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Use of invertebrate traits for the biomonitoring of European large rivers: the effects of sampling effort on genus richness and functional diversity

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1. Studies on biodiversity and ecosystem function require considering metrics for accurately describing the functional diversity of communities. The number of taxa (richness) is commonly used to characterise biological diversity. The disadvantage of richness as a measure of biological diversity is that all taxa are taken into account on an equal basis regardless of their abundance, their biological characteristics or their function in the ecosystem.

2. To circumvent this problem, we applied a recently described measure of biological diversity that incorporates dissimilarities among taxa. Dissimilarities were defined from biological traits (e.g. life history, morphology, physiology and behaviour) of stream invertebrate taxa and the resulting biological diversity index was considered as a surrogate for functional diversity.

3. As sampling effort is known to affect the number of taxa collected within a reach, we investigated how change in functional diversity is affected by sampling effort. We used stream invertebrate community data from three large European rivers to model accumulation curves and to assess the number of samples required to estimate (i.e. closeness to the maximal value) functional diversity and genera richness. We further evaluated the precision of estimates (i.e. similarity of temporal or spatial replicates) of the total functional diversity.

4. As expected, richness estimates were strongly dependent on sampling effort, and 10 replicate samples were found to underestimate actual richness. Moreover, richness estimates showed much variation with season and location. In contrast, functional diversity had greater accuracy with less sampling effort and the precision of the estimates was higher than richness both across sampling occasions and sampling reaches. These results are further arguments towards conducting research on the design of a biomonitoring tool based on biological traits.

Keywords: functional diversity, large river, macroinvertebrate community, sample effort, taxa richness

Introduction

Global extinction of species has prompted scientists to provide tools for evaluating biodiversity. Over the last decade, ecosystem management and European environmental policies have been orientated towards the enhancement of ecological functions across large geographical areas (Anonymous, 1999). Such objectives should benefit from theoretical and applied works which have focused on the functional diversity of communities using the life history traits of species (e.g. Corkum & Ciborowski, 1988; Statzner, Resh & Dolédec, 1994; Poff, 1997; Townsend, Dolédec & Scarsbrook, 1997; Minshall & Robinson, 1998; Statzner, Hildrew & Resh, 2001a; Usseglio-Polatera *et al.*, 2001; Snook & Milner, 2002).

A difficulty in reaching a consensus on the use of a universal index for measuring biodiversity suggests that different options be used (Duelli & Obrist, 2003), and the number of taxa (e.g. species richness) represents the simplest way to describe community diversity (Gotelli & Colwell, 2001). However, rare species are difficult to estimate and may disproportionately influence species richness (Gaston, 1994). The use of diversity indices such as Simpson (1949) or Shannon (1948) is complicated by the fact that some diversity metrics may give more weight to abundance while others may give more weight to the dominance of species (see e.g. Magurran, 1988). Finally, a major drawback of the use of both species richness and diversity indices is that all species are weighted equally regardless of their ecological function (see e.g. Hurlbert, 1971; Hill, 1973). Therefore, biodiversity indices usually account for neither the functional redundancy because of evolutionary constraints nor the biological differences among species associated to life history or physiology (Solow & Polasky, 1994).

A number of recent studies have focused on the use of Rao's quadratic diversity measure (Rao, 1982, 1986) for estimating species diversity (e.g. Izsak & Papp, 2000; Shimatami, 2001; Izsak & Szeidl, 2002). For example, from the complementary use of the unified theory of diversity of Rao and Euclidean metrics, Champely & Chessel (2002) proposed a diversity index, Euclidean diversity coefficient (EDC), that takes into account pairwise dissimilarities among species. Such dissimilarities take the form of a distance matrix, which enables the calculation of various biodiversity measures according to the type of similarity coefficient

used for characterising dissimilarities among species. For example, using traits for quantifying species differences may yield functional diversity, which in turn allows a shift from the usual biomonitoring of species towards the biomonitoring of ecosystem function (Ghilarov, 2000). However, few studies are based on an explicit measure of functional diversity (e.g. Diaz & Cabido, 2001; Petchey & Gaston, 2002; Bremner, Rogers & Frid, 2003).

When quantifying biodiversity we also need to consider the sampling effort required for estimating species richness (Elliott & Décamps, 1973; Willott, 2001; Cao, Williams & Larsen, 2002). Furthermore, sampling has to take into account the influence of environmental changes and the potential aggregation of organisms (Beisel *et al.*, 1998). The number of taxa at a site generally increases asymptotically with sampling effort, and accumulation curves have been used to illustrate this relationship (see e.g. Magurran, 1988; Vinson & Hawkins, 1996; Cao, Larsen & Hughes, 2001). Species accumulation curves are frequently used to estimate the expected number of species in a collection of samples, to estimate the minimum sample size required to characterise community diversity, to minimise sampling costs (Bartsch, Richardson & Naimo, 1998; Halse *et al.*, 2002) and as a means of data standardisation prior to among-site comparisons (e.g. Vinson & Hawkins, 1996; Gotelli & Colwell, 2001). Although the effect of sampling effort has been documented for species richness (Magurran, 1988) much less is known of how sampling effort may affect estimates of functional diversity.

In this paper we use aquatic invertebrate samples collected in different seasons and locations in three European large rivers to: (i) quantify functional diversity from the biological traits of aquatic stages of invertebrate species, (ii) compare sampling efforts required to achieve accuracy (i.e. closeness to the maximal value) for functional diversity and richness and (iii) evaluate the precision (i.e. similarity across replicates) of the estimates for both the functional diversity and richness.

Methods

Biological data

The invertebrate data were collected from three large (>40 m width) European rivers: the River Danube

(Fesl, Humpesch & Aschauer, 1999; Fesl, 2002; Humpesch, Fesl & Ruger, 2002), the River Rhine (Bournaud *et al.*, 1991) and the Loire River (France, M. Bacchi, pers. comm.).

Seasonal variation was assessed using data from a single reach of the River Danube (Bad Deutsch-Altenburg, Austria, 48°1'N, 16°9'E, located 1890 km from the mouth, width: 380 m). Ten quantitative macroinvertebrate samples from the river bottom were collected monthly (12 occasions) at four sampling points along a cross-section of the river with a modified Petersen grab (mean sampling area: 0.062 m²; mesh size: 0.2 mm; Humpesch, Anderwald & Petto, 1990). Inter-annual variation was assessed using data from a single reach on the River Rhine (Rhinau-Kappel, 48°3'N, 7°7'E, located 750 km from the mouth, width: 200 m). Microhabitats, including coarse and fine sediment and vegetation from the submerged bank, were sampled every kilometre according to the methodology of Bournaud & Coggerino (1986). Nineteen to 34 samples were collected in the old channel of the river (mean sampling area: 0.06 m²; mesh size: 0.5 mm) on six occasions between 1987 and 1990 (spring and summer seasons).

Spatial variation was considered using data collected from three reaches of the Loire River. These reaches were located at 612 km (Loire no. 1, 47°2'N, 3°0'E, width: 200 m) and at 297 km from the river mouth (Loire no. 2 and Loire no. 3, 47°3'N, 0°4'E, width: 300 m). Loire no. 1 and Loire no. 3 were located along the main course (free flowing) of the river, whereas Loire no. 2 was situated in a side arm connected to the main channel. In each of the Loire reaches, 33–42 samples were taken during July 1996 with a modified Surber type sampler (sampling area: 0.05 m²; mesh size: 0.5 mm).

All the macroinvertebrates were identified to species or the lowest practical taxonomic level. However, because of differences in taxonomic resolution and in sampling between the three data sets, we used a common basis for assemblage description. We selected the genus level as two previous studies (i.e. Doledec, Olivier & Statzner, 2000; Gayraud *et al.*, 2003) showed that species identification was not necessary for studies on functional diversity. Diptera and Oligochaeta were recorded to the family level in the Loire River, to the tribe level in the River Rhine and to the species level in the River Danube. Because of the poor knowledge on biological traits of Diptera and Oligochaeta, these two

groups were excluded from the functional description of assemblages. For the River Danube, we compared the accuracy and the precision of genus-level richness between the total data and the data excluding Diptera and Oligochaeta to check whether the exclusion of these groups affected the species accumulation curves. Moreover, we excluded the null sample (no taxa) in the simulations.

Biological traits of invertebrates

To describe the functional composition of assemblages we used 66 categories of 14 biological traits related to body morphology, life history, dissemination potential and feeding habits (Appendix). Data on traits were derived according to the available biological information on species (Doledec *et al.*, 2000; Statzner *et al.*, 2001b; Gayraud *et al.*, 2003). This information generally includes expert knowledge and various literature sources (Bournaud, Richoux & Usseglio-Polatera, 1992; Chevenet, Doledec & Chessel, 1994). A 'fuzzy coding' approach was used to quantify traits, where each genus was assigned an affinity (a_k) to each category ($1 \leq k \leq h$) for a given trait (Chevenet *et al.*, 1994). An affinity score of zero indicates no affinity, whilst an affinity score of three indicates a high affinity for a given trait category. For example, the final maximal body size of a species was classified into five length categories (Appendix). If all the individuals of a species were placed in one size category, affinity of that species was scored three. If most individuals were placed into one size category but a few were placed in a neighbouring category, the species would score two and one respectively, for the two categories. This information was treated as frequency distributions:

$$q_k = \frac{a_k}{\sum_{k=1}^h a_k} \text{ with } q_k \geq 0 \text{ and } \sum_{k=1}^h q_k = 1 \quad (1)$$

where q_k is the frequency of the trait category k ($1 \leq k \leq h$) and a_k is the assigned affinity.

Finally, we generated a set of biological traits for each genus by collating the affinities of species (frequencies) to the categories of each trait at the genus level. Overall, 283 genera were described completely in the trait database. The trait table was analysed with fuzzy correspondence analysis (Chevenet *et al.*, 1994) and we identified groups of genera

based on their biological traits using classification based on the Ward's linkage method (Ward, 1963).

Assessment of functional diversity

Ideally, functional diversity should be a measure of the functional differences among taxa in a community (Petchey & Gaston, 2002). Consequently, we assessed functional diversity of our invertebrate assemblages using the index developed by Champely & Chessel (2002). This index can be used to take dissimilarities among taxa into account based on their traits.

Consider a $N = [n_{ij}]$ community described by the occurrence of J taxa. Table $P = [p_{ij}]$ (with $p_{ij} = n_{ij} / \sum_{j=1}^J n_{ij}$) contains the frequencies of each taxon in each sample. Matrix $D = [d_{ij}]$ quantifies the distance (or difference) between the i th taxon and the j th taxon. Because of the general structure of the trait data sets, which are similar to tables that contain allele frequencies, we computed the dissimilarity among genera for each trait using the Edwards distance, a measure currently used for evaluating genetic distances among loci within a population (Edwards, 1971). As a result, the dissimilarity between the i th taxon and the j th taxon for a given biological trait was calculated as:

$$d_{ij} = \sqrt{1 - \sum_{k=1}^h \sqrt{q_{ik}} \sqrt{q_{jk}}} \quad (2)$$

where q_{ik} (or q_{jk}) is the frequency of the trait category k ($1 \leq k \leq h$) for the genus i (or j).

In Equation (2), d_{ij} ranges between zero, if the trait categories are identical in their proportion between taxon i and taxon j , and one, if the trait categories differ completely in their proportion between these two taxa. We calculated a dissimilarity matrix for each of the 14 traits to provide a full description of the functional diversity of invertebrate genera. The 14 individual matrices (eqn 2) were combined through their quadratic mean (Hartl & Clark, 1989) to derive a global dissimilarity matrix of biological traits, as:

$$D_t = \sqrt{\frac{1}{t} \sum_{s=1}^t D_s^2} \quad (3)$$

where t corresponds to the number of biological traits ($t = 14$ in our example). From eqn 3, we computed our functional diversity index for sample s as:

$$\frac{1}{2} \sum_{j_1=1}^J \sum_{j_2=1}^J p_{sj_1} p_{sj_2} (d_t)_{j_1 j_2}^2 \quad (4)$$

Finally, to evaluate the potential effect of rare genera on functional diversity, we estimated the differences of biological traits between rare and common genera for each sampling occasion. In our study, a genus was considered rare when its occurrence was less or equal to the first quartile (25%) on a given sampling occasion. Principal coordinate analysis (Gower, 1966) was done on each matrix of dissimilarity for each sampling occasion. Finally, we computed the between-groups inertia percentage (with group equal as rare or common) and compared the observed value to 999 simulated values (Romesburg, 1985).

Simulations and accuracy

A resampling procedure was used to simulate an increase in sampling effort (i.e. increase in the number of samples) and to compute accumulation curves for functional diversity and genus richness. For a given sampling effort, samples were randomly drawn 100 times without replacement. The resulting 100 simulated values of functional diversity (or genus richness) were averaged to provide a mean functional diversity (or genus richness) (see e.g. Cao *et al.*, 2001). As the functional diversity and the genus richness differed in their range of variation, we standardised their values between zero and one by dividing the functional diversity and genus richness by the maximal value calculated from all the samples. For a given number of samples the value on the standardised accumulation curve corresponded to a proportion of the total functional diversity (or genus richness) and thus represented accuracy (i.e. closeness to the maximal value).

Modelling and precision

We considered two types of models to assess the precision of our estimates of taxon richness and functional diversity, i.e. the stability in space or time of the standardised accumulation curves for a given sampling effort. We first computed a model common (5) for all the samples as:

$$f(k) = \frac{a \cdot k}{b + k} + \varepsilon \quad (5)$$

where k is the number of samples, a is the asymptote of the model (i.e. maximal standardised functional diversity or genus richness), b is the saturation factor (i.e. the value of k for which $f(k) = 1/2a$) and ε represents the error. Secondly, we computed a complete model (6) as:

$$f(k) = \frac{(\sum_{i=1}^h a_i \cdot S_i)k}{(\sum_{i=1}^h b_i \cdot S_i) + k} + \varepsilon \quad (6)$$

where a_i and b_i vary as a function of the sampling occasions or locations and S_i gives the membership ($S_i = 1$ for the i th sample and $S_i = 0$ for the others) of a sample for a sampling occasion or location.

To assess the significance of the differences among samples, we compared the deviance of the individual accumulation curves (for each sampling occasion or each location) to the common model using the Bayesian information criterion (7):

$$\text{BIC} = -2 \cdot LL + n_{\text{par}} \cdot \log(n_{\text{obs}}) \quad (7)$$

where LL is the log-likelihood value of the model, and n_{par} and n_{obs} are the number of parameters and

the number of observations, respectively (Schwarz, 1978).

All the routines necessary for calculating functional diversity, performing simulations and computing accuracy and modelling precision were implemented in the R freeware (<http://www.r-project.org/>; Ihaka & Gentleman, 1996). The sources of the R code are available from the first author. Fuzzy correspondence analysis, Principal coordinate analysis and permutation tests are available in the 'ade4' library.

Results

In the River Danube, the maximum taxa richness ranged between eight and 11 genera per sample, after the exclusion of Diptera and Oligochaeta (Table 1a), and the average richness per sample ranged between 3.3 and 5.9 genera (Table 1b). In comparison, the Loire River and the River Rhine had higher genus richness (excluding Diptera and Oligochaeta). The average richness per sample from the Loire River reaches ranged between 4.8 and 8.6 genera (Table 1b) and

Table 1 Richness characteristics based on genera collected from the River Loire, the River Danube and the River Rhine

Sampling occasion	date	(a)	(b)	(c)	(d)	(e)	(f)	(g)
Danube no. 1	September 1995	9	3.8	44	8	13	17	405
Danube no. 2	October 1995	10	5.9	65	8	15	21	535
Danube no. 3	November 1995	11	4.3	63	9	14	17	1525
Danube no. 4	December 1995	11	4.1	47	7	11	16	1737
Danube no. 5	January 1996	8	3.8	50	8	11	15	182
Danube no. 6	February 1996	11	4.1	50	8	14	18	349
Danube no. 7	March 1996	10	3.9	58	8	10	14	515
Danube no. 8	April 1996	9	3.9	49	9	11	15	302
Danube no. 9	May 1996	10	3.3	63	8	10	13	524
Danube no. 10	June 1996	8	3.7	56	7	12	15	459
Danube no. 11	July 1996	9	2.9	47	8	11	14	582
Danube no. 12	August 1996	9	4.8	58	7	12	15	376
Rhine no. 1	October 1987	17	7.4	–	17	35	48	2975
Rhine no. 2	July 1988	24	9.0	–	16	36	50	2174
Rhine no. 3	December 1988	15	5.9	–	13	24	29	1075
Rhine no. 4	July 1989	23	10.6	–	15	32	46	1817
Rhine no. 5	February 1990	25	8.8	–	18	32	45	1275
Rhine no. 6	July 1990	16	9.6	–	16	31	44	1211
Loire no. 1	July 1996	22	8.6	–	12	28	43	3379
Loire no. 2	July 1996	13	4.8	–	11	24	36	2477
Loire no. 3	July 1996	15	7.3	–	10	27	40	4831

a, maximum richness observed in one sample (without Diptera and Oligochaeta); b, average richness per sample (without Diptera and Oligochaeta); c, total richness including Diptera and Oligochaeta (Diptera and Oligochaeta not identified to the genus in the Loire River and in the River Rhine); d, total number of orders; e, total number of families; f, total number of genera without Diptera and Oligochaeta; g, average density per sample without Diptera and Oligochaeta (individuals m^{-2}).

maximal richness ranging between 13 and 22 genera (Table 1a). In comparison, samples of the River Rhine had an average richness per sample ranging between 5.9 and 10.6 genera and a maximal richness ranging between 15 and 25 genera (Table 1b). Differences in sampling methods may explain the variation of richness between the River Danube (sampled mainly in the channel) and the two others rivers (sampled mainly along the banks). Although exclusion of Diptera and Oligochaeta from the River Danube data set resulted a significant decrease in genera richness (Table 1c,d), correlation between the total simulated genus richness (with Diptera and Oligochaeta) and the simulated genus richness without these groups was high ($r = 0.83$, $P < 0.001$).

The first two axes of a fuzzy correspondence analysis performed on the biological traits of genera accounted for 21.8% of the total variability (Fig. 1a,

insert). Groups of genera differed in their traits along these two axes. The majority of insects including Trichoptera, Ephemeroptera, Plecoptera and Odonata were opposed along the first axis to other insects (Coleoptera and Heteroptera), Turbellaria, Hirudinea, Mollusca and Crustacea (Fig. 1b). Gastropoda and Crustacea genera were further separated from other taxa along the second axis. Classification confirmed the separation of genera into three entities (Fig. 1c). Traits contributing strongly to the separation of the groups along the first axis included reproductive characteristics (number of descendants per reproductive cycle, the number of cycles per individual and the life duration of adults). Parental care, flexibility of body and feeding habit could be added to these traits as their categories separated genera along the second axis. For example, group one (Mollusca Bivalvia and Crustacea) included genera having many descendants

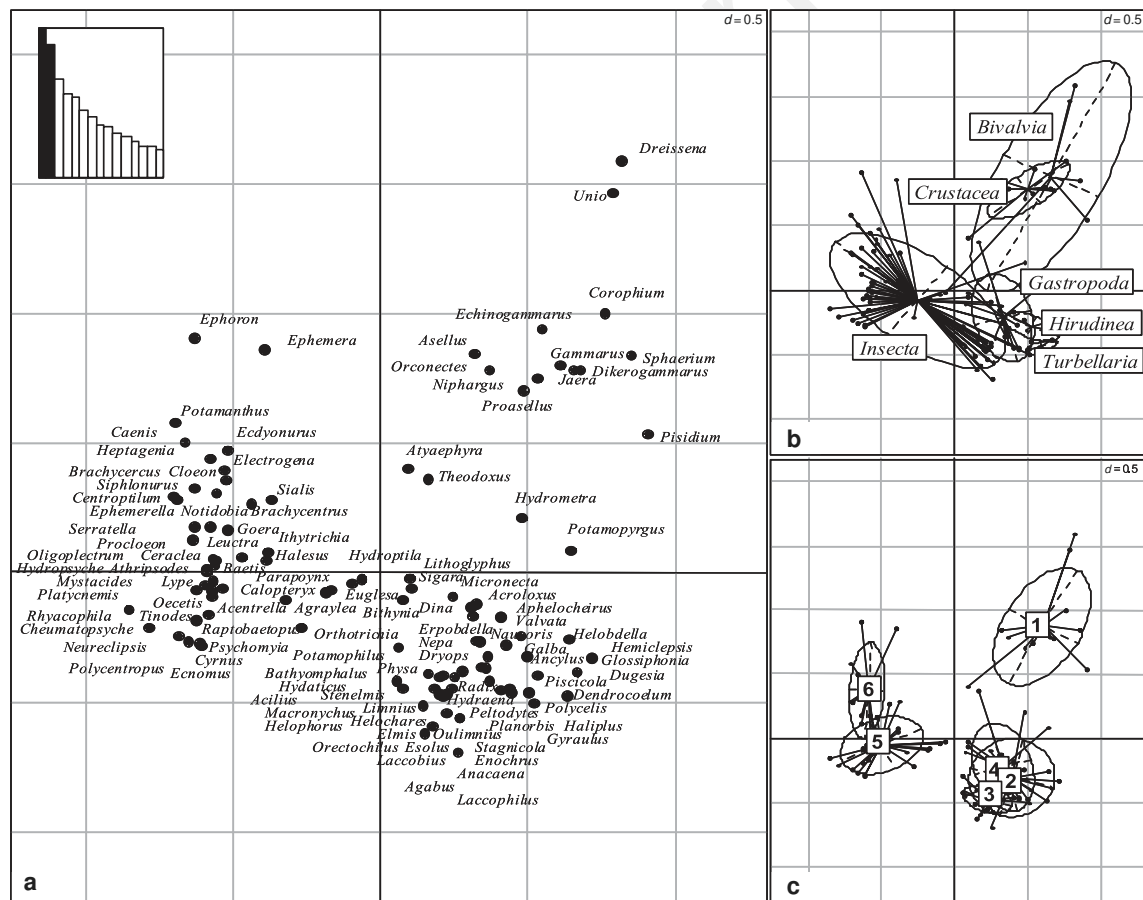


Fig. 1 Results of a fuzzy correspondence analysis of the biological trait table. (a) First factorial plane of the position of genera. Insert gives the histogram of eigenvalues. (b) Similar plane with genera grouped according to taxonomy. (c) Similar plane with genera grouped according to the six clusters identified by Ward's classification. In (b) and (c) each group is summarised by an ellipse.

per reproductive cycle (>3000), more than two cycles per individual, long-living adults and demonstrating ovoviviparity and were active filter-feeders. Groups 2–4 (Coleoptera, Heteroptera, Turbellaria, Hirudinea and Mollusca Gastropoda) were characterised by fewer descendants (<100), various types of egg deposition and possibly bud production (Turbellaria), higher flexibility of the body and frequently fed as piercers. Groups 5 and 6 (most insect genera) separated on the left side of the first axis and were characterised by many descendants per reproductive cycle (100–3000), one reproductive cycle per individual, short-living adults possibly depositing isolated eggs and having various feeding habits.

Finally, we evaluated the potential effect of rare genera on functional diversity by comparing the variance of biological traits between rare and common taxa. Low ratios of between to total variance (1.4–15.8%; Table 2) showed that rare genera generally had a close structure in their biological traits to that of common genera (Table 2). Permutation tests showed that only four tests out of 21 (Table 2) demonstrated a slight difference between rare and common taxa. For two of these tests, significance was close to $P = 0.05$. These results suggest an overall overlap of the traits between rare and common genera.

Seasonal variation (Danube reach)

Richness curves did not reach a plateau for any sampling occasion and differences among sampling occasions were evident (Fig. 2a). For example, a higher number of genera per sample was found in October (Danube no. 2; Fig. 2a) compared with other samplings occasions. In contrast, functional diversity tended to reach a plateau in a similar way across all sampling occasions and differences in the overall functional diversity between sampling occasions were weak (at both extremes, 20.7% for Danube no. 10 and 23.5% for Danube no. 12; Fig. 2b).

As expected, accuracy (i.e. the proportion of the maximum value) increased with sampling effort for all sampling occasions (Table 3). However, the increase was less for richness than for functional diversity (Danube; Table 3). For example, using one random sample, the richness accuracy ranged between 17.5 and 30.9%, whereas the functional diversity accuracy ranged between 36.6 and 82.5%. The standard deviation of richness accuracy calculated over 12 sampling occasions remained constant along with sampling effort, whereas the standard deviation of functional diversity accuracy decreased significantly (Table 3). Functional diversity accuracy aver-

Table 2 Effect of rare taxa on functional diversity. The 'total inertia', 'between-groups inertia', 'ratio' and 'P-value' correspond to the total inertia of the matrix of distance among genera, inertia explained by groups (rare or common), the ratio between 'between-groups inertia' and 'total inertia' and the P-values of the permutation tests (number of repetitions is equal to 999), respectively. The two last columns 'rare genera number' and 'common genera number' indicate for each sampling occasion the number of genera considered rare and common, respectively. $P < 0.05$ values in bold.

Sampling occasion	Total inertia	Between-groups inertia	Ratio (%)	P-value	Number of rare genera	Number of common genera
Danube no. 1	0.233	0.018	0.078	0.236	7	10
Danube no. 2	0.223	0.022	0.097	0.040	6	15
Danube no. 3	0.223	0.016	0.071	0.315	5	12
Danube no. 4	0.225	0.010	0.046	0.776	5	11
Danube no. 5	0.232	0.019	0.083	0.319	4	11
Danube no. 6	0.228	0.013	0.056	0.465	6	12
Danube no. 7	0.230	0.024	0.106	0.141	4	10
Danube no. 8	0.231	0.023	0.101	0.135	5	10
Danube no. 9	0.232	0.025	0.108	0.172	5	8
Danube no. 10	0.209	0.010	0.047	0.757	4	11
Danube no. 11	0.234	0.037	0.158	0.019	6	8
Danube no. 12	0.241	0.014	0.059	0.610	4	11
Rhine no. 1	0.233	0.005	0.020	0.492	15	33
Rhine no. 2	0.240	0.003	0.014	0.840	19	31
Rhine no. 3	0.235	0.017	0.074	0.012	12	17
Rhine no. 4	0.239	0.007	0.028	0.226	12	34
Rhine no. 5	0.226	0.005	0.023	0.407	12	33
Rhine no. 6	0.236	0.010	0.042	0.044	14	30
Loire no. 1	0.220	0.004	0.017	0.830	13	30
Loire no. 2	0.236	0.008	0.035	0.220	13	23
Loire no. 3	0.219	0.004	0.020	0.646	15	25

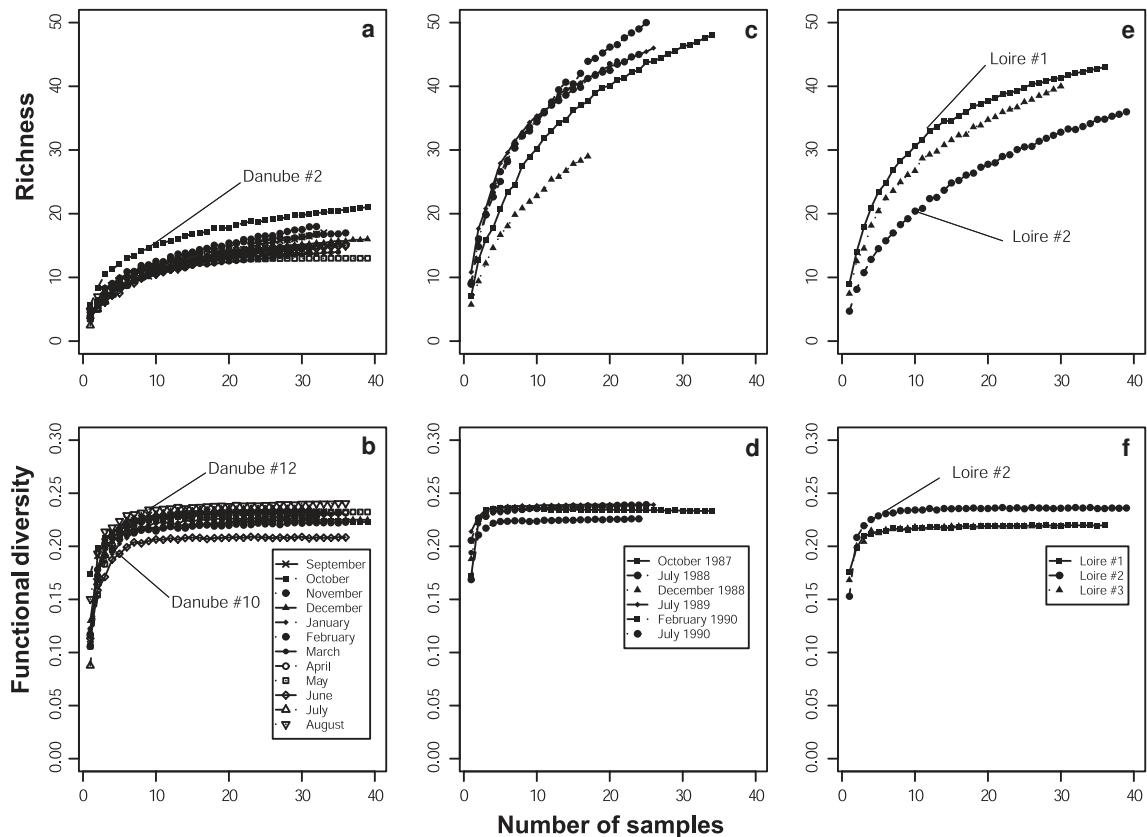


Fig. 2 Results of the simulations of richness (upper row) and functional diversity (lower row) in the River Danube (a, b), the River Rhine (c, d) and the Loire River (e, f) as a function of the sampling effort.

aged 92.4% with five random samples and 97.2% with 10 random samples. By contrast, average richness accuracy reached only 56.7% with five random samples and 72.8% with 10 random samples. Furthermore, as the number of samples increased from one to five the average functional diversity increased by 35.2%, whereas as the number of samples increased from five to 10 the mean functional diversity increased by only 4.8%. Similarly, values for average genus richness were 21.9 and 16.1% respectively (Table 3a).

The common and complete models demonstrated low residual standard errors for both genus richness and functional diversity (≤ 0.05 ; Table 4). The R^2 -values between the observed and adjusted values of both functional diversity and genus richness were $>90\%$ (Table 4). The complete model (i.e. including variation across the sampling occasions) of the functional diversity yielded a higher BIC than the common model (i.e. all the sampling occasions pooled together) demonstrating differences in functional diversity

across seasons (Table 4b). However, the differences between the two models were mainly because of the deviation of the second sampling occasion (Danube no. 2, see Fig. 3b). Moreover, these differences occurred only for a small number of samples and precision (i.e. degree of variation across sampling occasions) increased for about 10 random samples (Fig. 3b). In contrast, genus richness differed more between sampling occasions (BIC-values, see Table 4a; Fig. 3a), in spite of a good fit of the common model ($R^2 = 0.946$; Table 4a). Differences in R^2 -values remained relatively small (Table 4a).

Interannual variation (Rhine River reach)

Patterns of the data used to evaluate inter-annual variation were similar to those of the River Danube data (Fig. 2c,d). Using one random sample, the richness accuracy ranged between 14.7 and 23.5%, whereas the functional diversity accuracy ranged between 72.7 and 89.4% (Rhine; Table 3). The stand-

Table 3 (a) Richness and (b) functional diversity accuracies calculated for the three data sets

River	Sample no.	(a)			(b)		
		1	5	10	1	5	10
Danube	1	22.1 (± 14.5)	48.8 (± 11.4)	62.7 (± 10.0)	51.8 (± 37.8)	94.1 (± 7.8)	97.7 (± 5.5)
	2	28.1 (± 11.5)	58.5 (± 9.1)	72.7 (± 7.8)	76.2 (± 23.2)	96.4 (± 5.8)	99.2 (± 3.5)
	3	23.1 (± 16.5)	59.4 (± 15.2)	74.7 (± 10.7)	54.5 (± 39.8)	94.6 (± 4.6)	97.3 (± 3.9)
	4	24.6 (± 16.3)	56.5 (± 13.4)	74.4 (± 10.6)	66.7 (± 35.0)	92.9 (± 8.6)	96.7 (± 4.4)
	5	26.6 (± 12.6)	57.3 (± 13.0)	73.9 (± 8.6)	52.5 (± 28.2)	85.2 (± 11.7)	95.3 (± 5.7)
	6	23.1 (± 14.6)	50.4 (± 13.9)	67.4 (± 12.3)	46.3 (± 30.1)	89.3 (± 9.0)	95.2 (± 4.8)
	7	29.9 (± 16.3)	60.4 (± 15.3)	74.7 (± 12.5)	58.7 (± 32.6)	90.5 (± 11.6)	96.3 (± 4.4)
	8	17.5 (± 17.0)	49.8 (± 14.0)	68.3 (± 11.4)	82.5 (± 35.7)	98.0 (± 9.4)	98.9 (± 3.8)
	9	27.5 (± 18.2)	64.5 (± 16.8)	83.3 (± 11.4)	46.1 (± 36.3)	91.2 (± 13.5)	96.9 (± 5.7)
	10	24.7 (± 11.4)	50.8 (± 13.4)	66.6 (± 11.7)	54.8 (± 31.1)	92.5 (± 10.7)	98.2 (± 3.5)
	11	19.6 (± 13.9)	59.9 (± 16.1)	79.2 (± 14.1)	36.6 (± 36.7)	91.0 (± 10.8)	97.6 (± 4.4)
	12	30.9 (± 16.2)	64.9 (± 10.9)	75.9 (± 9.2)	60.0 (± 29.3)	93.2 (± 7.1)	97.6 (± 2.5)
	Mean (SD)	24.8 (± 4.0)	56.7 (± 5.6)	72.8 (± 5.7)	57.2 (± 12.9)	92.4 (± 3.4)	97.2 (± 1.3)
Rhine	1	14.7 (± 8.8)	43.2 (± 8.1)	62.9 (± 7.8)	72.7 (± 34.8)	100 (± 2.1)	100 (± 1.6)
	2	17.9 (± 11.3)	50.1 (± 12.9)	68.8 (± 10.5)	85.8 (± 19.0)	97.4 (± 2.7)	98.3 (± 2.0)
	3	19.8 (± 14.0)	57.5 (± 12.9)	78.5 (± 9.0)	79.6 (± 27.1)	99.2 (± 2.6)	99.9 (± 1.6)
	4	23.5 (± 11.1)	60.7 (± 8.2)	76.9 (± 6.5)	89.4 (± 13.3)	99.0 (± 2.1)	99.6 (± 1.4)
	5	20.1 (± 15.2)	59.1 (± 11.2)	77.4 (± 7.1)	74.7 (± 30.9)	98.9 (± 2.4)	99.0 (± 1.3)
	6	21.4 (± 9.8)	60.8 (± 7.3)	79.1 (± 5.5)	82.0 (± 23.4)	98.0 (± 2.4)	99.4 (± 1.3)
	Mean (SD)	19.5 (± 3.0)	55.2 (± 7.1)	73.9 (± 6.6)	80.7 (± 6.4)	98.7 (± 0.9)	99.3 (± 0.6)
Loire	1	20.1 (± 11.7)	53.5 (± 10.7)	70.2 (± 9.6)	84.8 (± 18.7)	96.1 (± 3.9)	98.4 (± 1.9)
	2	13.2 (± 8.4)	40.1 (± 8.6)	57.3 (± 7.9)	63.9 (± 28.3)	96.7 (± 3.0)	98.9 (± 2.6)
	3	17.1 (± 9.2)	49.3 (± 9.2)	68.0 (± 7.5)	78.9 (± 21.0)	97.9 (± 6.0)	99.0 (± 2.8)
	Mean (SD)	16.8 (± 3.5)	47.6 (± 6.8)	65.2 (± 6.9)	75.9 (± 10.8)	96.9 (± 1.0)	98.8 (± 0.3)

The estimates were computed for 1, 5 and 10 replicates, respectively. Standard deviations (SD) are indicated in brackets.

Table 4 Characteristics of the common and complete models of the standardised richness (a) and functional diversity (b)

River	Model	d.f.	(a)				(b)			
			RSE	Deviance	R^2	BIC	RSE	Deviance	R^2	BIC
Danube	Common	419	0.045	0.832	0.946	-1414.6	0.029	0.345	0.903	-1785.2
	Complete	397	0.026	0.273	0.983	-1750.1	0.021	0.177	0.951	-1932.1
Rhine	Common	145	0.055	0.441	0.937	-426.6	0.018	0.048	0.796	-751.9
	Complete	135	0.016	0.036	0.996	-746.7	0.016	0.034	0.855	-752.4
Loire	Common	103	0.052	0.283	0.943	-313.9	0.016	0.026	0.892	-564.8
	Complete	99	0.020	0.039	0.993	-502.8	0.013	0.016	0.933	-596.3

d.f., degree of freedom; RSE, residual standard error of the model; deviance, sum of the squared residuals to the fitted model; R^2 , squared correlation coefficient between the observed and adjusted values; BIC, Bayesian information criterion.

ard deviation of richness accuracy remained relatively constant or increased as a function of sampling effort (between one and five samples), whereas the standard deviation of functional diversity accuracy decreased (Table 3). The average functional diversity accuracy reached 98.7% with only five random samples. In contrast, richness accuracy equalled 55.2 and 73.9% with five and 10 random samples, respectively.

he complete and common models fitted well with the observed standardised richness and functional diversity for the six sampling occasions ($R^2 > 0.79$; Table 4).

For standardised richness, the complete model differed between the sampling occasions (Table 4a; Fig. 3c), whereas for standardised functional diversity, the difference was weak (Table 4b; Fig. 3d) and deviation low (BIC-values; Table 4b), suggesting an almost equal accuracy for the six sampling occasions.

Spatial variation (Loire reaches)

Similarly to the other two data sets, differences of saturation occurred between functional diversity

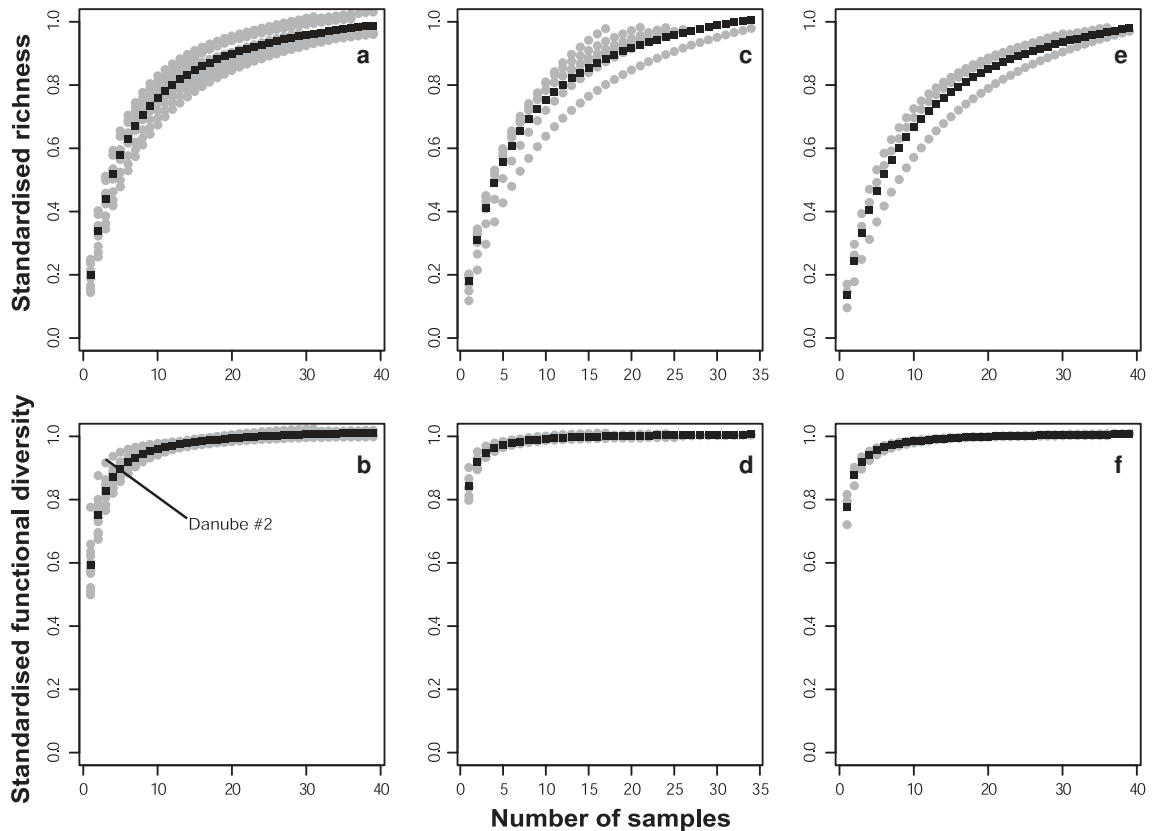


Fig. 3 Modelling of the standardised richness and the standardised functional diversity in the River Danube (a, b), the River Rhine (c, d) and the Loire River (e, f) as a function of the sampling effort. Grey symbols correspond to the complete models (one curve per sampling occasion or sampling site) and dark symbols correspond to the common models (one curve per data set).

(Fig. 2f) and richness (Fig. 2e) accumulation curves. Moreover, Loire reach no. 2, although exhibiting lower genus richness (Fig. 2e,f) demonstrated a slightly higher functional diversity than the other reaches. Using one random sample, richness accuracy ranged between 17.1 and 20.1% (Loire; Table 3a), whereas functional diversity accuracy ranged between 63.9 and 84.8% (Loire; Table 3b). The standard deviation of richness accuracy calculated for the three reaches remained relatively constant across sampling effort (increased from one to five), whereas the standard deviation of functional diversity accuracy decreased significantly (Table 3). Nearly 97% of the total functional diversity was achieved with only five random samples (Table 3b), and 98.8% was achieved with 10 random samples. By contrast, richness accuracy reached 47.6 and 65.2% with five and 10 random samples, respectively. Finally, as the number of samples increased from one to five, mean functional diversity increased by 21.0% and as the number of

samples increased from five to 10, mean functional diversity increased by only 1.9%. Equivalent values of 30.8 and 17.6%, respectively, were recorded for the mean richness (Table 3).

The common and complete models fitted well with the observed standardised richness and functional diversity for the three locations ($R^2 > 0.89$; Table 4), although the complete models had smaller BIC-values (Table 4). The richness model differed slightly for Loire reach no. 2 (Fig. 3e), whereas the difference was less obvious for functional diversity (Fig. 3f). In the latter case, BIC-values of the common and complete models were close and deviances were low (Table 4).

Discussion

Biological diversity assessment

Several authors have stressed the need for taking into account the magnitude of interspecific difference in

the design of diversity indices (e.g. Izsak & Papp, 2000; Shimatami, 2001). Approaches developed by Solow & Polasky (1994) and further expanded on by Champely & Chessel (2002) through the EDC are explicit proposals for fulfilling the above recommendations. The diversity index used in the present study was based on genus dissimilarities. However, EDC is far more general as it may be expanded to several types of distances. For example, studying marine nematode communities, Warwick & Clarke (1995) emphasised the limitation of common metrics of diversity for evaluating the integrity of ecosystems. They used the average taxonomic path length between pairs of individuals to define taxonomic diversity. The use of taxonomic or phylogenetic distances in the central distance matrix of EDC would yield taxonomic diversity as well.

We used biological traits (at the genus level) to quantify pairwise differences between taxa. Similarly, Petchey & Gaston (2002) have designed a functional diversity index from the total branch length of a dendrogram obtained from UPGMA performed on a trait matrix. Our trait matrix describes organism functions that may be linked to ecosystem function. For example, maximal size indicates the ratio of production/biomass and of production/respiration (Statzner, 1987). EDC derived from differences among pairwise taxa based on their traits thus represents an index of functional diversity. Finally, the critical advantage of using EDC over existing techniques is its clear mathematical definition, which meets the actual ecological needs of providing a standardised measure of biodiversity, which may apply at various organisational levels (from genes to communities).

Sampling effort

Community ecologists must frequently rely on estimates that describe some portion of the real composition of communities and the goal of sampling is to make these estimates as accurate as possible (Magurran, 1988). It has been shown elsewhere that taxon richness accuracy increases asymptotically with the number of samples taken from different habitats (e.g. Vinson & Hawkins, 1996; Li *et al.*, 2001). In our study, ten samples yielded 50% of the total richness (omitting Diptera and Oligochaeta) on one sampling occasion (River Danube or River Rhine) or at one location (Loire River). In small rivers (width <8 m), Li

et al. (2001) demonstrated that new taxa could be added in stream reaches after counting more than 50 samples. By contrast, Bradley & Ormerod (2002) studying second to third order streams detected about 70% of the taxa with one (combined riffle and margin sample) out of only five samples. Rather than the estimation of the number of taxa, we were interested in comparing the sampling accuracy and precision between taxon richness, a commonly used index of biodiversity, and a functional diversity index. In our example, contrasting with genus richness, almost 100% of the total functional diversity was obtained with 10 samples and five samples were adequate to obtain >90% of the functional diversity. Even with only one sample, functional diversity sampled more of the variability than genera richness (Table 2). Thus, estimates of functional diversity had greater accuracy than those genus richness because of trait similarity among genera and to the influence of abundant genera, which traits and ecological functions are given a prominent weight. Such a high accuracy could also result from a high degree of generality among the biological traits (i.e. all genera are considered to be functionally similar). However, Usseglio-Polatera *et al.* (2000) were able to show differences in traits among genera and could group genera according to specific strategies. In our study, the analysis of the matrix of dissimilarity and a classification procedure (Fig. 1) confirms the existence of groups of genera characterised by various life-history strategies that do not strictly overlap with taxonomy.

Comparison between the common and complete models underlined differences between sampling occasions for both genus richness and functional diversity, which suggests that precision varies with sampling effort. The instability of taxon richness was evident across sampling occasions. In contrast, precision was generally higher for functional diversity and increased with sampling effort so that each individual curve converged towards a similar asymptote. Besides temporal differences, spatial differences also affected richness estimates, whereas spatial differences were less obvious for functional diversity accuracy. Moreover, functional diversity demonstrated a high precision across reaches. For example, free-flowing reaches 400 km apart demonstrated close values of functional diversity, which support the spatial stability of the functional structure already observed across Europe (e.g. Statzner *et al.*, 2001b).

Our results suggest that functional diversity is a more reliable measure than taxon richness in describing communities using a small number of samples. Moreover, as species richness is often driven by rare species, a loss of species richness (in terms of rare species) may not severely change or impair the functionality of a stream community. This latter result shows the difficulty in making a causal connection between species diversity and ecosystem function and gives further argument to investigating whether functional characteristics of species take precedence over the number of species as a measure of this relationship (Grime, 1997).

Implications for biodiversity assessment of aquatic ecosystems

The use of biological traits in monitoring programs is only in its experimental phase (Dolédéc, Stätzner & Bournaud, 1999; Charvet *et al.*, 2000; Stätzner *et al.*, 2001b; Gayraud *et al.*, 2003), and at least two key elements may contribute to an operational monitoring tool based on aquatic invertebrate assemblages: (i) the taxonomic level and (ii) the number of samples needed for an accurate estimate of biological characteristics. Dolédéc *et al.* (2000) and Gayraud *et al.* (2003) have demonstrated that the use of a higher taxonomic level such as genera or even family has little effect on the functional response of invertebrate communities. In this paper, we show that five to 10 samples are sufficient for estimating the functional diversity in three European large rivers. Further studies are needed, however, to demonstrate whether such results apply along the entire course of rivers.

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Appendix 1 Biological traits and descriptions of the categories used to quantify biological differences among genera and functional diversity

No.	Biological trait	Category
1	Body size	≤5 mm >5–10 mm >10–20 mm >20–40 mm >40 mm
2	No. of descendants per reproductive cycle	≤100 >100–1000 >1000–3000 >3000
3	Reproductive cycle	≤ Bivoltine Univoltine ≥ Semivoltine
4	No. of reproductive cycles per individual	1 2 >2
5	Life duration of adults	≤1 day >1–10 days >10–30 days >30–365 days >365 days
6	Reproductive technique	Single individual Hermaphroditism Male and female
7	Parental care	Bud production Isolated eggs

Appendix 1 (Continued)

No.	Biological trait	Category
8	Dissemination potential in the water	Eggs in vegetation
		Cemented terrestrial eggs
		Cemented aquatic eggs
		Ovoviviparity
		≤10 m
9	Attachment to substrate	>10–100 m
		>100–1000 m
		>1000–10 000 m
		>10 000 m (by ships)
		Swimmer
10	Body flexibility	Crawler
		Burrower
		Temporary
		Permanently
11	Body form	None (≤10°)
		Low (>10–45°)
		High (>45°)
11	Body form	Streamlined
		Flattened
		Cylindrical

Appendix 1 (Continued)

No.	Biological trait	Category
12	Feeding habits	Spherical
		Engulfer
		Shredder
		Scraper
		Deposit-feeder
13	Food	Filter-feeder, active
		Filter-feeder, passive
		Piercer
		Detritus ≤1 mm
		Detritus >1–10 mm
		Detritus >10 mm
		Plants ≤1 mm
		Plants >1–10 mm
		Plants >10 mm
		Animals ≤1 mm
Animals >1–10 mm		
14	Respiration technique	Animals >10 mm
		Tegument
		Gill
		Plastron
		Aerial