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MACRO-INVERTEBRATE FUNCTIONAL GROUPS IN FRESHWATER AND MARINE SEDIMENTS: A COMMON MECHANISTIC CLASSIFICATION

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AQUATIC SEDIMENTS
MARINE AND FRESHWATER SEDIMENTS
FUNCTIONAL GROUPS
MACRO-INVERTEBRATES
BIOTURBATION

ABSTRACT. – Functional group definitions in aquatic ecology vary depending on the type of ecosystem (e.g., marine compared to fresh water ecosystems, stream compared to lake ecosystems). Since the benthic environment functions as the major storage and recycling compartment for virtually all material that flows in the aquatic system, biological processes that take place there are interesting models for identification of the different invertebrate functions. The accurate species function includes the effects of an organism on the abiotic as well as the biotic properties of the habitats. Therefore, a functional group may be defined as a group of species that share common biogeochemical and interspecific attributes. The main difficulty of applying this definition in aquatic ecosystems comes from the high diversity of organism functions (compared to terrestrial systems) that potentially exist at different levels: i) interspecific diversity supported by the large morphological and behavioural diversity of organisms, reinforced by a low degree of species redundancy; ii) intraspecific functional diversity due to changes in life history strategy during the life cycle, and enhanced by optimal foraging theory. The major question remains to find accurate functional group sizes and classifications that permit the distinction of the different biological activities involved in ecosystem key processes without missing other biological functions. After reviewing some of the problems in current functional classifications of benthic invertebrates, we propose a classification system based on the mechanical activities that characterize each species rather than consideration of the multiple consequences of these activities. This sorting strategy will result in a sub-classification of classical feeding groups into more precise functional groups. Such groups as bioturbation groups or functional feeding groups may be composed of representative taxa in both marine and freshwater environments.

SÉDIMENTS AQUATIQUES
SÉDIMENTS MARINS
SÉDIMENTS D'EAUX DOUCES
GROUPES FONCTIONNELS
MACRO-INVERTÉBRÉS
BIOTURBATION

RÉSUMÉ. – La définition des groupes fonctionnels en écologie aquatique dépend du type d'écosystème considéré (e.g. écosystèmes marins comparés aux écosystèmes d'eaux douces en distinguant les eaux douces courantes et les eaux stagnantes). Si le compartiment benthique assure le stockage et la transformation de la majorité de la matière transitant dans la colonne d'eau, les processus biologiques impliqués dans le fonctionnement de ce compartiment sont proposés comme base pour l'identification des modalités d'intervention des macro invertébrés benthiques. La fonction des macro-invertébrés benthiques doit inclure leurs interventions dans les propriétés biotiques et abiotiques de leur environnement immédiat. Ainsi un groupe fonctionnel peut être défini comme un groupe d'espèces partageant des effets communs d'ordre biogéochimique et intespécifique. La principale difficulté pour appliquer cette définition aux invertébrés des sédiments aquatiques se heurte à la forte diversité des fonctions des organismes qui s'exprime à différents niveaux : i) une diversité interspécifique alimentée par une importante hétérogénéité des traits morphologiques et comportementaux, et une redondance fonctionnelle encore faiblement mise en évidence ; ii) une diversité intraspécifique générée par les modifications de stratégie nutritionnelle au cours des cycles de vie, augmentée par les stratégies opportunistes. La principale question reste à déterminer la taille appropriée des groupes fonctionnels pour permettre d'expliquer la participation de ces organismes dans les fonctionnalités essentielles des écosystèmes sans cacher certaines fonctions biologiques à l'intérieur de groupes trop largement définis. Après avoir exposé quelques difficultés posées par l'élaboration des classifications fonctionnelles pour les invertébrés benthiques, un système de classification basé sur le type d'intervention mécanique caractérisant l'activité trophique et de bioturbation de chaque espèce est proposé. Les groupes fonctionnels ainsi définis constituent une sous-classification des modes trophiques actuels en précisant leurs modalités d'interventions. De tels groupes fonctionnels dénommés groupes de bioturbation et groupes fonctionnels trophiques doivent être composés d'organismes représentatifs des écosystèmes benthiques marins et d'eaux douces.

AREA OF CONCERN

Functional groups are defined differently in aquatic ecology depending on the ecosystem type (e.g., deep ocean, coastal zone, coral reef, estuary, lagoon, mangrove, river, lake, wetland, stream) and the concerned compartments (benthic *versus* planktonic). Usually, species of aquatic communities are grouped by ecological equivalency, such as guilds (Fauchald & Jumars 1979), trophic levels (Peerson *et al.* 1992, Pace *et al.* 1999), feeding groups (Cummins 1973, Merritt & Cummins 1996), non-trophic functional groups of consumers (Done *et al.* 1996), or organisms as ecosystem engineers (Jones *et al.* 1994). These efforts of classification are useful devices for understanding the complexity of ecological systems. Similar to approaches used in terrestrial ecology, aquatic research tends to elaborate functional groups in order to link ecosystem performance to biodiversity (Körner 1993, Gitay *et al.* 1996, Covich *et al.* 1999). Recent works on the concept of functional groups in different aquatic and terrestrial environments pointed out the variety of views on functional grouping for different organisms and ecosystems such as vertebrates (Blondel 2002), and vegetation communities (Lavorel & Garnier 2002). A previous reflexion intented to compare and homogenized functional group definitions across different ecological areas of investigations. In order to facilitate the emergence of common concepts among ecosystems, analyses focused on the inter-ecosystem similarities of the "functional group" concept and converging attributes appeared among ecosystems (Lavorel & Garnier 2001). The objective of the present review is to examine the potential to adapt the common concept of the functional groups to invertebrates of aquatic sediments.

The main difficulty in the application of this functional group concept to aquatic invertebrates is the remaining discrepancy on what is meant by "function" to describe their participation in ecosystem functioning. Our first focus is on the various meanings of function as it is used to discriminate the different types of functional groups in the aquatic ecosystems including marine and freshwater environments. Since the benthic environment represents the major storage and recycling compartment for virtually all material that flows in the aquatic system, relevant organism functions are most likely to be found in macrobenthic invertebrate communities (Here and below, macro-invertebrates reffer to macrofauna *sensu stricto* > 0,25 mm, as defined by Dinet *et al.* (1985)). Furthermore it is emphasized that biological processes that take place in aquatic sediment communities are interesting models for identification of invertebrate functions. After reviewing some of the difficulties in current functional classifications to reach a common definition of benthic invertebrate functional groups, a classification system based on similar functions in marine and freshwater ecosystems is described.

There exist an increasing interest in the "functional group" approach that provides an intermediate level of complexity to study causal relationships between biodiversity expressed at the taxonomic level and ecosystem function. Experimental development of this functional approach of the invertebrate community should bring insight to the testing of current hypotheses such as the rivet-popper hypothesis, the redundancy hypothesis, the key-stone species hypothesis, or the idiosyncratic hypothesis (Chapin *et al.* 1992, Lawton 1994, Mooney & Chapin 1994, Sala *et al.* 1996, Emmerson *et al.* 2001). Since the utility of the "functional group concept" for community structure analyses has been well demonstrated in earlier papers (Pearson & Rosenberg 1978, Bengtsson 1998, Pearson 2001, Steneck 2001), we will not discuss it further.

The diversity of the functions in the benthic communities

The feeding groups

The first type of functional group, which is based on energy sources, is the distinction between autotrophic and heterotrophic organisms. These large groups are subdivided into the well-known feeding subgroups of homogeneous trophic levels: primary producers, herbivores, carnivores, and detritus feeders. This last group has been associated with the benthic part of aquatic system. Trophic groups are now organized into web-like models with an intermediate level of complexity produced by introducing several functional groups for each trophic level. This functional grouping clusters species to depict linkages between consumers and the resources they potentially regulate (Hulot *et al.* 2000). Classifications based on trophic sources are useful for studies of food dynamics, trophic relationships, and the evolution of system complexity in changing environmental conditions, but the extrapolation of those functional groups to the benthic macro-invertebrates raises difficulties.

The lack of information on the organism functions in the sediments

All organism functions may not yet be identified. Furthermore, different opinions still exist on which essential ecosystem functions should be used as definitions for functional classification. Pearson (2001) made a thorough overview of the functional group concept in the soft-sediment marine benthos, with much insight into the development of the trophic group concept. He points out that "…the five broad groups traditionally recognized in the benthos, namely, herbivores, suspension feeders, detritic feeders, carnivores and omnivores, may be subdivided in many different ways depending on the level of detailed information available on the feeding behaviour and morphology of the species. Unfortunately, such information on even the most basic natural history of many benthic species is lacking in many, if not most, benthic habitats."

Facing the diversity of potentially existing functions in a benthic community, the major question remains to find an accurate strategy for the classification of benthic invertebrates that permits the distinction of the different biological activities involved in ecosystem key processes without missing other biological functions.

In the task of selecting pertinent species traits and functions, taxonomic relatedness will probably remain a poor indicator of potential species effects, as demonstrated by Steneck (2001) who stated: "Species that are closely related evolutionarily are not necessarily morphologically or functionally similar." This observation is particularly easy to demonstrate in the aquatic environment; therefore, other classification criteria should be used.

Consequently, one of the major difficulties in the task of classifying species into functional groups comes from the large diversity of functions that is characteristic of most aquatic ecosystems. Different reasons may be discussed to explain this functional diversity.

Inter ecosystem diversity (pelagos *versus* benthos)

One commun point to all aquatic systems is the ubiquitous distinction between the classification of pelagic and benthic communities. In the pelagic zones of lakes and even more of oceans, strong ecological interactions of the major species are based on trophic interactions with a system-wide spatial scale. In benthic systems, the spatial scale of effects appears much more variable at the water-sediment interface. This scale ranges from the sediment particle scale, with biofilm communities to the mosaic unit scale with benthic community patches. Trophic impacts exist in all aquatic sediments, and benthic organisms have been classified into trophic groups. However, evidence of the benthic communities' involvement in determining how organic matter is processed in sediments (Rhoads 1974, Aller 1982, Krantzberg 1985), such as their ability to influence non-trophic geochemical parameters via bioturbation processes, has led to the identification of other functions for benthic species based on different functional criteria. Various types of biological processes may take place in the aquatic sediments that potentially interact with the organic matter transformation. The size of sediment particles in the animal environment appears to be one major discriminant factor that conditions the type and intensity of organism's intervention.

Interspecific diversity

Functional biodiversity in marine aquatic systems is due to a large number of species from many different phyla (May 1988, Ray & Grassle 1991). In contrast, limnic and terrestrial biodiversity is due to large numbers of species from fewer phyla. This difference implies the coexistence of an abundance of respiratory and metabolic pathways with very different ways of living in marine aquatic ecosystems, with consequences on functional diversity by creating different types of surviving strategies (Chandler *et al.* 1996).

Consequently, classification of benthic communities on a feeding basis may obscure distinct species effects within the same feeding groups and does not yield consistent information on their different ways to use food resources. An example is given by the widely distributed detritus feeder group that becomes dominant in non-solid substrates. Several detritic feeders perform a variety of functions at the sediment-water interface, including the regulation of organic matter degradation, carbon burial, microbial grazing and gardening, bioturbation, and biogenic structure formation. These activities influence sediment diagenesis and nutrient flux both directly (by modifying sediment geometry and distribution) and indirectly (by promoting microbial activities and growth rates) (Diaz

& Schaffer 1990). The large diversity of behaviours and metabolic pathways in the detritic feeder group asks for the reconsideration of this group that should perhaps be divided into subgroups to give evidence of the different types of interventions.

Intraspecific functional diversity

Some organisms show plasticity in their feeding strategy depending on i) the period of their life cycle, such as the polychaete *Nereis virens* (Desrosiers *et al.* 1994) and most insects, and ii) the type of resource available according to the optimal foraging theory (Pyke 1984, Jumars & Wheatcroft 1989). This intraspecific functional diversity implicits that many possible functions appear for a single species depending on the ecosystem function in question and the period of the study. We can use insects to illustrate this point, since essentially all aquatic insects are omnivorous, at least in their early instars (Cummins & Klug 1979). In this case, classification based on later larval feeding strategies may not represent the food sources and feeding effects of the whole population. Also, several marine polychaete worms, such as nereids, are difficult to assign to a single feeding mode since they feed according to the optimal foraging theory and may vary in their diet throughout their life cycle, including the benthic and pelagic phases (Miron *et al.* 1990, Olivier *et al.* 1993, Olivier *et al.* 1996). This point makes classification with simple feeding references quite impossible for a large number of benthic invertebrates.

Evolution of the functional group definitions

A plurial definition of the functional groups

The exploration models of theoretical ecology can bring useful and objective insights for the research of the most valuable functions to take into consideration for classifications setting. The development of such models to quantitatively test the stability and complexity of ecosystem relationships (Michalski & Arditi 1999) demonstrates that a community's efficiency is not purely linked to the complexity of the trophic interactions, but is more accurately related to the nature of the ongoing relationships including trophic and non-trophic functions. Relationships that modify trophic interactions are called rheagogic (Michalski & Arditi 1999) effects. These non-trophic functions may include amensalism, competition, mutualism, ecosystem engineering, and bioturbation. In particular, the relevance and crucial role of these relationships in the ability and efficiency of the theoretical communities to use their non-biotic resources is demonstrated. Based on the qualitative consideration of the same types of biological effects, Jones *et al. (*1994) defined "ecosystem engineers" as those organisms that provide strong interactions with bacterial communities, organic matter diagenesis, and nutrient exchanges with the overlying water. They cause physical state changes in biotic or abiotic material and in so doing facilitate the benthic part of element cycles. More precisely, Jones and co-authors defined "allogenic engineers" as those organisms that change the environment by transforming living or non-living material from one physical state to another via mechanical or other means. Allogenic engineers typically include all bioturbator group representatives and some of the functional feeding groups defined by Merrit & Cummins (1996) that potentially modify the availability of food to other organisms such as shredders and grazers.

In agreement with functional group definitions in terrestrial ecosystems, a common functional group classification strategy should relate species with similar interventions in ecosystem energy fluxes and equilibrium. To this end, accurate species classification have evolved towards a more pluralistic conception of the species function that should include their effects on the abiotic and biotic properties of the habitats. In this sense functional groups may be defined as groups of species that share common biogeochemical and interspecific effects.

To apply this "plurial" definition of the invertebrate function to benthic communities, one solution, with respect to the large functional diversity of species, could be to identify the different functions of each organism. This solution implies the necessity of completing several functional classification determinations, with each classification focusing on one type of ecosystem service. As an example, the accuracy of trophic functional groups is widely demonstrated for energy transfert studies when, for the same community, functional bioturbation group sorting appears more adapted to understanding organic matter recycling processes. This type of classification may end up with multifunctional groups rather than mono-functional groups. Pearson's (2001) definition of these multifunctional groups is "a group of organisms that respond in a similar way to environmental challenges." Although this solution seems scientifically attractive, it may not be simple to get an exhaustive list of all the functions performed by a benthic species. We may not even be sure that all functions have been identified.

A single mechanistic function at the source of multiple effects

A second solution emerges from the examination of each classification limit in the marine and freshwater environments and leads to the suggestion of a sorting strategy based on the origins of species interventions rather than on the effects of the activities on the water-sediment interface properties. In the absence of further information that objectively indicates the major consequence of each benthic activity, organism interventions may be identified using the type of biologically mediated mechanical processes that induce significant changes in sediment properties, mainly physical ones. The main advantage of this strategy is that it permits the elimination of the multiple functional consequences of one single species activity. An example of the distinction between mechanical activity and its multiple consequences is provided by the infauna biofilm grazer group. This activity may provide different effects that significantly influence physical, chemical, and biological properties of the hyporheic zone of the ecosystem (Mermillod-Blondin 2000): it prevents the clogging of porous sediment by the continuous creation of new interstitial passages in the sediment column, it supplies oxygen and nutrients to isolated spots in the sediment, it maintains the bacterial population in exponential growth, and it lowers the biofilm biomass in the corresponding sediment layer.

A common classification strategy for functional group classification

It is not surprising to find common functional characteristics in organisms living in similar types of soft sediments in both freshwater and marine environments (Lake 1990). Examples of such similar characteristics include organisms that live in the deposit sediments of estuaries, lagoons, lakes, backwaters, and dams, where granulometry is dominated by fine particles and supplies of allochtonous and autochtonous organic matter are sufficient to support benthic communities. In these ecosystems, benthic activities are highly diverse and the diversity of species functions is assumed to follow the same pattern.

Development of a common classification to both marine and fresh water communities may led to functional groups with composition made of representative taxa from both environments. As an example of this advantage, bioturbation groups currently include organisms that live in marine soft bottom habitats, but the biodiffusor, regenerator, and conveyor groups are also represented by insect larvae such as mayflies, midges (Matisoff & Wang 2000), stoneflies (Brooke & Peckarsky 1996), and oligochaetes (Fisher *et al.* 1980, Guerin 1994, Mermillod-Blondin *et al.* 2001).

In the search for understanding how organisms influence their environment, it is suggested to consider all types of mechanical interventions using the already available functional classifications on the bases of trophic functions when no other mechanical intervention exists and including non-trophic functions when they exist.

A common classification for marine and freshwater invertebrates may combine current classifications that have been shown to be functionally useful in their own area. This classification should include classical bioturbation groups and other mechanical interventions when bioturbation is not possible. Since the activities of species that live in macroporous substrata may also affect sediment properties *via* organic matter processing, the functional feeding groups previously described by Cummins (1974) should be included in the general classification. It remains particularly relevant for those organisms that feed on detritus or living organic matter without participating in bioturbation processes.

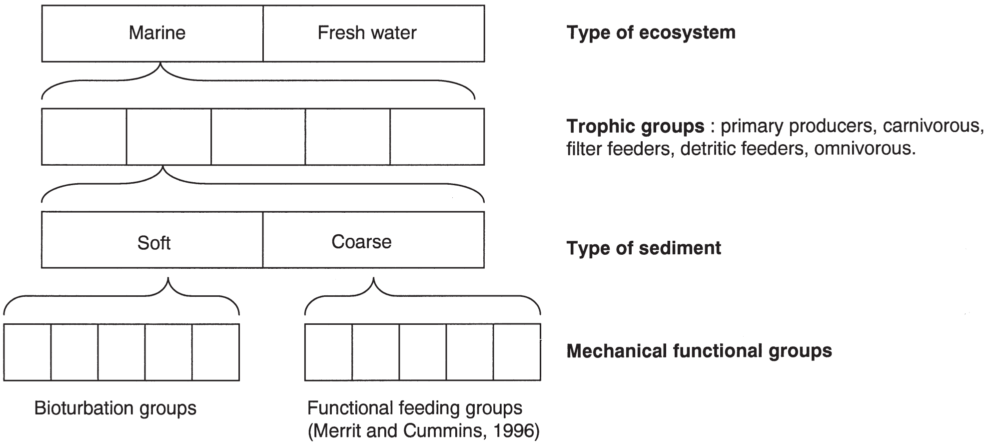

Fig. 1. – Different levels of information for macro-invertebrate classification of marine and freshwater sediments. Different functional groups exist depending on the granulometry of the sediment. Both type of mechanical functional groups (bioturbation and functional feeding groups) (Merrit & Cummins 1996) may be composed of species from marine and freshwater sediments.

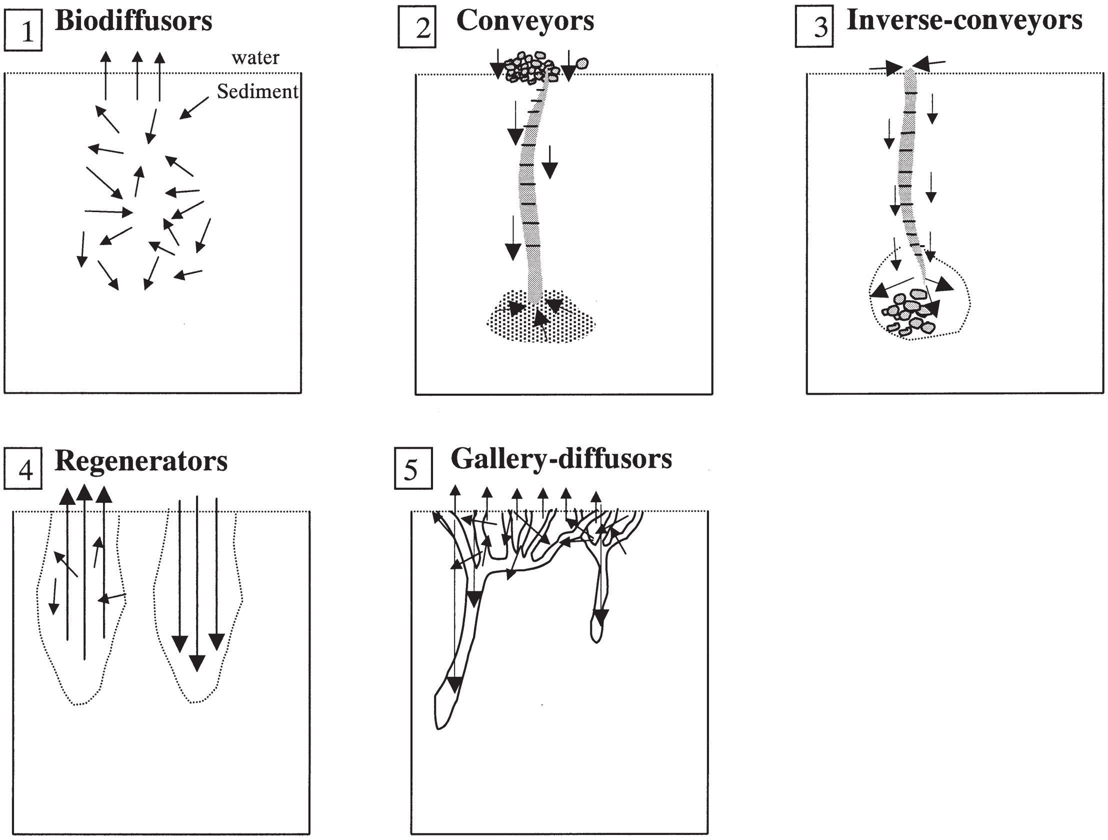

Fig. 2. – Schematic representation of the physical and biological reworking mechanisms of 1. biodiffusors, 2. conveyors, 3. Inverse-conveyors, 4. regenerators, and 5. gallery-diffusors (François 1999). The size of the arrow heads is representative of the intensity of the particle fluxes.

Facing this duality of the occurrence of two major types of mechanical interventions (Bioturbation groups and Functional feeding groups in the sense of Cummins), a first selection should be made with the old criteria of substrate granulometry, as presented in the following paragraphs.

The identification of these functional bioturbation groups does not preclude the importance of trophic group studies. The relevance of the trophic groups in the functional classification of benthic organisms should be taken into account for organisms living on hard substrate or soft bottoms that predominantly work to reduce biomass. These organisms that include herbivores, suspension feeders and carnivores may still be classified depending on their feeding strategies.

The consideration of this supplementary function based on mechanical intervention will result in a sub-classification of classical feeding groups into more precise functional feeding groups such as bioturbation groups for soft-sediment communities and functional feeding groups in macro-porous sediments of river-beds (Fig. 1).

Functional groups in soft sediments

When current velocity is low and sediment is soft, bioturbation phenomena have profound effects on the physical, geochemical, and biological properties of the substratum (e.g., Rhoads 1974, Aller 1982, Krantzberg 1985, Palmer *et al.* 1997). Through activities such as feeding, defecation, and movement, organisms living in the upper layers of lake, wetland, and ocean sediments cause sediment and pore water reworking and irrigation. Bioturbation affects the stratigraphic records by spatially redistributing sedimentary materials, such as microfossils and sediment associated radionuclides (e.g., Berger & Heath 1968, Guinasso & Schink 1975, Aller & Cochran 1976, Smith *et al.* 1986). By mixing biogenic particles, bioturbation also affects biogeochemical cycles, such as those of CO_2 and nutrients. Bioturbation also has a profound impact on pollutant distributions such as metals or hydrocarbon (Schink & Guinasso 1977, Yokoyama *et al.* 1985, Gilbert *et al.* 1996, Gilbert *et al.* 2001) by controlling their burial and delayed release (Lee & Swartz 1980, Reynoldson 1987, Salomons *et al.* 1987). In addition, bioturbation phenomena, through "feed-back" effects, exert a significant influence on the sediment's biological components, such as macrofauna (Flint & Kalke 1983, Posey 1990, Botto & Iribarne 1999), meiofauna (Reise 1983, Billheimer & Coull 1988, Moodley *et al.* 1998), and micro-organisms (Driscoll 1975, Fukuhara *et al.* 1980, Yingst & Rhoads 1980, Daumas & Bianchi 1984, Reichardt 1988, Van de Bund *et al.* 1994, Traunspurger *et al.* 1997). According to the literature, four types of bioturbation groups (Fig. 2) have been distinguished: biodiffusors, conveyors, inverse conveyors, and regenerators (Gardner *et al.* 1987, Gerino 1992, François *et al.* 1997, François 1999).

The *biodiffusor group* includes species whose activities result in diffusive sediment transport. They move sediment particles in a random manner over short distances and some surface biodiffusors are called bulldozers. These include organisms like the bivalves *Ruditapes decussatus* and *Venerupis aurea* (Gerino 1992, François *et al.* 1999) and the amphipods *Pontoporeia hoyi* (Robbins *et al.* 1979).

The *conveyor group* includes head-downward, vertically oriented species that remove sediment at depth in the substratum and expel it at the sediment surface. They cause an "active" non local transport of sediment from the bottom up through their gut and "passive" and advective transport all around them from the sediment-water interface to the bottom of their feeding zone due to sediment discharge at the interface and to sediment subsidence into the ingestion cavity. Major conveyors are tubificid oligochaetes in lake sediments (e.g., Fisher *et al.* 1980) and the polychaetes Maldanidae (Aller 1982) and Capitellidae.

The *inverse conveyor group* includes head-upward, vertically oriented species that cause an "active" non-local transport of sediment through their gut from the sediment-water interface to their egestion depth. Smith *et al.* (1986) described this behaviour pattern for worms of the phylum Sipunculida.

The *regenerator group* includes galleries digging species, such as the fiddler crab, that transfers sediment from depth to the surface where it is washed away (Gardner *et al.* 1987). This behaviour has two effects: 1. a biodiffusive mixing with a high output of sediment into the water column during digging, and 2. a net movement of the surficial sediment to the bottom of the burrow after it has been deserted; this mechanism being another type of non-local transport.

A fifth functional group (Fig. 2) should be mentioned that is called the *gallery-diffusor group* by François *et al.* (2001a) or the bioirrigator group elsewhere. This group includes species whose main activities are to dig systems of galleries, tubes, or burrows in sediment and to practice bioirrigation. This activity leads to a non local transport of matter from the surface to the deep part of the tubes due to egestion of faeces and to solute diffusion through the burrow walls. The well-known polychaete *Nereis diversicolor* is representative of this group.

Functional groups in coarse sediments

When the sediment composition is influenced by strong hydrodynamics and is characterized by coarse particles with adjacent hyporheic liquid fluxes, benthic species are not able to rework sediment. However, in the benthic boundary layer, benthic metazoan activities possibly influence the rates of organic matter and nutrient recycling through the tied relationships developed with the microbial standing crop. Invertebrates may potentially influence organic matter transformation by the way they influence microbial communities growth (Mermillod-Bondin *et al.* 2002). Biofilm grazing activities stimulate growth of bacterial communities and permit accessibility of solute to isolated interstitial zones (Merritt & Cummins 1996, Boulton *et al.* 1998, Mermillod-Blondin 2000). When sediment is coarse, benthic infaunal invertebrates act as nutrients vectors by enhancing disposability of products to microbiological reactive interstitial zones. Other invertebrates, that scrape interstitial biofilm initiate microbial activities by removing the dead parts of the biofilm. These organisms, by directly or indirectly modulating resource availability (other than themselves) to other species, accomplish non-trophic functions. Since these "non trophic" and mechanistic functions may enhance biogeochemical reactions in the interstitial matrix, they may be as important as trophic functions to the fate of the whole nutrient load.

In the River Continuum Concept (Vannote *et al.* 1980) authors categorize consumers into distinct functional feeding groups that use a particular resource class. Benthic organism classification within the river system is based on the morpho-behavioural mechanism of food processing. *Shredders* utilize coarse particulate matter (> 1 mm) such as leaf litter and depend to a large extent on the associated microbial biomass. *Collectors* filter fine and ultra-fine particulate organic matter from transported matter. *Scrapers* (*grazers*) are adapted primarily for shearing attached algae from surface particles, but this group also includes detritivorous infauna that graze on interstitial biofilm. The functional feeding groups of the predators (engulfers and piercers) and "gathering collectors" that feed on deposit should be added to this classification in order to cover the whole benthic community of streams. The ingestion of a wide range of food items in each of these functional feeding group results in groups composition made of a mixture of herbivory, detritivory and carnivory (Merritt & Cummins 1996).

Functional groups in environmental gradients

As mentioned by Pearson (2001), (Pearson & Rosenberg 1978, Rosenberg 2001), functional groups provide a clearer understanding of the influence of changing environment conditions along vertical and latitudinal gradients on the benthic faunal distribution. If functional structural assemblages are closely tied to environmental conditions, the studies of species interventions in changing conditions may add helpful information to the classification of functional groups. The implicit method of trait identifications from emergent groups of plant species (Lavorel *et al.* 1997) is based on natural correlations of biological attributes obtained in different conditions of disturbance. Exhaustive identifications of aquatic macro-invertebrate traits are provided by Charvet *et al.* (2000), Doledec *et al.* (2000), and a previous study (Charvet 1999), who list "biological traits" such as reproductive characteristics, mobility, resistant forms, feeding habits, respiration, size, life duration, and aquatic stage, and "ecological traits" such as temperature preferences, trophic level, saprobity, biogeographic distribution, longitudinal zonation, substratum, and current velocity. A comparison of this method with the present classification of functional groups (resulting from mechanical function types of species sorting) should reveal convergent results.

As an example of the advantage of this combined classification method, the evolution of functional groups after just one perturbation reveals convergences in the freshwater and marine environment. Studies of adaptive responses to changes in ecosystem constraints in muddy sea floors (Rhoads 1974, Rhoads *et al.* 1978) reveal major modifications of species habits including pellet production, depth of ingestion, vertical range of burrows, the organism's vertical position, and reproductive strategies. The increasing diversity of bioturbation processes are mentioned as the result of the community's succession after disturbances that potentially facilitate the colonisation of later species (Rhoads 1974). The replacements of species and the increasing number of different species that characterise a successional process get their equivalencies in terms of functional groups that start from single conveyor communities and evolve toward complete functionally diverse communities.

Modelling as a tool for functional group sorting

The development of experimental approaches with appropriate model applications for data treatment yields powerful insights into the investigation of functional groups. Laboratory experiments with model systems (Lawton 1995) and *in situ* experiments that test species combination effects on key ecosystem parameters and conservative tracers are generally helpful to reach these objectives. Unfortunately, experimental approaches are usually lacking for stream ecosystems where interactions between biotic and abiotic processes complicate the experimental design and interpretation of results (Huston 1997). The treatment and analysis of data should be conducted with mathematical models whose formulations depend on the level of precision required. Bioturbation models provide an example of modelling usefulness for the task of functional species sorting. The classical biological transport-reaction model application permits one to quantify the intensity of the functions related to different types of biological sediment transports. This type of model may be helpful for the comparison of species or community effects without *a priori* knowledge of their intervention modes. More precise species effects are quantified with five elementary models, each formalizing the sediment reworking resulting from one of the five bioturbation functional groups. The combination of these five elementary models in a global model is particularly well suited for testing hypotheses and for checking and predicting the effects of multiple species assemblages (François *et al.* 2001b).

Conclusion

The present review of functional group definitions did not demonstrate any restrictions to the application of a common concept and classification strategy to both marine and freshwater benthic species. The functional groups that currently prevail in the literature have been based on the identification of species functions, but there are still a large number of species effects that have not been examined.

The classification of benthic invertebrates into functional groups is handicapped by the large diversity of functions and roles, including O_2 diffusion, organic matter mineralisation, sediment reworking, and bacterial activation, that are filled by invertebrate organisms in the sediment and are involved in the highest key functions of the ecosystem, like nutrient retention. For the majority of benthic ecosystems, our current knowledge is insufficient to set a single functional nomenclature based on the large diversity of effects (Wall 1999) that are expressed by each benthic species and also within a single species during its life cycle.

The general marine and freshwater approach permits a classification strategy that focuses on the species mode of intervention in their environment. This alternative provides a solution to the questions of how to find the main function of an organism and how to manage distinct species effects within the same group. The main advantage of this strategy is to bring an intermediate level of complexity based on mechanistic effects that permit a description of the biodiversity / functional group /

ecosystem service relationships. The suggested classification strategy is a mixture of functional groups that are currently used and that belong to both marine and freshwater environments, each classification being efficient in its own range of environmental conditions.

It is concluded that in the scope of further determining an organism's participation in key functions and services of ecosystems, it is useful to sort aquatic organisms into well defined and general functional group classifications. Facing the immense work that remains to be done in this sense, and since all species of a group may not act with the same intensity, it may be worthwhile taking the opposite approach, that is, to clearly define the key processes that drive ecosystem performance. This inverse strategy would permit one to directly identify the relevant organisms that most regulate each of these key processes and provide arguments in setting accurate nomenclature for functional group classification.

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