Spatial and temporal variability of benthic macroinvertebrates in running waters -implications for biomonitoring

Literature review

by

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1.0 Introduction

This literature review will focus on the spatial and temporal factors regulating the benthic macroinvertebrate communities in streams and rivers. Although benthic macroinvertebrates have been used for a long time as a biomonitoring tool, the spatial and temporal variability of the communities has often been neglected. This variability may confound the results of water quality biomonitoring, possibly resulting in inferring incorrect conclusions of the impact of anthropogenic stress on the benthic fauna. A better understanding of the effects of spatial and temporal variability of benthic macroinvertebrates is important for improving our knowledge of factor(s) influencing the structure and function of aquatic ecosystems, and subsequently the management of aquatic biodiversity.

1.1 Biomonitoring using macroinvertebrates

Benthic macroinvertebrates are "...organisms that inhabit the bottom substrates (sediments, debris, logs, macrophytes, filamentous algae, etc) of freshwater habitats" (Rosenberg and Resh 1993). They are usually considered to be organisms large enough to bee seen without magnification, i.e. retained in a net with a mesh size of 200 to 500 μm (De Pauw and Vanhooren 1983; Rosenberg and Resh 1993; Sladecek *et al.* 1982; Wiederholm 1980). These organisms, together with algae, are the most widely used indicators for assessing the quality of fresh water according to a literature survey presented by Hellawell (1986). In reality benthic macroinvertebrate studies are alone the most widespread biological water quality assessment tool (Metcalfe 1989; Sladecek *et al.* 1982; Whitton 1979; Wiederholm 1980).

The use of benthic macroinvertebrates in biomonitoring started in the late 19th century in Germany with the saprobien system, which focused on organic pollution and the associated decrease in dissolved oxygen (Kolkwitz and Marson 1909). This method focused largely on the presence of microorganisms belonging to the plankton and periphyton communities (Metcalfe 1989) and a list of indicator organisms that could be used to indicate different levels of pollution was constructed (Sladecek 1979). Since then, more than 50 other approaches for biomonitoring using macroinvertebrates have evolved (De Pauw and Vanhooren 1983).

1.1.1 Macroinvertebrates as biomonitoring tools: advantages

Several authors have summarized the advantages of using benthic macroinvertebrates in biomonitoring (Hawkes 1979; Hellawell 1986; Metcalfe 1989; Rosenberg and Resh 1993; Sladecek *et al.* 1982). In brief, macroinvertebrates are ubiquitous, sedentary and have a relatively long lifespan. Because of these and many other features they are good representatives of local conditions and they integrate changes in environmental conditions over a period of time. There are generally a large number of species present at a site and the taxonomy of the organisms is relatively well known. The animals can easily be sampled using inexpensive equipment. Since the communities are diverse, the benthic fauna will display a wide spectrum of responses to different kinds of pollution. These responses are often well established, as well as the different environmental requirements the species have. Benthic macroinvertebrates are also well suited for experimental approaches to biomonitoring and a large number of toxicity tests involving benthic macroinvertebrates have been developed. Lastly, by using biological monitoring methods actual changes in the populations and communities of the biota can be measured as opposed to chemical methods where the results have to be interpreted on a biological basis.

1.1.2 Macroinvertebrates as biomonitoring tools: disadvantages

There are also several disadvantages of using benthic macroinvertebrates as biomonitoring tools (Hawkes 1979; Rosenberg and Resh 1993; Sladecek *et al.* 1982). It is difficult to sample macroinvertebrates quantitatively and their distribution can be affected by other environmental factors than pollution, e.g. water current and sediment content. Benthic macroinvertebrates are not sensitive to all kinds of pollution and their distribution varies with season. Because of their drift behavior they may be found at sites and in habitats where they normally should not be encountered. Some taxa are difficult to identify, which can cost a lot of time and produce incorrect identification of certain groups, e.g. some Chironomidae, Trichoptera, and Oligochaeta.

1.2 Analysis methods

The approach for assessing spatial and temporal change of benthic macroinvertebrate communities can be divided into two main groups: univariate and multivariate methods.

Univariate studies looks at one response variable at a time whereas multivariate statistics are used to interpret a large set of response variables and sampled sites at the same time.

1.2.1 Univariate methods

In its simplest form, univariate methods can be the quantification of some community parameter such as taxon richness or density of individuals (Norris and Georges 1993). Another common method, in univariate studies, is to compute an index value. There are three main categories: diversity, biotic and similarity indices (Washington 1984). A diversity index is a numerical expression, based on taxa richness, evenness and abundance (Johnson 1995), that "...supposedly indicates the state of the community" (Norris and Georges 1993), since it is assumed that an undisturbed environment will contain a higher diversity and species richness than a polluted one (Metcalfe 1989). The number of existing diversity indices is very large, but the Shannon-Wiener index, also called Shannon's H´ (Shannon and Weaver 1949) is most commonly used in biomonitoring of benthic fauna (Metcalfe 1989; Resh and McElravy 1993). Another common diversity index used in running waters (Resh and McElravy 1993) is Simpson's diversity index (Simpson 1949).

In the biotic indices and scores methods, the organisms found in a sample are given scores based on how tolerant or sensitive they are to a pollutant; based on field work or laboratory experiments, this is called the indicator organism concept (Johnson *et al.* 1993). The scores for the different organisms are combined into a single value and this value can be used as an index of the level of water pollution (Washington 1984). The difference between a biotic index and a biotic score is that a biotic score also includes a measure of the abundance of the organisms (Metcalfe 1989). Biotic indices and scores are often specific both to certain pollution (mainly organic) and to a geographic area (Norris and Georges 1993). There are six major biotic indices used in running waters of Europe according to Metcalfe (1989). The Trent Biotic index (Woodiwiss 1964) was originally developed for the Trent River in England, but has since been modified for a large number of countries in Europe (Hawkes 1979). It is also the base for most biotic indices used today (Metcalfe 1989). One of the first extensions of the TBI was Chandler's Biotic Score, originally developed for upland rivers in Scotland (Chandler 1970). It differed from the TBI because it included measures of abundance and is based on a more extensive list of macroinvertebrates (Metcalfe 1989). The British Monitoring Working Party (BMWP) improved the biotic indices/scores methods when they developed the BMWP score for national use in UK (Armitage *et al.* 1983). Both Chandler's Biotic score and the BMWP score have been modified to average score per taxon (ASPT), where the final score is divided by the number of scoring taxa (Pinder and Farr 1987). The Indice Biotique, developed in France (Tuffery and Verneaux 1968), the Belgian Biotic Index (De Pauw and Vanhooren 1983) and the Indice Biologique Global (AFNOR 1985) are other extensions of the Trent Biotic Index. Similarity indices measure the similarity in structure of two communities, often by looking at the similarity of species shared by two areas (Washington 1984). Jaccard's index (Jaccard 1908), which expresses the species shared between two sites as a percentage is according to Washington (1984) the most widespread similarity index in aquatic studies.. The percentage similarity, PCS (Whittaker 1952) is another similarity index and compares the number of species and their relative abundance. Other similarity indices that have been used in aquatic ecology are the Bray-Curtis index or the Bray-Curtis dissimilarity index (Bray and Curtis 1957), Sørensens index (Sørensen 1948), Pinkham and Pearson's index (Pinkham and Pearson 1976) and the Euclidean or ecological distance (Williams 1971).

1.2.2 Multivariate methods

Classification, ordination, and discriminant analysis are some of the most widely used multivariate techniques in water quality assessment using macroinvertebrates (Norris and Georges 1993). Classification comprises a group of methods where the investigated objects are arranged into small homogenous groups or clusters (Everitt and Dunn 1991). Two Way INdicator SPecies ANalysis (TWINSPAN) is a polythetic, divisive, hierarchical classification method (Hill 1979), that has often been used in macroinvertebrate studies (e.g. Johnson and Wiederholm 1989; Ormerod and Edwards 1987; Rutt *et al.* 1990; Wright *et al.* 1984). Unweighted Pair Groups Using ArithMetic Average (UPGMA) (Sneath and Sokal 1973) is another classification technique that is agglomerative and hierarchical. Belbin *et al.* (1992) have further developed this method and introduced flexible UPGMA, a clustering technique which has to some extent been used to analyze data of benthic macrofauna (e.g. Marchant *et al.* 1994; Marchant *et al.* 1997; Pardo and Armitage 1997; Parsons and Norris 1996).

"Ordination is a procedure for adapting a multidimensional swarm of data points in such a way that when it is projected onto a two-space (such as a sheet of paper) any intrinsic pattern the swarm may possess becomes apparent" (Pielou 1984). Two types of ordination techniques are indirect and direct gradient analysis. In indirect gradient analysis the axes are constructed from the variation among the sampled communities and thereafter interpreted in terms of environmental gradients (ter Braak and Prentice 1988). These techniques include methods such as Principal component analysis (PCA) and Correspondence Analysis (CA) (Hill 1974). Direct gradient analysis is a group of methods where each species abundance or probability of occurrence is described directly as a function of the measured environmental variables. It includes methods such as Redundancy Analysis (RDA) (Rao 1964; van den Wollenberg 1977), and Canonical Correspondence Analysis (CCA) (ter Braak 1986; ter Braak 1987). This last method has been widely used in ecology and benthic macroinvertebrate studies (see Birks *et al.* 1994 for a review). CCA uses measured environmental gradients and extracts from these new synthetic gradients using multiple regression that maximizes the niche separation of the species (ter Braak and Verdonschot 1995).

1.2.3 Analysis of time series data

When analyzing time series one is usually interested in analyzing for trends, where time is the explanatory variable (Helsel and Hirsch 1992). Trend analysis is a formal way of testing if the long term mean of the analyzed variable is changing over time (Loftis *et al.* 1991). This can be done either by the use of parametric methods, using linear models (i.e. regression), or by the use of nonparametric methods using rank correlation (i.e. the Mann-Kendall test for trend) (Loftis *et al.* 1991). Another method that can be used for trend testing of water quality data is spectral analysis as described by Chatfield (1984). It is very common in environmental time series to find changes between different seasons. If the seasonality is not removed, true trends over time may be very difficult to detect (Helsel and Hirsch 1992). There are several ways to remove seasonal components such as parametric, semiparametric and nonparametric methods. One may use multiple regression with periodic functions, where sine and cosine terms are included in a multiple regression to account for seasonality (Helsel and Hirsch 1992). A nonparametric method that can be used is the seasonal Mann-Kendall test (Hirsch *et al.* 1982), where the Mann-Kendall test is computed for each season separately and then an overall test for trend is performed. Trends at several sampled sites can also be analyzed at the same time i.e. multivariate trend tests. In an article comparing univariate and multivariate trend tests Loftis *et al.* (1991) found that the multivariate approaches are to be recommended, since they perform better in most cases.

1.3 Modeling

Multivariate techniques can be used in predictive modeling. In UK a model called River InVertebrate Prediction And Classification System (RIVPACS) has been developed. In this model classification, ordination, and discriminant analysis are used to give site-specific predictions of what species composition of macroinvertebrates can be expected in the absence of anthropogenic stress (e.g. Wright *et al.* 1984; Wright *et al.* 1988; Wright *et al.* 1993). Other similar approaches are the AUStralian RIVer Assessment Scheme (AusRivAS) (Simpson *et al.* 1997) and the Canadian model BEnthic Assessment of SedimenT (BEAST) (Reynoldson *et al.* 1995; Reynoldson *et al.* 1997).

2.0 Theories explaining macroinvertebrate community composition in running waters

A number of both descriptive and more theoretical approaches have been used to try to explain the difference in benthic macroinvertebrate communities in space and time. Some of the most important ones are described below.

2.1 Longitudinal zonation

Already in the beginning of the studies of running waters, a zonal distribution of the fauna was found and described (e.g. Shelford 1911; Steinmann 1907; Thienemann 1912). In western Europe these zonations were based on fish, but the same kind of zonation has been described for many groups of invertebrates (see Hynes 1970 for a review). A few studies of this kind have also been conducted in Sweden (Badcock 1953; Brinck and Wingstrand 1949, 1951; Müller 1954). Illies and Botosaneanu (1963) tried to combine the information from all studies on zonations and construct a universal system that could be applied to all watercourses. Working in the Fulda River in North Germany, Illies found that at certain points along the river more species appeared or disappeared, these points seemed to mark faunal divisions. These zones corresponded reasonably well with the earlier established fish zones, and Illies developed the idea that these zones are real ecological entities. He defined three main zones of running waters and termed them: *crenon,* the spring (*Eucrenon*) and spring brook (*Hypocrenon*) section. *Rhitron*, the stony stream to small river (can be divided into *epi-*, *meta-* and *hyporithron*) and *potamon* the larger river section of running waters (can also be divided into *epi-* and *metopotamon*). This scheme has been subject to some criticism, mainly concerning the division of the zones into parts. In addition, Thorup (1966) suggested that the faunal discontinuities found in the Fulda River were caused by local pollution. Hynes (1961) also found in a short and uniform stretch of the epirithron section of a Welsh stream, that although the list of species did not change, there was a change in the abundance of the most common species. As Hynes (1970) puts it "... it is possible therefore, at least in the lower rithron and the potamon, to make some meaningful subdivisions within zones, but as with the zones themselves a rigid classificatory approach rapidly loses touch with the complexities of reality".

2.2 Island biogeography theory

One of the general relationships concerning diversity in nature is predicted by island biogeography theory. The theory is not at all confined to islands; lakes and streams are islands in a ´sea´of land (Begon *et al.* 1990), they state "there can be few natural communities lacking at least some element of ´islandness´ ". According to island biogeography theory there exists a positive relationship between area and species richness, described by the formula:

$S = cA^z$

where S = species richness, A = area of the habitat, c and z are parameters determined from the data. The slope parameter z quantifies the increase rate in species richness with area size and frequently falls between 0.2 and 0.4 (Allan 1995). A number of studies have also confirmed that the species-area relationship equation applies to rivers, although estimates of z varies widely (Allan 1995), see Brönmark *et al.* (1984) for a Scandinavian example. Begon *et al.* (1990) gives three complementary explanations for the species richness of island communities. (i) Habitat diversity. Larger areas contain more habitats and should thus offer optimal conditions for a larger number of species. This factor can however easily be confounded with the fact that smaller areas also probably contain fewer individuals and thus by chance may contain fewer species (Giller and Malmqvist 1998). (ii) ´The equilibrium theory of island biogeography´ (MacArthur and Wilson 1967). The balance between immigration and extinction determines the number of species on an island. This balance is dynamic, with species continually going extinct and being replaced (through immigration) by the same or other species. The immigration rate will be higher at islands closer to the source of immigration and on larger islands, since larger islands represents a larger target for the colonizers. As the number of resident species on an island increases, the extinction rate will also increase, since with more species, competitive exclusion becomes more likely, and the population size of each species is on average smaller, making it more vulnerable to chance extinction. The same is true for smaller islands, since smaller islands will typically have smaller population sizes. (iii) The evolutionary aspect. None of the theories above takes into account evolution. On an isolated island, the rate at which new species evolve can be as fast or faster than the rate at which new colonists arrive, and thus the communities of islands may be only incompletely understood by ecological processes (Begon *et al.* 1990).

2.3 The River Continuum Concept (RCC)

The River Continuum Concept as proposed by Vannote *et al.* (1980) views the stream ecosystem as longitudinally changing physical templates (geomorphology, hydrology, energy input and organic matter transport), which are overlain by biological adaptations. The RCC includes a number of predictions of longitudinal change along the continuum. The lotic communities can be divided into three broad groups according to RCC: headwaters (stream order 1-3), medium-sized streams (4-6) and large rivers (>6). Headwater streams are strongly influenced by riparian vegetation, which reduces autotrophic production by shading and contributes large amounts of allochthonous detritus. The gross primary productivity to community respiration (P/R) is <1 and the stream community is dominated by shredders and collectors due to the large amounts of CPOM and FPOM coming into the system. As stream size increases, the importance of terrestrial organic inputs decreases and autochthonous primary production and transport of organic material from upstream sources becomes more important. This shift from heterotrophy to autotrophy is primarily dependent upon the degree of shading. In deciduous and coniferous forests, the transition is probably at order 3, whereas at higher latitudes and altitudes where the riparian zone is restricted, the transition to autotrophy is in order 1. The medium sized rivers, relying on algal and rooted vascular plant production is thought to have a (P/R) >1. Here grazers and collectors dominate the benthic community. Large rivers receive fine organic particulate organic matter from upstream processes of dead leaves and woody debris. The effect of riparian vegetation is insignificant, but light and turbidity may limit primary production. Here collectors dominate the benthic community. RCC also predicts maximum species diversity at medium sized rivers, where the variation, especially in temperature is the greatest, and thereby a larger number of species will occur at their temperature optima at least during some part of the day.

A number of studies have looked at the predictions made by the RCC. Hawkins *et al.* (1982) tested whether alterations in terrestrial vegetation had predictable consequences for the stream communities. They compared stream sections flowing through old-growth coniferous stands, recently clear-cut stands and deciduous forest that had re-grown since logging. Some of the predictions made by RCC were met, but opening of the canopy did not lead to the expected shifts in functional group composition. All functional feeding groups were more abundant in the open stream and shredders were not more abundant under forest canopy, as expected. In New Zealand, Winterbourn *et al.* (1981) found little correspondence between the RCC and invertebrate communities. Food specialization was minimal, shredders were absent and energy inputs from organic microlayers were more important than CPOM, FPOM, and algae. One possible explanation is the biogeographical isolation and the depauperate fauna of New Zealand, but Winterbourn *et al.* (1981) suggests that a highly unpredictable hydrological regime can override expectations from the RCC. The RCC predicts that there is a gradual downstream change in physical properties. That has been criticized by Statzner and Borchardt (1994), they argue that changes in ecological patterns seem to occur at the intersection between stream sections with high hydrological stress and sections with low hydrological stress. Staztner and Higler (1985) also criticize the hypothesis that medium sized streams should contain the highest diversity, since it only relates in macroinvertebrates and that fish and plankton have their highest diversity in high-order streams. In tropical areas, the temperature regime is most variable in low-order streams. The original RCC has been modified to take into account the influence of climate, geology, tributary effects (Bruns *et al.* 1984) and local geomorphological controls (Minshall *et al.* 1985). These modifications (e.g. tributary effects, nutrient spiraling, riparian influence and serial discontinuity) (Ward and Stanford 1983) is compatible with the RCC and enhance its utility according to Cummins *et al.* (1995). A description of the rivers in the Nordic countries, based on the RCC concept can be found in Petersen *et al.* (1995).

2.4 Hierarchy theory

In hierarchy theory, the local species community is seen as products of biotic and abiotic factors at multiple spatial and temporal scales (Allen and Starr 1982). Poff (1997) suggests that "species can be described in terms of their functional relationships to various habitat features". These features can be defined at different spatial scales and organized hierarchically from microhabitat patch to watershed or basin. Poff (1997) considers these habitat scale features to be filters, influencing the probability that a species will be able to persist in the local community. For a species present in the regional species pool to be able to be potentially present in the local community, it has to "pass" through the "filters" i.e. the environmental conditions present. All species are assumed to be able to disperse to all localities in the region given long enough time scales, so the absence or low abundance of a species at a local reflects the actions of selective filters. To pass through the filters the species must have certain organismal traits that match the selective characteristics of the filter(s). Poff (1997) specify four levels of filters, which he argues are "a minimum number that spans the relevant scales for a wide range of lotic species, both invertebrates and vertebrates". These four levels are: watershed/basin filters, stream valley bottom or stream reach, channel unit (e.g. riffle/pool), and microhabitat (e.g. sediment patch).

2.5 The patch dynamics concept

The patch dynamics concept focuses on temporal phenomena and disturbance and colonization plays important roles (Townsend 1989). In his 1989 paper Townsend describes five types of communities that can be included in a patch dynamics concept. (i) *Niche controlled communities*: competition is the important structuring factor and coexisting species must differ in their trophic niches. Another type of models views communities as comprising of a number of cells (with identical conditions and resources) with competition within cells, dispersal between cells and stochastic elements in the model (Yodzis 1986). (ii) *Dominance controlled communities*: if there are strongly competitive species in the system, initial colonizers of cells may not necessarily maintain their presence in a cell, but may still persist in the patchy environment as a whole. (iii) *Founder controlled communities*: if all species have similar competitive abilities initial colonizers will not be outcompeted and the community composition is essentially dependent on the original sequence of colonization. (iv) *Relict controlled communities*: if not all species are removed at disturbance, the species that are able to persist will have advantages when other species recolonize. (v) *Mobility controlled communities*: in environments where the disturbance rate and mobility of organisms is high, competition may be of minor importance and only occur intermittently and never proceed to competitive exclusion.

3.0 The importance of scale factors

In the following sections, the environmental and biological factors at different scales that effect the variability of benthic macroinvertebrate communities will be reviewed. These factors are important to be able to draw the right conclusions of water quality assessment studies. Knowledge of these scale factors is also very important to better understand the structure and function of aquatic ecosystems and subsequently how these systems should be managed.

3.1 Scale in running waters

Running water ecosystems have a high level of spatio-temporal variability and can be divided into four dimensions according to Ward (1989). (i) The upstream downstream longitudinal dimension, (ii) exchange between the riparian zone, the floodplain and the channel, i.e. the lateral dimension, (iii) the vertical dimension, interactions between the running water and the ground water and (iv) time which "...superimposes a temporal hierarchy on the three spatial dimensions" (Ward 1989).

3.2 Spatial and temporal variability and biomonitoring

In biomonitoring studies of environmental impact, the objective is to separate the change generated by anthropogenic stress from the natural spatial and temporal variability (Johnson 1998). If the natural variability is large and the anthropogenic induced change is small it will be difficult to detect a real change in the measured variable(s) caused by the pollutant (Johnson 1998). A few studies have examined the variability of benthic macroinvertebrate indicator metrics used in water quality assessment, both in running waters (Barbour *et al.* 1992; Hannaford and Resh 1995; Resh 1994) and in lakes (Johnson 1995; Johnson 1998). The variability in the indicator metric(s) can be divided into three parts, (i) measurement error, (ii) the within site spatial and temporal variability and (iii) among site variability. The within site variability can be regarded as noise whereas among site variability often is the parameter of interest in biomonitoring studies (Johnson 1998). The variability of the different metrics, such as diversity indices and biotic scores/indices can be measured as the coefficient of variation, which expresses the standard deviation as a percentage of the mean and is a measure of the relative variation. The studies mentioned above emphasize that different indicator metrics have very different coefficients of variations and changes caused by anthropogenic stress can therefore be difficult to detect. This is due to the large variability in the measured indicator metrics, part of this variability is caused by natural spatial and temporal variability of the benthic macroinvertebrate species (Johnson 1995; Johnson 1998).

4.0 Importance of biotic and abiotic factors

Whether biotic forces structures the local community by keeping the community at or near equilibrium or if variable and unpredictable abiotic factors are the important ones, and species found together are those favored by the local physical conditions of the moment has long been debated (Diamond and Case 1986; Strong *et al.* 1984). Running water ecosystems appear to be variable and harsh environments, and it is often suggested that abiotic factors may have a great influence in these ecosystems (Allan 1995). In the following part of this literature review the biotic and abiotic factors commonly believed to be of main importance in running waters is examined.

4.1 Biotic factors

Begon *et al.* (1990) identifies five main types of interactions between organisms: competition, predation, parasitism, mutualism, and detrivory. In his 1970 book "The Ecology of Running Waters", Noel Hynes distinguishes three types of biotic factors: predation, disease and competition. In the following section two of these types will be considered: competition (inter- and intraspecific) and predation (by invertebrates and by fish).

4.1.1 Competition

Begon *et al.* (1990) defines competition as: "...an interaction between individuals, brought about by a shared requirement for a resource in limited supply, and leading to a reduction in survivorship, growth and/or reproduction of the competing individuals concerned". Morin (1999) states that competition involves a mutually negative interaction between a pair of species. Schoener (1983) distinguishes two main types of competition: *exploitation competition*, the depletion of resources by one individual is disadvantageous for another individual and *interference competition* which involves a direct interaction between the individuals, usually of an aggressive nature, e.g. when one individual excludes another from a preferred area. Competition theory became dominant in ecology in the 1950s and resource partitioning and the fact that species differed in their niches was seen as evidence that competition was widespread. By the late 1970s niche differences between species was no longer seen as an indication of competition. It is difficult to demonstrate the occurrence of competition. Conell (1980) discusses the criteria that must be met for competition to take place, and a large number of competition studies have shown ambiguous results (Giller and Malmqvist 1998). Among sessile, territorial insects (e.g. hydropsychids and simuliids) space is an important limiting resource (e.g. McAuliffe 1984; Hemphill 1988). Among mobile grazers (e.g. certain ephemeropterans, trichopterans and gastropods) competition for food resources (algae) may lead to local reduction or extinction of those taxa most sensitive to low food densities (e.g. Gresens 1995; Hawkins and Furnish 1987; Kohler 1992; Kohler and Wiley 1997). In many cases competition may only take place if the abiotic factors (e.g. flow) are relatively stable (i.e. abiotic factors is important in ´harsh´ stream environments and biotic factors in ´benign´ environments) (Peckarsky 1983). Competition can also be important episodically (e.g. during certain seasons, when there is limited amounts of food or when population densities are high) (Allan 1995).

4.1.2 Predation

Begon *et al.* (1990) defines predation as: "...consumption of one organism (the prey) by another organism (the predator), in which the prey is alive when the predator first attacks it". Most streams contain a variety of vertebrate (fish) and invertebrate predators (e.g. stoneflies, rhyacophilid caddisflies, dragonflies and some dipterans). Vertebrate predators are considered to be more voracious than invertebrate predators (Sih and Wooster 1994). Invertebrate predators on the other hand virtually always cause reductions in prey densities (e.g. Cooper *et al.* 1990; Oberndorfer *et al.* 1984; Peckarsky and Dodson 1980; Walde and Davies 1984) whereas the results of studies of vertebrate predators show ambiguous results. Some have found strong negative effects by fish on benthic prey (e.g. Cooper *et al.* 1990; Flecker 1984; Feltmate and Williams 1989; Gilliam *et al.* 1989; Power 1990; 1992) whereas others have found small or no effects (e.g. Allan 1982; Culp 1986; Flecker and Allan 1984; Reice and Edwards 1986). Habitat complexity, methodological differences between studies, prey dispersal that swamp the effects of fish and experiments being conducted over different scales have been suggested as explanations to these differences (Cooper *et al.* 1990; Peckarsky *et al.* 1997; Wooster 1994; Wooster *et al.* 1997). Another explanation suggested by Dahl and Greenberg (1996) is that the feeding mechanism of predatory fish affects the impact they have on the benthic community. They argue that fish eating solely benthic prey should have a larger effect than fish that also have drifting animals (i.e., many terrestrial ones) in their diet. A further complication is that vertebrate predators have both invertebrate predators and herbivores in their diet (Wooster 1994). The vertebrate predators should have a direct effect on the invertebrate predators, whereas their effects on the herbivorous invertebrates are more complex. They have a direct negative effect on the herbivores but also a positive effect since they decrease the number of invertebrate predators that can potentially have a negative effect on the herbivores (Wooster 1994). Dahl and Greenberg 1997 studied the predatory effects of one vertebrate predator *Salmo trutta* and one invertebrate predator *Erpobdella octoculata* and they found indeed that the presence of brown trout caused the leeches to consume less prey. When both predators were present, their impact on *Baetis* and *Epehemerella ignita* was lower than when each predator was alone (Dahl and Greenberg 1997).

4.2 Abiotic factors

Running water ecosystems appear to be variable and harsh environments, and it is often suggested that abiotic factors may have a great influence in these ecosystems (Allan 1995). In the following section some of the abiotic factors thought to be of main importance for the benthic community structure in running waters are examined.

4.2.1 Temperature

The annual water temperature regime of a stream or river has several components: maximum and minimum temperature, total annual, and diel variation, the rate of seasonal change and number of degree-days (Vinson and Hawkins 1998). Temperature is a factor, which is correlated with several others such as altitude, latitude, and season and, in spring- or lake-fed streams distance from source. The findings that certain species will not be found in waters above certain temperatures is probably due to the lower availability of oxygen in warmer waters (Hynes 1970). Temperature varies with season in temperate areas and here low winter temperatures may slow down growth rates of benthic invertebrates. As a result, the higher the altitude and latitude, the later the emergence of many stream insects e.g. Plecopterans in Sweden (Brinck 1949). Ice is also intimately connected to temperature, the freezing of streams and rivers seldom lead to deoxygenation and may in fact protect the water from further cooling (Hynes 1970). Increased water temperature leads to increased feeding and ingestion rates, but also to higher metabolic rates and respiration, and most life history components of benthic invertebrates such as larval growth rates, number of generations per year, and adult size is influenced by temperature (Giller and Malmqvist 1998). Species that occupy a narrow temperature range are called stenothermal, whereas species that can tolerate large variations in temperature are called eurythermal. In the River Continuum Concept (Vannote *et al.* 1980) it is predicted that maximum species diversity will be found at the middle reaches where the amplitude of water temperature is the highest (i.e. most species will during some part of the year find a favorable temperature here). Despite the large influence of the RCC, few studies have actually tested whether these predictions are correct or not (Vinson and Hawkins 1998). In a literature survey on insect richness from both temperate and tropical areas Jacobsen *et al.* (1997) found a linear relationship between maximum annual water temperature and insect richness. Because of this species richness is lower at higher altitudes and latitudes than at lower altitudes and latitudes.

4.2.2 Oxygen

According to Hynes (1970) oxygen is not an important factor in clean rivers (where it does not drop to low levels), except under two conditions: during continuous ice-cover for long periods and if there are large autumn leaf-falls into almost dry streams. In some parts of the river, however, e.g. in stagnant backwaters and among dense vegetation oxygen levels may fall in summertime. Since lotic insects have different abilities to actively move water, they also differ in their ability to tolerate low flow, i.e., many lotic invertebrates are dependent on current to transport oxygen to the integument, since a number of species do not have specialized gills to do this. As was mentioned above oxygen is less soluble in warm than in cold water and the likelihood of oxygen distress is thereby higher in warmer water. Warm water will also cause higher metabolic activities and thereby higher oxygen consumption in the benthic fauna.

4.2.3 Current velocity

A number of stream benthic macroinvertebrates are dependent on a certain current speed either for respiratory requirements or for the transport food particles (Hynes 1970). Hynes (1970) also concludes "...the current speed is a factor of major importance in running water, and that it controls the occurrence and abundance of species and hence the whole structure of the animal community". Flow regime for a stream (seasonal / annual discharge pattern) is influenced by large-scale variables such as climate, drainage basin morphology and geology. There are three main types of flow: laminar, turbulent and transitional. In laminar flow the water moves in parallel layers i.e., they are thought to "slide" pass each other whereas in turbulent flow the water is characterized by irregular movement and the water is mixing. The transitional flow is intermediate between the laminar and turbulent flow. In reality the laminar flow is very rare and will only occur in pipes and above smooth mud surfaces. In a stream, the water moves slower as one gets closer to the bottom and a boundary layer is created, the upper limit of the boundary layer is found where the current is no longer influenced by the bottom. Very close to the bottom there may be a laminar sublayer, where the shear stress is zero and flow is greatly reduced. The current velocity in itself also represents a direct physical force that acts on the organisms both in the water column and at the bottom of the stream or river. Many running water benthic macroinvertebrates have a streamlined shape or different types of suckers or hooks to avoid being swept away by the current and to maintain the preferred orientation in the stream. The speed of the current influences the size of the substrate particles (see below) and current velocity is also important for the transport of e.g. food and oxygen to the organisms (see above). In their review of factors influencing biodiversity in streams, Vinson and Hawkins (1998) found two studies where richness was negatively correlated with current speed or discharge and three other studies where taxa richness was positively correlated with either of them. Current velocity changes in space e.g. between riffles (fast flowing) and pools (slow flowing) areas and in time e.g. increase after rainfalls. Whether pools and riffles differ in taxa richness is not totally clear according to Vinson and Hawkins (1998), Logan and Brooker (1983) found no significant differences in taxa richness between riffles and pools, whereas other studies cited in Vinson and Hawkins (1998) did find significant differences between the two.

4.2.4 Substrate

The substratum is intimately connected to current velocity (see above). One way to classify the particle size of the inorganic substrate is with the Wentworth scale (Cummins 1962; Tolkamp 1980), the classification is based on the diameter of each particle and each size class is twice the preceding one. It is well established that certain species are confined to certain substrate types i.e.

the mayfly *Ephemera danica* are found mainly at particle sizes 0.05-3 mm (Percival and Whitehead 1926). As the substrate type changes so does the fauna (e.g. Berg *et al.* 1948; Illies 1958; Marlier 1951; Percival and Whitehead 1930; Thorup 1966; Vonnegut 1937). The stability and heterogeneity of the substrate are important factors determining diversity, biomass and benthic fauna density in streams. The more stable the streambed is the higher the abundance and diversity of macroinvertebrates. The stability itself increases with mean particle size, and high amounts of organic material found on the inorganic substrate also increases abundance and diversity (Giller and Malmqvist 1998). The substrates though to be the poorest i.e., the most unstable substrates are sandy ones, this is also a relatively uniform substrate. It is generally thought that the higher the heterogeneity of the substrate, the higher the taxon richness found. According to Vinson and Hawkins (1998) this assumption is scale dependent. On individual stones there are more taxa on complex stones than on stones with simple surfaces, but on individual substrate surfaces Vinson and Hawkins (1998) only found higher taxa richness at more heterogeneous patches in 4 out of 10 studies. They also found a number of studies showing that more taxa was found on larger than on smaller substrates (individual stones), but also a few studies that showed the opposite.

4.2.5 Multivariate studies

The analysis of large benthic macroinvertbrate datasets is usually done with classification and ordination (see above). Usually the environmental variables explaining the largest part of the variability in benthic fauna is reported. In Great Britain the benthic fauna community have been used to produce a stream and river prediction and classification scheme (RIVPACS) (see e.g. Furse *et al.* 1984; Moss *et al.* 1987; Ormerod and Edwards 1987 ; Wright *et al.* 1984 and above). In their 1984 paper Wright *et al.* uses 28 environmental variables to predict the classification of 268 sampled sites across Great Britain. The most important variables were substratum type, water chemistry and factors that express position downstream. Later on Moss *et al.* (1987) continued to test what environmental variables best discriminated among their benthic macroinvertebrate classification groups and found that reducing the number of variables from 28 to five did not change the prediction strength very much. These five variables were: distance from source, altitude, air temperature range, mean air temperature, mean substratum particle size. By 1995 some 700 sites were planned to be included in the classification scheme and eight environmental variables were used in all predictions: distance from source, mean substratum, altitude, discharge category, mean water width, mean water depth, latitude, longitude together with five optional environmental variables. In another study in Great Britain, Ruse (1996) sampled the River Mole catchment and during the four sampling years, 116 samples was taken. Out of the 37 measured environmental variables, 13 were deemed significant. The most important of these was distance from source, altitude, temperature range and substrate particle size. Gower *et al.* (1994) sampled benthic macroinvertebrates at 46 sites on twelve metal contaminated Cornish streams in south-west England. At the same time 39 environmental variables were recorded and 17 of these were included in further analysis. The environmental variables that correlated best with the first ordination axis was: copper, aluminium, alkalinity, pH, dissolved organic matter, and algal cover and with the second axis: discharge. In Australia AusRivAS (see above), a prediction system similar to the British RIVPACS have been developed. Smith *et al.* (1999) sampled 188 minimally disturbed sites in Western Australia and 44 physical and chemical variables were also recorded. Four models were built using two habitats, macrophytes and channel and two seasons, the dry and the wet season. In their 1999 paper, Smith *et al.* give the results from the channel habitat in the wet season model including 146 sites. Initially in their model, seven physical and two chemical variables were included, but after testing their model against data collected the following year it was found that changes in water chemistry was not followed by changes in the invertebrate fauna. Thus only the seven physical variables: latitude, longitude, altitude, distance from source, mean annual discharge, flow pattern (episodic, seasonal, perennial etc.), mean river width, and mean depth was included in the model. In a similar sampling scheme in Victoria, Australia, Marchant *et al.* (1999) took benthic macroinvertebrate samples from 199 edge habitats and 163 main channel habitats from 25 drainage basins. Their results showed that the edge community varied longitudinally within the drainage basin (catchment area upstream of site, distance from source, water temperature, riparian vegetation, conductivity, alkalinity and nitrogen). In the main channel habitat variables such as temperature, catchment area upstream of site, mean width, altitude, longitude, conductivity, alkalinity and nitrogen were the most important to discriminate among the macroinvertebrate classification site groups. In another interesting Australian study Faith and Norris (1989) divide their benthic macroinvertebrate taxa into common (40 taxa) and rare (229 taxa). The common taxa were highly correlated with physico-chemical variables related to temperature (minimum and maximum), stream order, altitude, particle size and water chemistry (chloride, sodium, potassium, total phosphate and benthic organic matter). The rare taxa were highly correlated with the same physico-chemical variables as the common and additional ones such as: current velocity (minimum and maximum), conductivity and several water chemistry variables. In northwestern North America Corkum (1989) evaluated the contribution of biogeographical and on-site, hydrological variables to discriminate among benthic invertebrates from 100 river sites. Biogeographical variables were better predictors of the benthic fauna classification than on site hydrological variables. Included in the first function to discriminate among site groupings was: basin drainages, distance from source, latitude, forest, added from the second function was: physiographic region, Cenozoic bedrock and altitude, finally current velocity was a major correlate with both functions. Richards and Host (1993) sampled macroinvertebrates within the Saginaw Bay catchment in central Michigan, USA. The main part of explained variability in the benthic fauna was attributed to physical habitat factors i.e., substrate and riparian zone characteristics. In northern Sweden, Malmqvist and Mäki (1994) examined the relationship between lotic macroinvertebrates and environmental variables from 60 riffle sites. The variables most strongly associated with the benthic fauna were: drainage area, altitude, alkalinity, water color, phosphate and the presence of macrophytes. In another study in the county of Dalarna, Sweden, Malmqvist and Hoffsten (1997) found that the size of the drainage basin, pH, percentage of lakes in the drainage basin, nitrogen and altitude to be important factors explaining macroinvertebrate distributions.

5.0 Summary

Benthic macroinvertebrates are "...organisms that inhabit the bottom substrates (sediments, debris, logs, macrophytes, filamentous algae, etc) of freshwater habitats" (Rosenberg and Resh 1993). These organisms, together with algae, are the most widely used indicators for assessing the quality of fresh water according to a literature survey presented by Hellawell (1986). In reality benthic macroinvertebrate studies are alone the most widespread biological water quality assessment tool (Metcalfe 1989; Sladecek *et al.* 1982; Whitton 1979; Wiederholm 1980). Several authors have summarized the advantages of using benthic macroinvertebrates in biomonitoring (Hawkes 1979; Hellawell 1986; Metcalfe 1989; Rosenberg and Resh 1993; Sladecek *et al.* 1982). The approach for assessing spatial and temporal change of benthic macroinvertebrate communities can be divided into two main groups: univariate and multivariate analysis methods. Univariate studies looks at one response variable at a time whereas multivariate statistics looks at a large set of variables and a large set of sites at the same time. In biomonitoring studies of environmental impact, the objective is to separate the change generated by anthropogenic stress from the natural spatial and temporal variability (Johnson 1998). If the natural variability is large and the anthropogenic induced change is small it will be difficult to detect a real change in the measured variable(s) caused by the pollutant (Johnson 1998). Whether biotic forces structures the local community by keeping the community at or near equilibrium or if variable and unpredictable abiotic factors are the important ones, and species found together are those favored by the local physical conditions of the moment has long been debated (Strong *et al.* 1984, Diamond and Case 1986). Running water ecosystems appear to be variable and harsh environments, and it is often suggested that abiotic factors may have a great influence in these ecosystems (Allan 1995). A number of theories explaining macroinvertebrate community composition in streams have been put forward, in this literature review five of these are presented: longitudinal zonation, island biogeography theory, the River Continuum Concept (RCC), hierarchy theory, and the Patch Dynamics Concept. The most important biotic (competition and predation) and abiotic (temperature, oxygen, current velocity, and substrate composition) as well as a number of multivariate studies trying to explain the differences in benthic fauna community using environmental variables have been presented in this review. In the multivariate studies, drainage area, current velocity, altitude, latitude, longitude and temperature were among the best environmental variables to explain variability in benthic macroinvertebrate data.

6.0 References

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