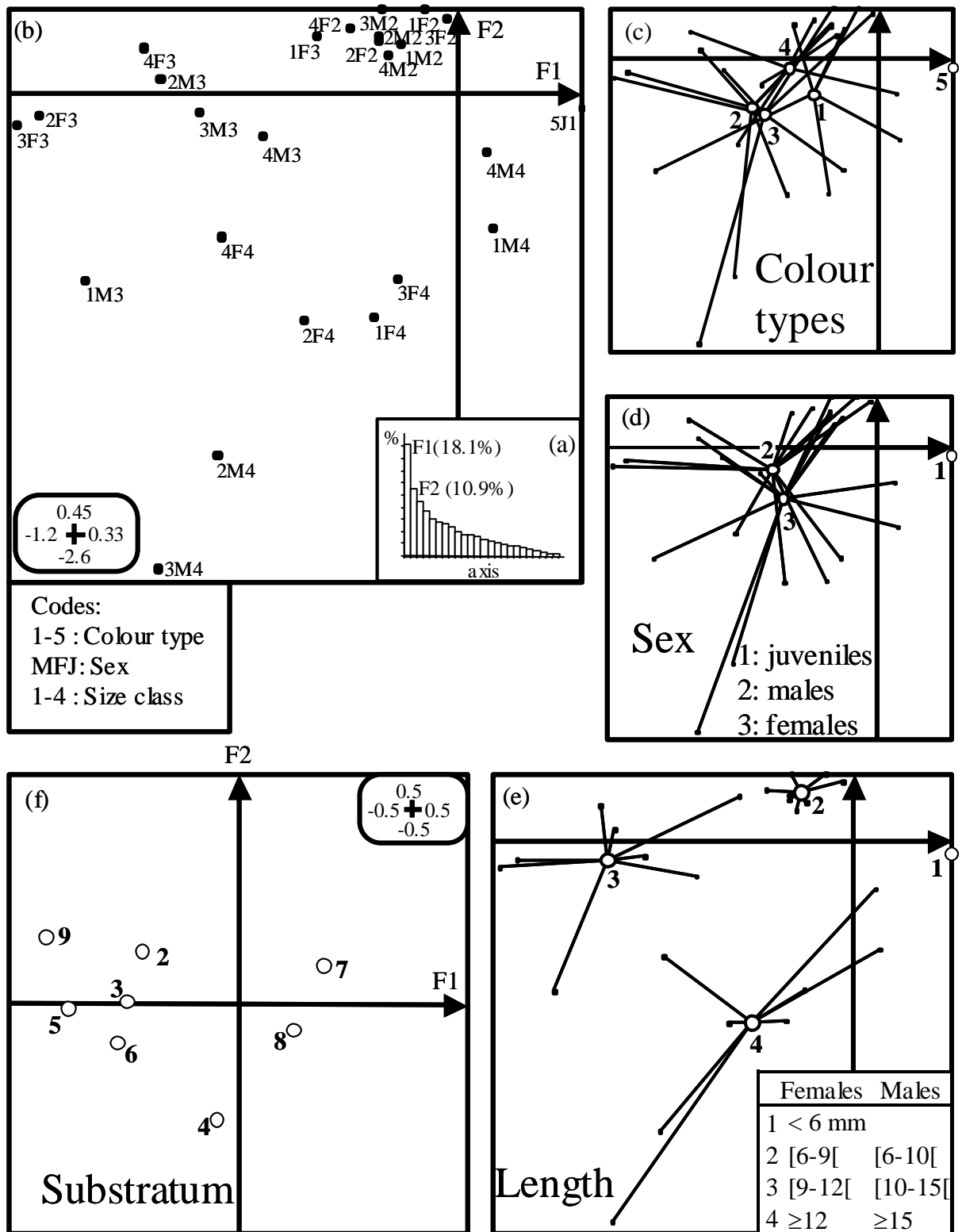


Figure 2. DEVIN S., PISCART C., BEISEL J.N. and MORETEAU J.C.

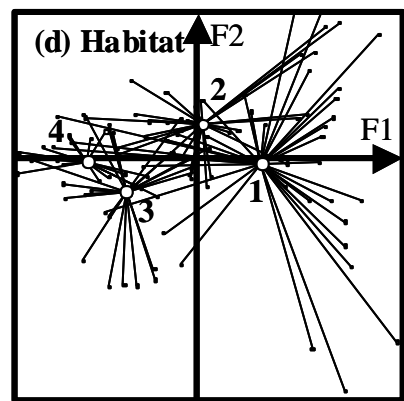
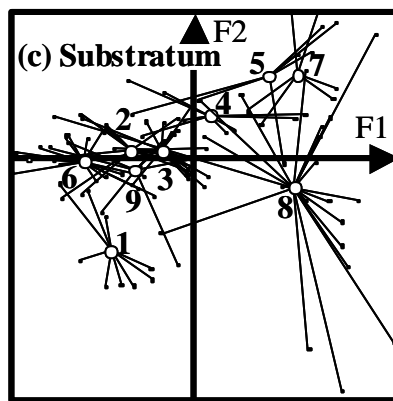
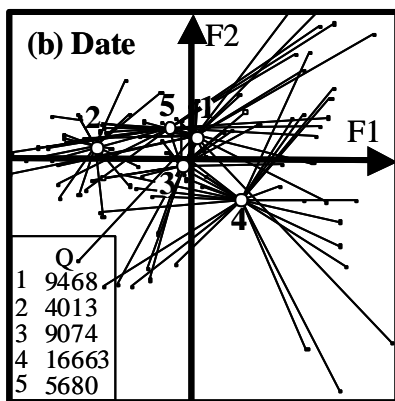
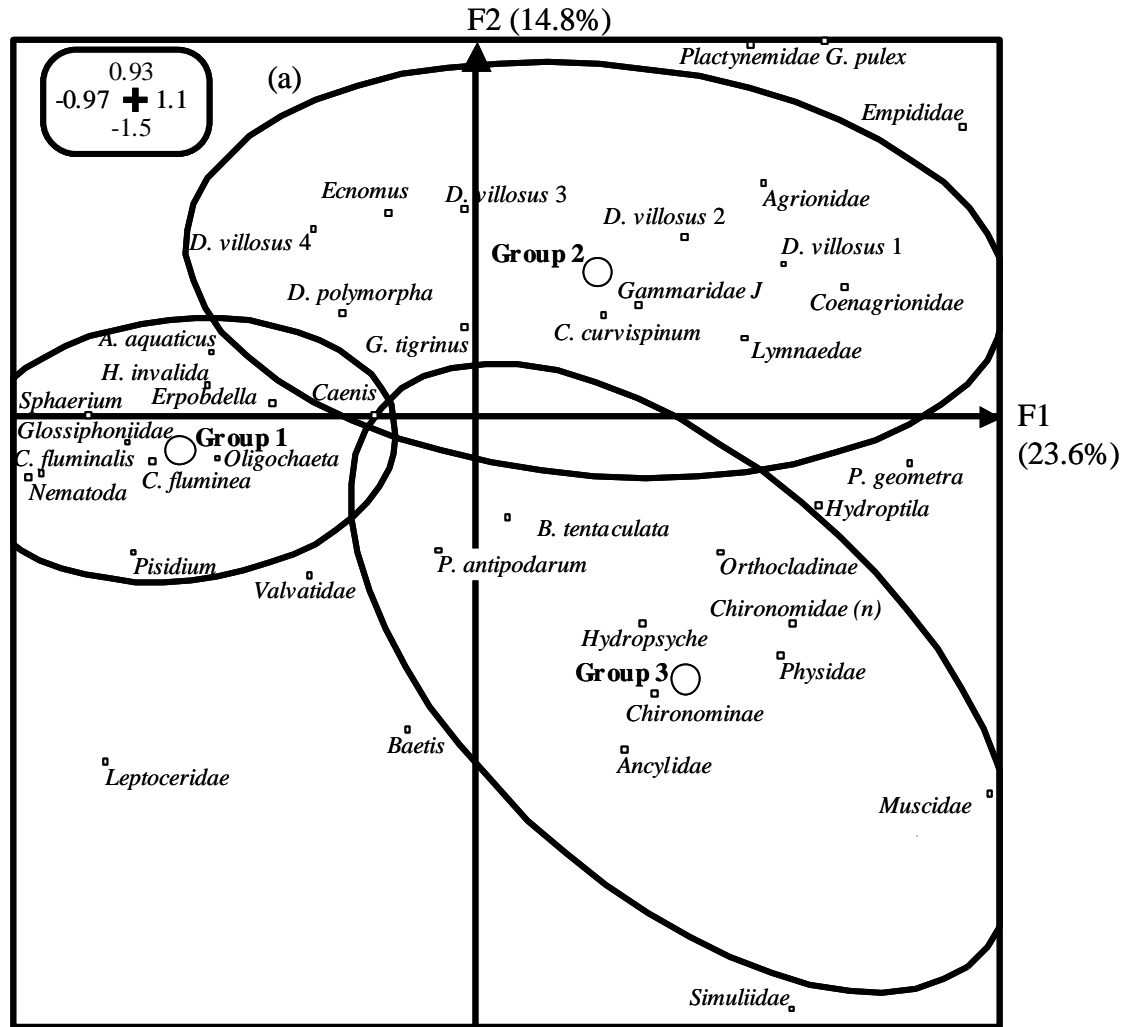


Figure 3. DEVIN S., PISCART C., BEISEL J.N. and MORETEAU J.C.

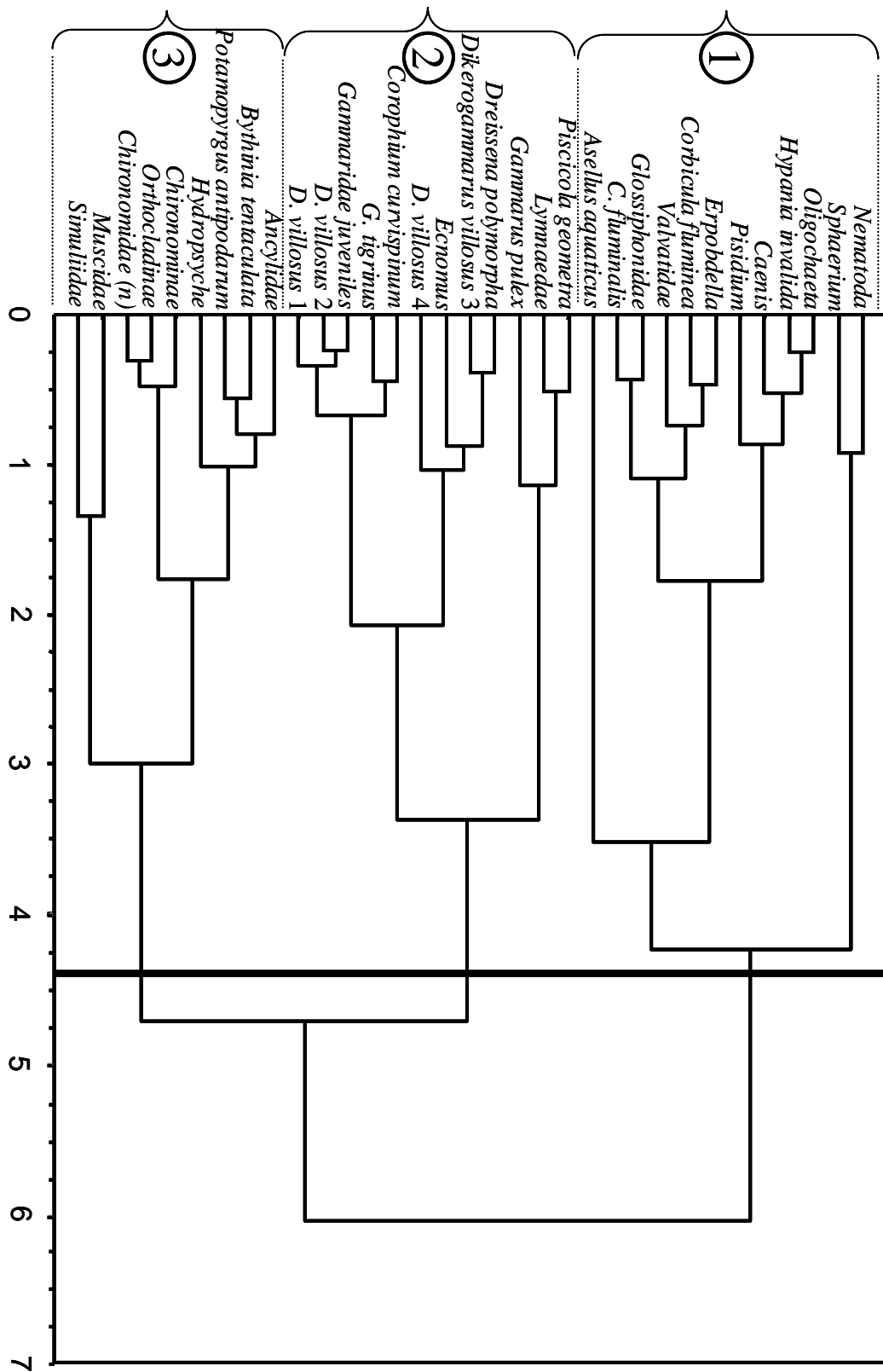


Figure 4. DEVIN S., PISCART C., BEISEL J.N. and MORETEAU J.C.