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Biological and ecological characteristics of invasive species: a gammarid study

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Abstract. Knowledge of characteristics helpful in screening potential invaders and in elaborating strategies to limit their success is highly desirable. We focused on gammarid amphipods from Western Europe and North America to discover biological and/or ecological traits that may explain successful invasion by these species. Two typologies were considered: an analytical one, with groups built on the basis of biological or ecological similarities, and an empirical one, with groups constituted a priori according to a species' invasive status and its fresh or brackish water origin. The results obtained are discussed in the light of three hypotheses that may influence invasiveness: biotic potential, species size and euryoeciousness. The analysis revealed a particular ecological profile for invaders, with a strong influence of salinity tolerance, but no typology was found based on biological characteristics. Invasiveness cannot be predicted from a limited number of criteria, and is the result of a combination of several characteristics. Invasive species therefore exhibit a particular ecological profile rather than a biological one, contrary to most classical explanations.

Key-words: biological invasions, biological traits, ecological traits, Gammaridae, profiling invader.

Introduction

Research on biological invasions has largely focused on the impacts of introduced species and on methods of their control. Recently, focus has turned to the development of tools to prevent invasions. In addition to technical prevention methods, such as ballast water treatment, attention is given to identify potential future invaders from their biological and ecological characteristics (e.g. Ricciardi and Rasmussen 1998; Hayes and Sliwa 2003).

The invasion process itself may be divided into three to five distinct stages (Vermeij 1996; Kolar and Lodge 2001; Colautti and MacIsaac 2004). After transport and introduction into a recipient ecosystem, any species that maintains a population through local reproduction and recruitment without the introduction of new individuals is called an exotic (stage III according to Colautti and MacIsaac 2004). If it reaches high densities and spreads further, it becomes invasive (stage V, Colautti and MacIsaac 2004), and impacts the recipient ecosystem. Here, we use this definition of an invasive species and, following Kolar and Lodge (2001), we define indigenous (autochthonous) species as taxa restricted to their native ranges.

A species' traits determine its success or failure in the transition between the different stages of the invasion process, and only particular trait combinations are assumed to make a species invasive. Some studies have adopted a quantitative approach for determining what these traits are (Kolar and Lodge 2001). Most deal with plant or bird invaders, with particular attention for island ecosystems (Kolar and Lodge 2001, Lloret et al. 2005). For invertebrates, their role is more difficult to analyze due to a lack of data on failed introductions (Vasquez and Simberloff 2001). To the best of our knowledge, studies using a quantitative approach are lacking for aquatic invertebrate species, but a few empirical descriptions of potential traits have been proposed (Ricciardi and Rasmussen 1998; van der Velde et al. 2000; bij de Vaate et al. 2002). Biological

(autoecological) characteristics are suspected to play a major role and have been more frequently investigated than ecological characteristics. All studies have considered traits individually, potentially underestimating a possible cumulative / antagonistic effect of traits on invasiveness.

In this study, we use a quantitative method to investigate a combination of biological and ecological traits involved in invasion success. We assume that an organism's biological traits reflect the biotic characteristics and the ecological functions of the species, whereas its ecological traits describe its potential environmental tolerance. This study focused on gammarid amphipods, frequent in biological invasions, paying attention to Western Europe and North America, two well documented recipient areas. Gammarids are amphibiotic and constitute a taxonomic group of phylogenetically related species with variable bio-ecological features (Illies 1978; Sainte Marie 1991). We considered species from fresh and brackish water origin.

We investigate two questions: (1) could a typology based on a combination of biological or ecological traits be related to the invasive character of the species, and (2) does a given trait considered alone discriminate between invasive and non-invasive species? The results are discussed in the framework of three conceptual hypotheses about invasiveness:

H1: Invasive species exhibit a higher biotic potential (typically an r-strategy) than non-invasive ones (Lodge 1993; Williamson 1996; van der Velde et al. 2000; bij de Vaate et al. 2002).

H2: Body size influences invasion success (Roy et al. 2002).

H3: Invasive species tolerate a wider range of environmental conditions (Ricciardi and Rasmussen 1998).

Material and methods

Bibliographic analysis: traits and species studied

We selected 10 biological and 7 ecological traits (Table 1) and documented features related to the life cycle of taxa ('maximal size', 'size distribution', 'hatching length', 'minimal size at sexual maturity', 'mean fecundity', 'maximal egg number', 'sex-ratio', 'number of generations per year', 'life-span'), aspects of nutrition ('diet'), different habitat conditions ('salinity', 'temperature tolerance', 'altitude', 'longitudinal distribution', 'microhabitat', 'current velocity'). Traits common to all species, such as respiration mode or locomotion, were not taken into account. The size distribution variable reflects the distribution usually observed in field of individual among size class. The mean fecundity is the mean number of eggs observed considering all size classes. The microhabitat variable reflects the distribution at the scale of the bottom substrate. In addition, ecological traits include the mean density observed where the species occurred.

In order to document the biological and ecological traits of the highest possible number of species, all accessible references dating from 1911 to 2003 were consulted. In all, eighteen fresh and brackish water species were included (Table 2), viz. almost all gammarids common in Western Europe (Eastern distribution limit: Germany-Switzerland-Italy; Illies 1978; Leppäkoski et al. 2002), as well as the most common North American freshwater species (Barnard and Barnard 1983). Among 18 species considered, seven are known to be invasive (Dick and Elwood 1992; Devin et al. 2005; Table 2).

Fuzzy coding and statistical analysis

Data were retained in an array where lines represent the 18 species and columns represent the 17 biological and ecological variables. Each variable was subdivided into several modalities (Table 1) with limits allowing an equal distribution of species score among them. The affinity (score) of a species for each modality was assigned using a fuzzy coding approach (Chevenet et al. 1994). This procedure standardizes the description of each species by assigning it a score from 0 (no affinity) to 3 or 5 (high affinity) (Table 1) and is particularly effective for the description of variables for which several modalities might be simultaneously involved.

Two multiple correspondence analyses (MCA) adapted to fuzzy coding were performed on this data set, one for the biological and one for the ecological traits (Chevenet et al., 1994). From the MCA performed on this data set, axes representing about 70% of the total inertia were kept. A cluster analysis was then performed on the factorial coordinates of the species on the MCA axes to define whether invasive species grouped together. The multivariate analyses were performed using ADE-4 software, a package for multivariate analysis and graphic display (Thioulouse et al. 1997). Species classification was done using Ward's method applied to Euclidean distances (Statsoft, Statistica 7).

Inferential analyses were performed to assess which traits best discriminate (1) groups obtained from the species traits typology or (2) groups constituted a priori of invasive or non-invasive species. Kruskal-Wallis tests were first performed on the species' traits among groups obtained with the cluster analysis, for each modality of all traits. The differences were tested modality by modality between groups identified as different in terms of their bio/ecological profile. This approach on groups obtained by cluster analysis is innovative by comparison with studies based on groups built *a priori*, only depending on invasive status. In a second step, Kruskal-Wallis tests were performed between groups defined according to their observed

invasive character. If a difference was detected, a post-hoc analysis was used to determine precise differences (Statsoft, Statistica 7).

Results

Species classification

Biological traits

Eigenvalues of the MCA on biological traits indicated two main factors important to the structure of species description data (Fig. 1). Species, positioned on the factorial plane according to their biological characteristics, were grouped according to their invasive status. The figure reveals that the groups were poorly separated, with the scatter plots of all species belonging to a group strongly overlapping. The best differentiation of the three groups was achieved along the F2 axis, which corresponded to parameters related to fecundity, size and life cycle.

The dendrogram based on biological traits showed that the 18 gammarid species could be divided in three groups according to their biological profiles, but with a mix of invasive and non-invasive species (Fig. 2). The classification revealed no pattern related to their invasive status. In order to define which biological traits structure the dendrogram, Kruskal-Wallis tests showed that the three groups differ by the trait “species size”. We found significant differences for maximum size, size distribution, hatching length and size at sexual maturity (Table 3, $p < 0.05$ each). Finally, feeding habits (presence or absence of animal elements in the diet) also varied among groups, but with no significant differences in pairwise comparisons. No modality revealed different profiles between the two first groups.

Ecological traits

Eigenvalues of the MCA on ecological traits indicated two factors that were potentially important to the structure of species description data (Fig. 3). The species, positioned on the factorial plane according to their ecological characteristics grouped according to their invasive status. The ecological characteristics of species allowed a separation of invasive (IS) and autochthonous groups (F-AS) on the F1 axis, and of IS and brackish water autochthonous groups (B-AS) on the F2 axis with group centers well-separated and minimal overlap of their scatter plots. It seems that all variables contributed to discriminate the three groups.

The dendrogram based on ecological traits (Fig. 4) distinguished two main groups: brackish or freshwater species with salinity tolerance up to 4 ‰ (group 1) and strictly freshwater species (with salinity tolerance below 2 ‰) (group 2). Focusing on the former, a subdivision into two clusters showed a clumping of brackish water species (group 1b). The other subgroup was constituted of all invasive species considered, and one non-invasive species, the North-American *Gammarus fasciatus* (group 1a). Groups 1 and 2 were significantly different as regards salinity tolerance, altitudinal and upstream-downstream distribution, densities, and current velocity (Table 4). Species belonging to the first group are more salinity tolerant, are present in high densities, in downstream sectors, where altitude and current velocity are low. No modality exhibited significant differences between the subgroups 1a and 1b.

Biological and ecological traits of invasive vs autochthonous gammarids

Our 18 species could also be *a priori* subdivided into three groups according to their invasive character and their ability to live in brackish water, as reported in the literature. The three categories thus defined were: autochthonous freshwater species (thereafter called “F-AS”), brackish water autochthonous species (B-AS), and invasive species (IS).

Biological traits

Among the ten variables studied, only two, representing 3 modalities out of 29, showed significant differences among groups (Table 5). IS, B-AS and F-AS exhibited different mean fecundity and maximum egg number. Between group comparisons revealed that the only difference observed was a higher maximum egg number for B-AS if compared to F-AS.

Ecological traits

Four among the seven variables studied, representing 9 modalities out of 22, showed significant differences among groups (Table 5). IS, B-AS and F-AS exhibited different salinity and current velocity preferenda, as well as different altitudinal and upstream-downstream distributions.

Between group comparisons produced no evidence for differences between IS and B-AS. As a whole, invasive species occurred in downstream sectors of rivers, where current velocity is low. Moreover, they exhibit a wide salinity tolerance (euryecious species), and have an equal affinity to each modality of this variable, while the two other groups are more restricted to either fresh- or brackish-waters (stenoecious species).

Discussion

Investigations of invasive gammarids highlight that the discrimination between invasive and non-invasive species is difficult on the basis of biological or ecological traits considered individually. However, the analysis combining ecological traits demonstrated a clumping of invasive species within one group. As a result, we hypothesize that a combination of several biological and ecological characteristics could lead to a better general definition of an invader

profile. The results of two types of analysis (combination of traits and individual traits) link some species characteristics to invasiveness through three hypotheses. The three hypothesis did not converge to a global theory explaining invasiveness, and need to be considered separately. For example, H1 and H2 are contradictory hypotheses, r-strategic species being generally small.

H1: Invasive species exhibit a higher biotic potential than non invasive ones (Lodge 1993; Williamson 1996; van der Velde et al. 2000; bij de Vaate et al. 2002). Three main variables define the biotic potential, i.e. a strategy for rapid colonization of the recipient ecosystem: sexual precocity, average fecundity and the number of generations per year. The species classification revealed that traits related to biotic potential were not predominant in the constitution of groups, which was dominated by size-related traits.

Moreover, the separate consideration of each of these variables did not lead to a significant result. Invasive species were not significantly different from fresh or brackish water autochthonous species in biotic potential. The most significant trend observed was a lower mean fecundity and egg number, depending on salinity tolerance. For example, *G. pulex* and *G. duebeni* have similar fecundity (Sainte Marie 1991) and number of generations per year, but *G. pulex* invaded Northern Ireland streams where it outcompeted the native *G. duebeni*.

High biotic potential is an attribute frequently shared by invasive species, but also by non invasive species, and is useful but neither essential nor sufficient for a species to become invasive.

H2: Body size influences invasion success (Roy et al. 2002).

In many groups, life-history features leading to faster population growth tend to negatively correlate with body size, r-strategists being smaller than K-strategists. However,

according to Roy et al. (2002) large species are more likely to invade than small ones, a pattern observed throughout the Pleistocene. This controversial link between size and invasiveness is difficult to prove, and contradictory results have been obtained in marine bivalves (Miller et al. 2002; Roy et al. 2002), depending on species considered. In gammarids, a positive size-fecundity relationship exists within each species (Sainte-Marie 1991), but not among species, due to variations of parameters such as egg size.

Our results indicate that body size was not related to invasiveness. Firstly, the cluster analysis, which reflected a size gradient, result in a mix between invasive and non invasive species. Secondly, analysis of each modality showed that no significant differences existed between IS, F-AS and B-AS. As a result, we cannot draw a conclusion between body size of gammarids and traits leading to faster population growth.

The role of size in the invasion process is still unclear and comparisons with results for birds (Cassey 2001; Duncan et al. 2001) and plants (Bazzaz 1986) are useless as adaptation specifics of invertebrate to aquatic habitats has to be taken into account. For lotic invertebrates, Statzner (1987) pointed out that the ratios for production/biomass and production/respiration are closely related to the maximal size achieved. As other ecological functions are potentially indicated by these traits, in particular physiological ones (Peters 1983), the role of body size needs to be investigated further.

H3: Invasive species are able to tolerate a wider range of environmental conditions

(Ricciardi and Rasmussen 1998).

Several ecological parameters taken into account are related to euryeciousness: water salinity and temperature, current velocity, altitude and microhabitat. For most of them, no differences could be observed among groups. The variable that best discriminates the *a posteriori*

ecological groups obtained by the cluster analysis is the range of salinity in which a species can live and reproduce. This particularity is not specific to invasive species and some non-invasive species also present broad environmental tolerance. Among them, *G. duebeni* exhibits the highest euryhalinity (0 to 48 ‰, Hynes 1954), yet it is not known for its invasive potential. However, this trait discriminates invasive species in the cluster analysis as well as when traits were considered individually (Kruskal-Wallis test, $p < 0.001$ for the three modalities).

Salinity tolerance is a primordial feature that conditions the potential shift between saline and freshwater habitats (Lee and Bell 1999). In the Baltic Sea, a hot spot of xenodiversity, the whole salinity gradient from up to 22 to less than 2 ‰ offers a wide range of hospitable conditions. The western Baltic region is more salted and more invaded than the inner Baltic (Leppäkoski et al., 2002), and highly euryhaline species of both marine and freshwater origin already established in adjacent water bodies are considered as potential invaders of the brackish Baltic (Leppäkoski, 2004). In the Caspian Sea, the salinity could have constituted a natural barrier to the spread of the invasive ctenophore *Mnemiopsis leidyi*, not observed in 2000 where salinity is less than 4.3 ‰ (Shiganova, et al., 2004). Moreover, convergent salinity conditions in donor and recipient ecosystems is suspected to play a key role in the recent success of invaders found in San Francisco Bay, the Baltic Sea or the North American Great Lakes (MacIsaac et al. 2001). In Europe, several authors hypothesized that pollution in the last decades increased the ionic contents of large rivers allowing salt tolerant species to spread in new basins, even if some invaders also thrive in purely fresh waters (Ketelaars, 2004). Piscart et al. (2005) observed along a sixth-order stream section that an increase of anthropogenic salinity from 0.2 to 2.6 ‰ drastically affected the species composition of macroinvertebrate communities and promoted the establishment of salt-tolerant exotic species.

As mentioned for our first hypothesis, a combination seems essential. Wide salinity tolerance increased the probability that a species would disperse and establish itself in new ecosystems, but it should be combined with other traits to define an ecological profile specific to invasive species. Moreover, the presence of *G. fasciatus*, a North-America gammarid, in the same ecological cluster than invasive species point out that the factors we considered are not sufficient to characterize precisely invasiveness.

In conclusion, for gammarids, ecological characteristics appear to efficiently discriminate invasive species, contrary to biological ones. This implies that a high biotic potential (described by biological traits) may contribute to the rapid spread of an introduced species, but also that, prior to spreading, species cannot become established without wide environmental tolerance (described by ecological traits). In this sense, ecological attributes are necessary, though biological features favored the invasion, but are accessory to its success. Despite these trends, the definition of a specific biological profile is complicated by the variations in the biotic context of the recipient area.

Finally, while none of the three main hypothesis investigated can be rejected, taken individually they are not sufficient to fully explain the invasive character of gammarids. The invader profile consists of a combination of features that allow a species to disperse, establish and densely populate a recipient ecosystem.

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Table 1. Biological and ecological variables taken into account and the modalities defined for each variable.

Biological traits		Ecological traits	
Variables	Modalities	Variables	Modalities
Maximal size (mm)	[0-16[[16-20[[20-+[Water salinity (‰)	[0-2[[2-4[[4-+[
Size distribution (juveniles excluded, mm)	[0-10[[10-13[[13-+[Temperature tolerance	Psychrophilous Eurythermal Thermophilous
Hatching length (mm)	[0-1.5[[1.5-2[[2-+[Altitude (m)	[0-500[[500-1000[[1000-+[
Minimal size at sexual maturity (Females, mm)	[0-5.5[[5.5-6.5[[6.5-+[Distribution	Rithron Potamon Estuary Lentic waters
Mean fecundity	[0-20[[20-25[[25-+[Density (ind/m ²)	[0-100[[100-1000[[1000-+[
Maximal egg number	[0-30[[30-60[[60-+[Microhabitat	Organic Sedimentation Erosion
Sex-ratio	F>M F=M F<M	Current velocity	Slow Medium Fast
Number of generations per year	1 2 >2		
Life span	<1 year 1 year > 1 year		
Diet	Detritivorous Omnivorous		

Table 2. Geographic origin, preferences in habitat salinity and invasive character of the 18 gammarid species analysed. Invasive species are in bold characters.

Species	Western Europe	North America	Freshwater	Brackishwater
<i>Gammarus limnaeus</i>		x	x	
<i>Gammarus pseudolimneaus</i>		x	x	
<i>Gammarus minus</i>		x	x	
<i>Gammarus fasciatus</i>		x	x	
<i>Gammarus troglophilus</i>		x	x	
<i>Gammarus lacustris</i>	x	x	x	
<i>Gammarus tigrinus</i>	x	x	x	x
<i>Gammarus pulex</i>	x		x	
<i>Gammarus inaequicauda</i>	x			x
<i>Gammarus duebeni</i>	x		x	x
<i>Gammarus fossarum</i>	x		x	
<i>Gammarus aequicauda</i>	x			x
<i>Gammarus locusta</i>	x			x
<i>Gammarus roeselii</i>	x		x	
<i>Echinogammarus ischnus</i>	x		x	x
<i>Echinogammarus berilloni</i>	x		x	
<i>Dikerogammarus haemobaphes</i>	x		x	x
<i>Dikerogammarus villosus</i>	x		x	x

Table 3. Non-parametric Kruskal-Wallis ANOVA performed on groups constituted after the cluster analysis on biological traits. Only significant modalities ($p < 0.05$) were presented. No differences were found between groups 1 and 2.

n.s.: not significant

Variable	Modality	Kruskal-Wallis p	Between groups differences	
			1-3	2-3
Maximum size (mm)	[0-16[<0.001	0.02	<0.001
	[16-20[0.04	n.s.	n.s.
	[20-+[0.01	n.s.	0.01
Size distr. (mm)	[0-10[0.01	n.s.	0.04
	[13-+[0.03	n.s.	n.s.
Hatching length (mm)	[2-+[<0.001	n.s.	n.s.
Sexual maturity (mm)	[0-5.5[<0.001	0.007	0.02
	[6.5-+[0.005	n.s.	0.01
Diet	Detritivorous	0.01	n.s.	n.s.
	Omnivorous	0.01	n.s.	n.s.

Table 4. Non-parametric Kruskal-Wallis ANOVA performed on groups constituted after the cluster analysis on ecological traits. Only significant modalities ($p < 0.05$) were presented. No differences were found between subgroups 1a and 1b.

n.s.: not significant

Variable	Modality	Kruskal-Wallis p	Between groups differences	
			1a-2	1b-2
Water salinity (‰)	[0-2[<0.001	0.02	<0.001
	[2-4[<0.001	<0.001	n.s.
	[4-+[<0.001	n.s.	<0.001
Altitude (m)	[0-500[<0.001	0.005	0.03
	[500-1000[<0.001	0.005	0.03
Distribution	Rhitron	<0.001	0.03	0.01
	Potamon	0.007	0.04	n.s.
	Lentic waters	0.02	n.s.	0.03
Density (ind/m ²)	[1000-+[0.01	0.05	n.s.
Water velocity	Slow	0.05	n.s.	n.s.

Table 5. Non-parametric Kruskal-Wallis ANOVA performed on the three groups constituted a priori according to the invasive status of species and their fresh or brackishwater origin. Only significant modalities ($p < 0.05$) were presented. No differences were found between invasive and brackishwater autochthonous species.

n.s.: not significant

	Variable	Modality	Kruskal-Wallis	Between groups differences	
			p	Invasive versus freshwater autochthonous species	Brackish versus freshwater autochthonous species
Biological traits	Mean fecundity	[25-+[0.05	n.s.	n.s.
	Maximum egg number	[30-60[0.04	n.s.	n.s.
		[60-+[0.02	n.s.	0.03
Ecological traits	Water salinity	[0-2[<0.001	0.03	<0.001
		[2-4[<0.001	0.01	n.s.
		[4-+[<0.001	n.s.	<0.001
	Altitude (m)	[0-500[<0.001	0.02	n.s.
		[500-1000[<0.001	0.02	n.s.
	Distribution	Rhitron	<0.001	0.02	0.01
		Potamon	0.01	n.s.	n.s.
Lentic waters		0.02	n.s.	0.04	
Water velocity	Slow	0.01	n.s.	0.05	

Figure captions

Figure 1: Multiple correspondence analysis of the biological characteristics for the 18 gammarid species. The distribution of the species on the factorial plane F1-F2 is to be compared to the factorial plane of the modalities of the 10 biological variables . IS: Invasive species, F-AS: Freshwater autochthonous species and B-AS: Brackish water autochthonous species.

Figure 2: Cluster analysis using results of a multiple correspondence analysis (MCA) of the biological traits array [18 species x 29 Modalities], performed on the factorial coordinates of the 5 first axes of the MCA (68.9% of the total variation). Invasive species are in bold characters.

Figure3: Multiple correspondence analysis of the ecological characteristics for the 18 gammarid species. The distribution of the species on the factorial plane F1-F2 is to be compared to the factorial plane of the modalities of the 7 ecological variables . IS: Invasive species, F-AS: Freshwater autochthonous species and B-AS: Brackish water autochthonous species.

Figure 4: Cluster analysis using results of a multiple correspondence analysis (MCA) of the ecological traits array [18 species x 22 Modalities], performed on the factorial coordinates of the 4 first axes of the MCA (73.6% of the total variation). Invasive species are in bold characters.

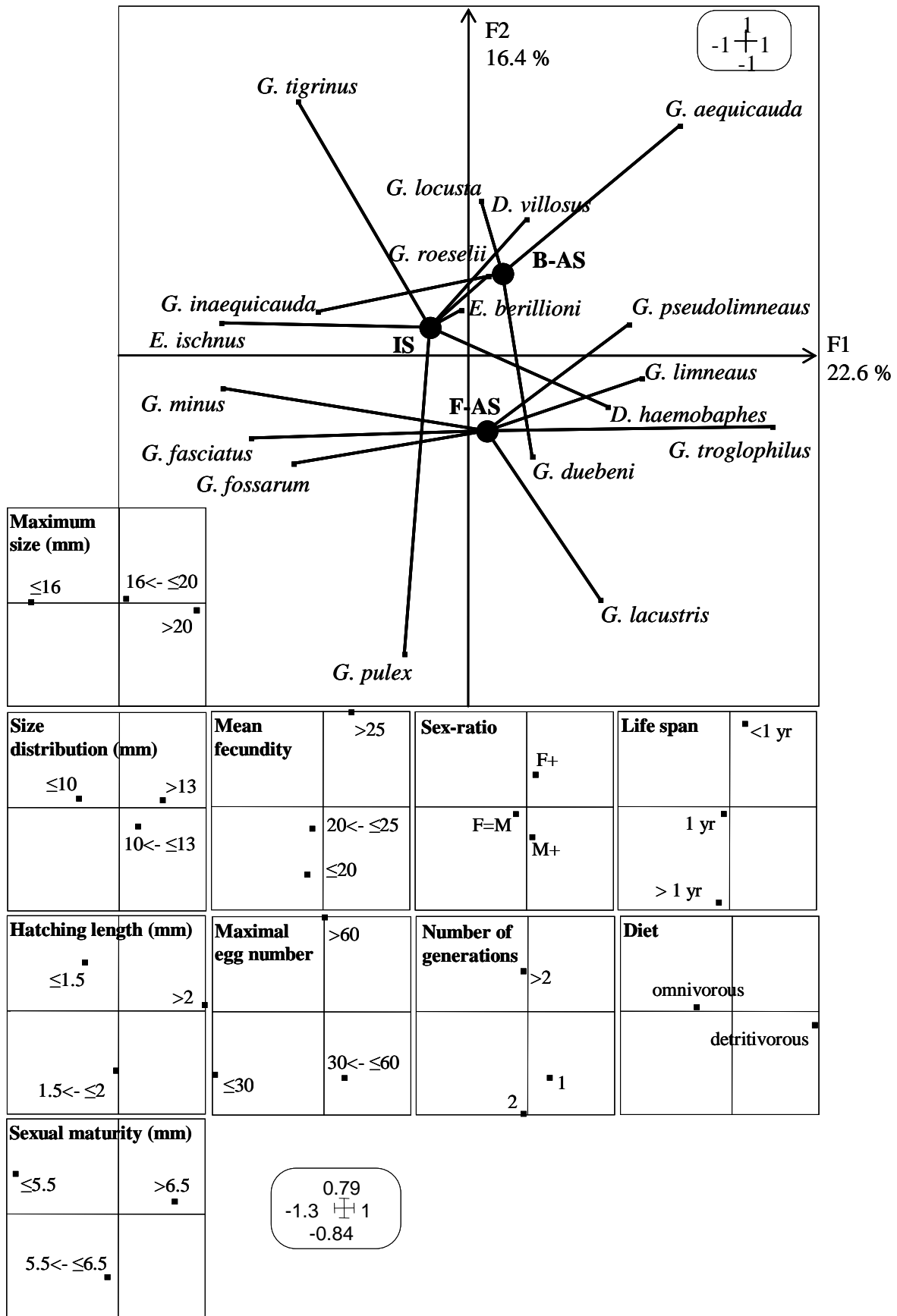


Figure 1.

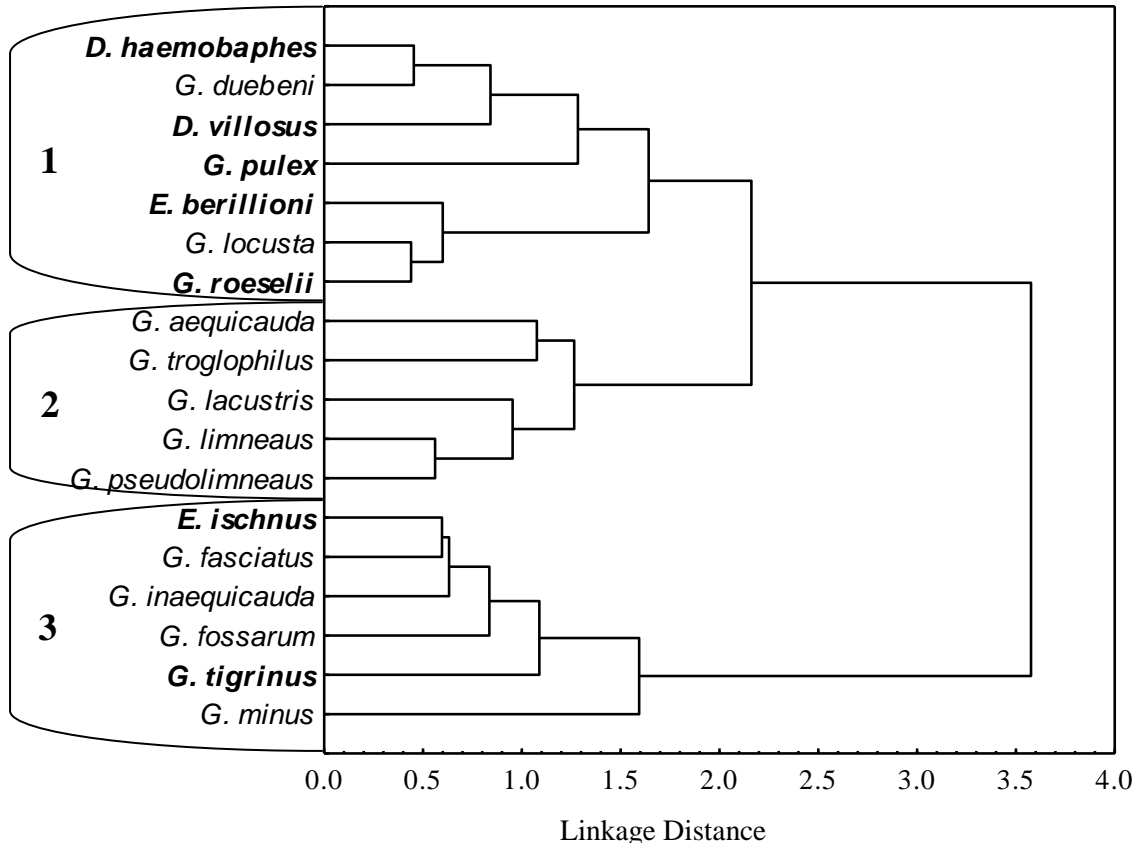


Figure 2.

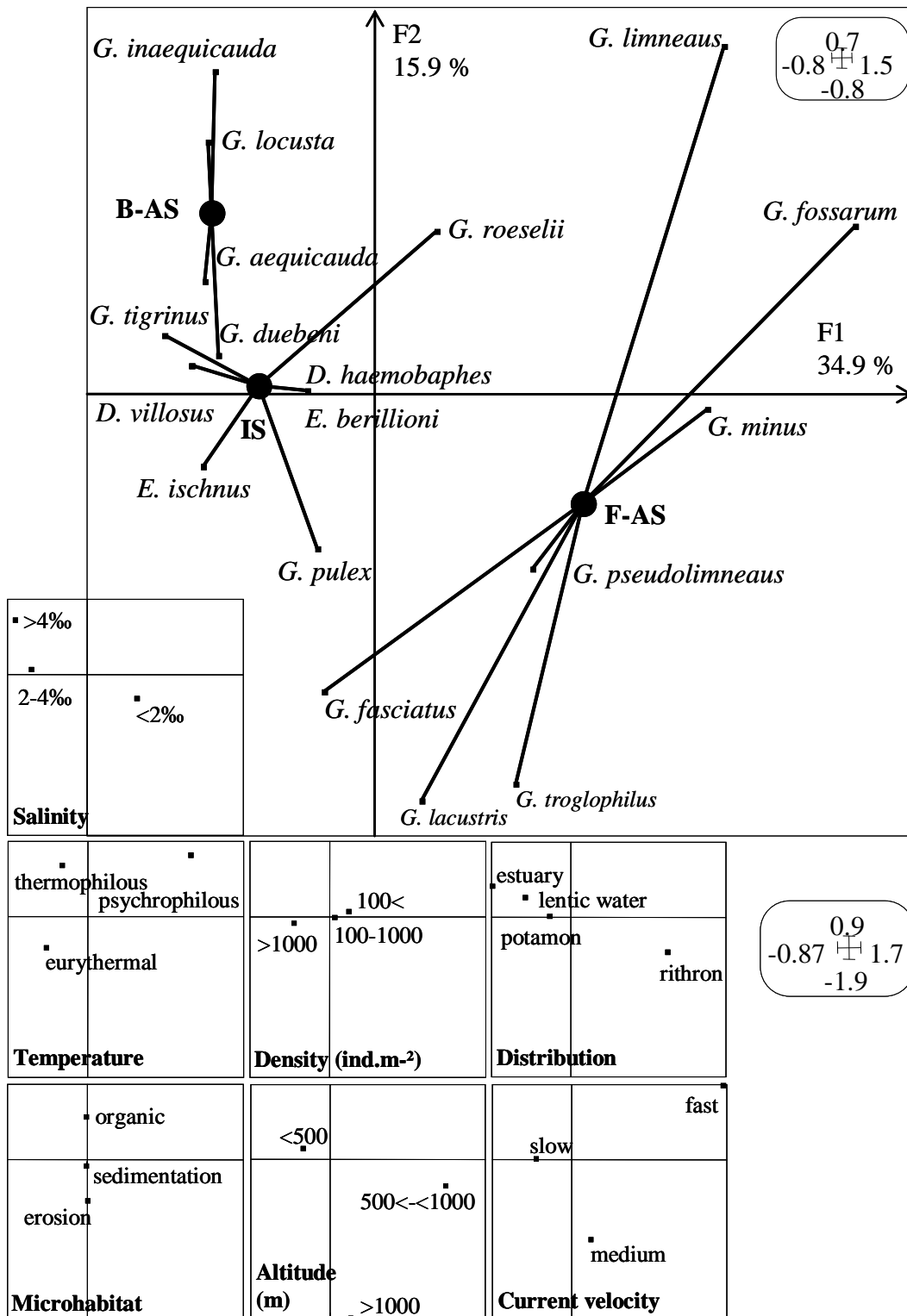


Figure 3.

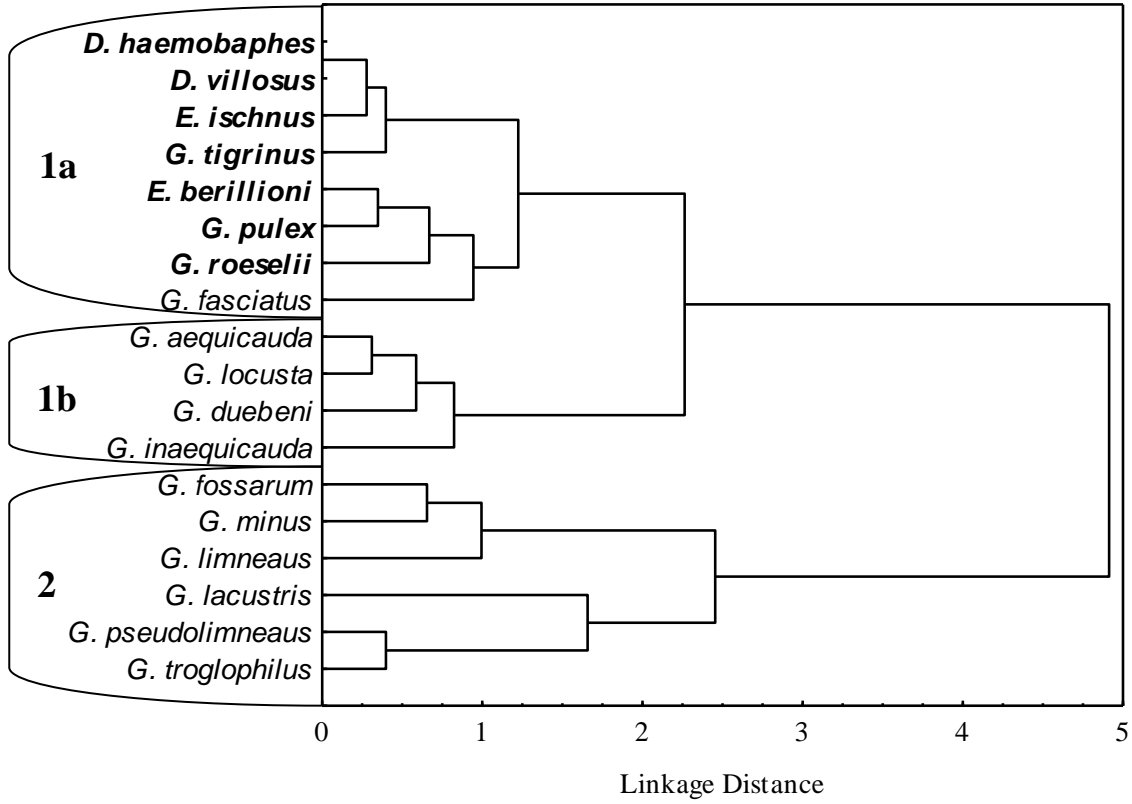


Figure 4.