

OPINION

Long-term studies of freshwater macroinvertebrates: a review of the frequency, duration and ecological significance

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SUMMARY

1. The importance of a long-term ecological perspective is well documented, yet the availability of long-term data remains limited. This paper highlights the value of long-term ecological studies of freshwater macroinvertebrates by reviewing both the availability of long-term data and recent ecological contributions based on them.
2. A survey of recent literature on stream macroinvertebrates identified 46 papers published between 1987 and 2004 that included long-term (i.e. ≥ 5 years) data. Most recently published long-term studies of stream macroinvertebrates began collecting data in the 1970s and 1980s and their duration (time between first and last year sampled) was relatively brief (median = 9 years, maximum = 96 years). Most studies did not expand their temporal perspective by incorporating older data collected by other researchers.
3. Recent long-term studies of macroinvertebrates have made major contributions to our understanding of interannual variation and cycles, complex abiotic and biotic interactions, and natural and anthropogenic disturbance and recovery. Without these studies, we would know much less about the magnitude of natural temporal variation, the importance of physical and biological disturbance and interactions, the role of pathogens and introduced species, the overall impact of pollution and the effectiveness of protection and remediation efforts.
4. If we are to encourage long-term perspectives in our science, we need to facilitate the transfer of individual studies, as well as knowledge and data, among scientists. This includes efforts to archive and annotate data more effectively, so that they can be more easily incorporated into future research.

Keywords: annual variation, aquatic insect, benthic, study design, temporal variability

Introduction

Early ecologists recognised that environmental conditions were temporally dynamic (McIntosh, 1985) and that the temporal length of a study contributed significantly to its conclusions, generalisations and/or predictions. For example, observations distributed

across several days or months may differ from those that span years or decades because longer studies have a greater probability of observing or helping to explain slow, rare, subtle or complex changes in natural environments (e.g. Strayer *et al.*, 1986; Likens, 1989; Elliott, 1990; Risser, 1991; Cody & Smallwood, 1996). Weatherhead (1986) observed that authors noted unusual events less frequently in longer studies, presumably because the longer temporal perspective modified the definition of an unusual event. Although the value of long-term ecological perspectives is well

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documented (e.g. Strayer *et al.*, 1986; Likens, 1989; Elliott, 1990; Risser, 1991; Cody & Smallwood, 1996), the collection of long-term data is still limited by funding constraints, personal or institutional changes in research directions, research careers that last a maximum of 30–40 years and the absence or inaccessibility of comparable data from older research (e.g. Statzner, Resh & Roux, 1994). The purpose of this paper is to illustrate the value of long-term ecological studies of freshwater macroinvertebrates by examining the availability and characteristics of long-term data and describing recent contributions such long-term studies have made to lotic and lentic ecology.

There is a number of classic long-term studies of terrestrial macroinvertebrates (Taylor, 1989). Many of these species are agricultural or forest insect pests of considerable economic significance, which contributed to the initiation and maintenance of the long-term studies. The Rothamsted Insect Survey is probably the most important in terms of spatial and temporal scale (Taylor, 1986; Woiwod & Harrington, 1994). The Hungarian Light-trap Network is a survey similar in scale to the Rothamsted Insect Survey, but less well known (Szentkirályi, 2002). Other classic long-term studies of terrestrial insects include those that Andrewartha & Birch (1954) chose to illustrate general ecological principles in their well-known textbook. Long-term studies of terrestrial macroinvertebrates have documented population dynamics, provided insight into factors affecting distribution and abundance and facilitated pest management and conservation efforts. Because data for terrestrial macroinvertebrates are available for a variety of species, it is not surprising that terrestrial macroinvertebrates played a prominent role in a recent analyses of plant and animal responses to global warming (Parmesan & Yohe, 2003; Root *et al.*, 2003).

Long-term studies are also available for fish from a wide variety of freshwater ecosystems (e.g. Waters, 1983; Erman, 1986; Elliott, 1990; Peterson & Kwak, 1999; Bronte *et al.*, 2003; Gudbergsson, 2004) and, as with terrestrial macroinvertebrates, it seems likely that economic and cultural factors associated with sport and commercial fishing played a role in determining the direction and duration of many of these studies. In addition to contributing significantly to our general understanding of temporal stability in natural populations and communities (e.g. Elliott, 1985; Grossman, Dowd & Crawford, 1990; Strange, Moyle

& Foin, 1993; Grossman *et al.*, 1998; Grenouillet *et al.*, 2001; Oberdorff, Hugueny & Vigneron, 2001), these studies have provided an invaluable perspective on fish fauna responses to habitat modification, flow regulation, climate change and introduced species (e.g. Erman, 1986; Peterson & Kwak, 1999; Aparicio *et al.*, 2000; Eby, Fagan & Minckley, 2003; Gido, Schaefer & Pigg, 2004).

For freshwater macroinvertebrates, the most extensive (temporally and spatially) long-term data have been collected for mosquitoes (Culicidae) and black flies (Simuliidae) as part of pest and disease control programmes. Most of these data remain unpublished, but the published studies have contributed to our understanding of predator/prey interactions, local and regional impacts of weather on population dynamics and spatial variability in population dynamics (e.g. Day & Curtis, 1993; McCreddie, Adler & Masteller, 1994; Lounibos *et al.*, 1997; Wegbreit & Reisen, 2000; Nakamura *et al.*, 2002; DeGaetano, 2005). Most freshwater macroinvertebrates are not economically or medically important and their distribution and abundance have not been commonly measured as part of fisheries or pest management programmes. In addition, because macroinvertebrate communities include many species that can experience rapid and dramatic changes in abundance, relative to longer-lived species such as fish, it can be laborious to generate samples that are temporally representative for long-term analyses (Ladle, 1990). As a result, the temporal perspective in our understanding of freshwater macroinvertebrate ecology is often short (e.g. Resh & Rosenberg, 1989). One exception has been the burrowing mayflies (e.g. *Hexagenia*, *Ephemera*, *Ephoron* and *Palingenia* spp.), a group of freshwater macroinvertebrates that has for decades been subject to long-term ecological study. Adults of these mayflies are often among the largest aquatic insects and their massive, synchronised emergences are often viewed either with awe or as a public nuisance. The dramatic reduction or loss of burrowing mayfly emergences from the Laurentian Great Lakes and the large rivers in the Mississippi River basin in 1950s was a stark indicator of the severity of water pollution across a wide area in the U.S.A. and Canada (e.g. Fremling, 1964; Carr & Hiltunen, 1965). Conversely, their reappearance more than 30 years later has been noted in the popular press (e.g. Masteller & Obert, 2000) and has been used to illustrate water quality improve-

ments resulting from environmental regulations (Fremling & Johnson, 1990; Schloesser *et al.*, 2000; Schloesser & Nalepa, 2001). *Ephoron virgo* (Olivier 1791) exhibited a similar pattern by recently reappearing in the River Rhine after being absent for decades (Kureck & Fontes, 1996).

Long-term perspective in recent studies of freshwater macroinvertebrates

We searched Biological Abstracts between January 1989 and April 2002, as well as our personal literature collections from 1987 to 2004, for research involving long-term studies of stream macroinvertebrates. The literature inventory was limited to ecological studies of stream and river macroinvertebrates, in part because it was the literature best known by the authors and this helped us to evaluate the thoroughness of the search. While this inventory is not complete, we believe it is a representative subset and that the patterns we observed are illustrative for both lentic and lotic macroinvertebrates. We defined a priori a long-term study as one that spanned at least 5 years, which we believe is the minimum time needed to interpret a meaningful representative range of conditions such as wet and dry years or cool and warm years. It also appears to be the minimum time needed to observe responses to some short-term climatic cycles (e.g. El Niños occur every 2–7 years), but obviously not long enough to address decadal or multidecadal phenomena (e.g. Hurrell, 1995; Allan, 2000; Hurrell *et al.*, 2003; Stenseth *et al.*, 2003; Straile *et al.*, 2003). McElravy (1988) observed that only about 5% of hydrobiological studies published between 1980 and 1987 were longer than 3 years and similarly we expected to find relatively few papers that spanned ≥ 5 years.

Our search of Biological Abstracts identified 5645 articles published during the 160-month period that addressed freshwater macroinvertebrates (e.g. mayflies, stoneflies, caddisflies, or chironomid midges). Of these, only 188 (i.e. 3%) had either 'long-term' or 'annual' in the title, abstract or key words. Of these, only 26 actually included stream macroinvertebrate data spanning ≥ 5 years. Twenty additional papers from our personal literature collections included long-term stream macroinvertebrate data and were published between 1987 and 2004. Data from these 46 papers addressed a total of 236 sites and the scope

ranged from studies of a single species at one site to entire macroinvertebrate assemblages at multiple sites. There is some redundancy among studies in that data from some sites are incorporated into more than one paper. For example, portions of the data from 30 years of sampling adult insect emergence from the Breitenbach (a tributary of the Fulda, Germany) have appeared in four different papers (Statzner & Resh, 1993; Wagner, Dapper & Schmidt, 2000; Obach *et al.*, 2001; Wagner, 2002). Studies using data from the same sites were considered independent analyses if the questions asked or data analysed were not identical. Studies of interannual variation associated with natural conditions or as part of water quality assessment programmes were most common in the recently published papers we examined. Other studies were natural experiments focused on extreme disturbances such as forest fires, severe floods or droughts. Finally, some studies were planned experiments involving large-scale manipulations such as deforestation or pollution remediation.

Few of the recently published studies included data collected before 1970 and only one included data from before 1940 (Fig. 1). This appears to reflect the limited data available because ecological studies of freshwater macroinvertebrates were less common more than 60 years ago than they are today and fewer topics were addressed (Minshall, 1988; Resh & Rosenberg, 1989; Wallace, 1992). Hynes (1970) noted in the first comprehensive book on lotic ecology that, of the more than 1500 references he cited, over half were <10 years old. Most of the long-term studies that we examined began with data from the 1970s (21%) or 1980s (63%). The bias toward this period reflects, in part, the initiation of national or regional water quality assess-

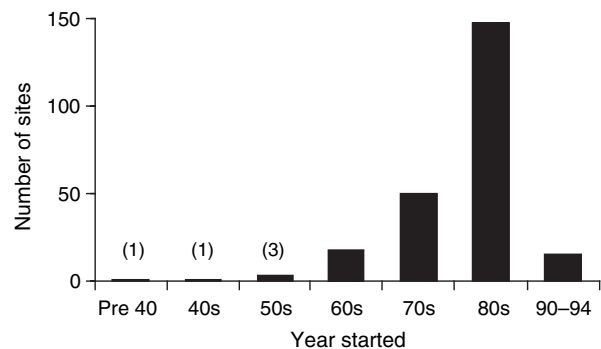


Fig. 1 Number of long-term study sites at which data collection began in each year between 1901 and 1994.

ment programmes. For example, of the 148 sites with data beginning in the 1980s, 68% were from stream assessment programmes in New Zealand (Scarsbrook, Boothroyd & Quinn, 2000) and acid rain studies in Wales (Weatherley & Ormerod, 1990; Bradley & Ormerod, 2001, 2002). Studies starting in the 1990s are not well represented in these recently published papers. Given the time needed for researchers to develop and publish long-term research, we expect that studies that started in the 1990s are only now beginning to appear in the peer-reviewed literature and much of it remains unpublished or in the grey literature. Because most recently published long-term studies relied on data that began to be collected in the 1970s or 1980s, the duration of these studies is limited to about 30 years or less (Fig. 2). It also means long-term perspectives in recent publications are generally not being formed by incorporating older data (e.g. from the 1940s through 1960s) into analyses.

Across the 236 sites with long-term data, study duration ranged from 5 to 96 years (Figs 2 & 3). Most (85%) lasted 5–10 (63%) or 11–15 (22%) years. The majority (65%) of the sites were subject to continuous sampling (i.e. data collected every year; Fig. 3). Among the sites with discontinuous data (data missing from one or more years), the number of years sampled relative to the duration of the study ranged greatly. In some cases, data were missing for only one of several years (e.g. Bradley & Ormerod, 2001, 2002). In other cases, data were missing from most if not all years between the first and last year sampled (e.g. Townsend, Hildrew & Schofield, 1987; Johnson, Brown & Covell, 1994; Grubaugh & Wallace, 1995; Strayer & Fetterman, 1999; Woodward, Jones & Hildrew, 2002). Discontinuous data sets contained data from an average of 47% of the years (range =

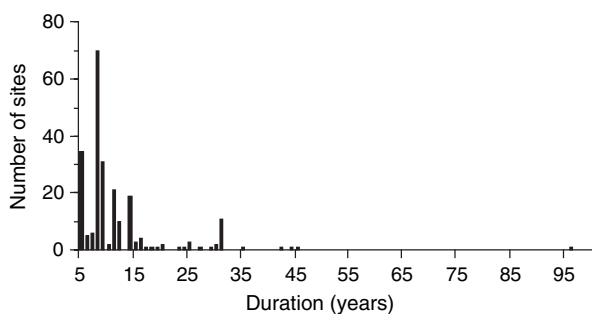


Fig. 2 Frequency of long-term studies expressed as the total number of sites versus study duration (years between the first and last year sampled).

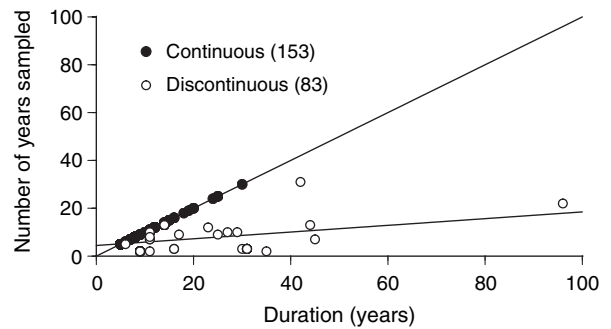


Fig. 3 Comparison of the number of years sampled in continuous studies (i.e. annual data) and discontinuous studies (i.e. data not available from all years) versus study duration. The total number of sites is in parentheses. Lines are 1 : 1 for continuous studies and a simple linear regression ($r^2 = 0.11$, $P < 0.05$) for discontinuous studies.

6–93%) and some analyses included data from researchers not participating in the current publication. For example, Vinson's (2001) analysis of the long-term dynamics of stream invertebrates below Flaming Gorge Dam on the Green River involved a 50-year perspective developed with data from 14 sources. The median duration in our literature survey was 9 years across all studies, 8 years for continuous studies and 11 years for discontinuous studies. The longest continuous study was 30 years of adult insect emergence from the Breitenbach (Obach *et al.*, 2001). Of the 34 sites with data spanning >15 years, 24 (71%) had discontinuous data. Thus, discontinuous data are more commonly associated with longer duration studies.

The above results indicate that the temporal perspective for most studies of freshwater macroinvertebrates in the recent literature is short. Among 'long-term' studies of freshwater macroinvertebrates, the temporal perspective is still generally limited relative to rare events such as severe disturbances (e.g. floods, fires and hurricanes with return intervals of >50 years), cyclical phenomena such as climatic cycles, or slow phenomena such as forest maturation or anthropogenic changes that affect land cover, pollutants or climate. In addition, as we noted above, older studies (i.e. pre 1970) are not commonly being revisited to generate a long-term perspective in the current literature. Although still temporally limited, recent publications based on long-term studies have made important contributions to our understanding of aquatic and terrestrial (i.e. catchment) ecosystems.

Recent contributions to lotic and lentic ecology

The studies highlighted below were picked to illustrate recent contributions of long-term studies of freshwater macroinvertebrates to lotic and lentic ecology. They show how long-term studies can establish a baseline from which interannual variation in environmental conditions (natural or anthropogenic) can be measured and interpreted, increase the probability of detecting and understanding phenomena that are long-term in their dynamic and help explain complex phenomena that are poorly understood and cannot be predicted from short-term studies. These insights have helped to formulate hypotheses that integrate short- and long-term perspectives and to provide direction for research and policy.

Examples of interannual variation and cycles

The measurement and understanding of interannual variation in freshwater macroinvertebrate populations and assemblages are just beginning, in part because of the brevity of most data sets (see above) and also because of the complexity of this natural variation. Life spans for most freshwater macroinvertebrate species range from <1 month to >2 years for many arthropods and worms and from 1 to 10–150 years for some molluscs (e.g. Comfort, 1957; Bauer, 1992; Wallace & Anderson, 1996; Huryn & Wallace, 2000; Ziuhanov *et al.*, 2000). This makes it difficult to generalise about the relationship between the macroinvertebrates and their environment because the interaction may reflect daily, seasonal or annual events, depending on the species and location.

Similar to the terrestrial studies of Andrewartha & Birch (1954), Wagner *et al.* (2000) found that stream insects respond strongly to weather conditions (temperature and hydrologic regime). The authors examined 24 years of emergence for two mayfly species from the Breitenbach and found that variation in annual emergence reflected annual variation in stream discharge. *Baetis rhodani* (Pictet) was most abundant in years with continuously high discharge and with seasonal discharge, while *Baetis vernus* Curtis was most abundant in years with non-seasonal events. A 7-year study of freshwater macroinvertebrates in a coastal California stream also found that population

densities and community structure differed significantly among wet, average and drought years and this appeared to reflect variation in the hydrologic regime (McElravy, Lamberti & Resh, 1989). Molles & Dahm (1990) suggested that the McElravy *et al.* (1989) data represented evidence that climatic cycles (i.e. an El Niño/La Niña cycle) had a significant impact on stream macroinvertebrates. Bradley & Ormerod (2001) found similar evidence of a relationship between climatic cycles and stream invertebrates over a 14-year period across eight streams in Wales. Macroinvertebrate persistence (as measured by rank abundances and similarity) exhibited synchronous cyclical patterns across streams with different chemistry and land use. The patterns paralleled the North Atlantic Oscillation, although the mechanisms producing the approximately 8-year cycle were not clear. In an Estonian lake, Kangur *et al.* (1998) observed both short-term (3–4 year) and long-term (11 year) periodicities in chironomid and oligochaete abundances between 1964 and 1996. They suggested that solar activity contributed to the long-term periodicity.

While climatic conditions can influence interannual variation in macroinvertebrate populations, cyclical patterns can be an expression of other factors. A 20-year study of chironomids emerging from Lake Myvatn in Iceland found that abundance varied up to several orders of magnitude among years (Gardarsson *et al.*, 2004). Emergence numbers for several univoltine and bivoltine species oscillated with an approximately 7-year cycle, whereas other chironomid species exhibited no cyclical pattern. Based on a detailed analysis of the dominant chironomid *Tanytarsus gracilentus* (Holmgren) and the ecologically similar *Microspectra lindrothi* (Goetghebuer), it appears that consumer–resource interactions, rather than predator–prey interactions, create the cyclical dynamics in abundance and body size and amplify interannual variation that results from other factors (e.g. temperature, rainfall, wind; Einarsson *et al.*, 2002). High chironomid densities deplete sediment food resources while low chironomid densities allow resource quality or quantity to recover. The long period between emergence peaks (seven to 14 generations) indicates that depleted resources may be slow to regenerate. Einarsson & Örnólfssdóttir (2004) suggest that cycling of food resources and sediment conditions associated with chironomid populations also affects benthic Cladocera in Lake Myvatn.

Imbedded within studies of interannual variation and cycles can be the impact of severe disturbances that occur naturally, are relatively rare and can have long-lasting effects.

Examples of severe disturbance

Our survey of the recent literature suggests that severe natural disturbance was a focus of lotic research. Macroinvertebrates in streams and rivers experience a variety of abiotic disturbances that differ in frequency and severity. Severe disturbance that physically restructures stream channels and catchments and results in catastrophic mortality for macroinvertebrates tends to be infrequent, and the degree of change and rate of recovery are often undocumented. Recent long-term studies have examined the impact and long-term recovery of stream macroinvertebrates following wildfires and severe weather. A series of long-term studies in western North America found that the fires appeared to have little direct effect on stream macroinvertebrates. However, the stream macroinvertebrates were severely affected by physical disturbances associated with increased runoff and erosion from the deforested landscape (Minshall *et al.*, 2001a; Minshall, Royer & Robinson, 2001b; Vieira *et al.*, 2004). The recovery trajectory of streams impacted by wildfires was more rapid than expected, although normal environmental variation (i.e. precipitation events) affected this trajectory as an increase in stream discharge can result in significant setbacks. Minshall (2003) predicts that stream ecosystems impacted by severe forest fires will not stabilise for at least 10–15 years.

A long-term study in a perennial Neotropical stream in Puerto Rico has documented the response of freshwater shrimp species to a severe hurricane (Hugo), followed 4 years later by a prolonged drought (Covich *et al.*, 1996; Covich, Crowl & Scatena, 2003). Both disturbances affected shrimp abundance along elevation gradients – the distribution of *Atya lanipes* Holthuis and *Xiphocaris elongata* (Guérin-Méneville), changed in response to disturbance, whereas that of *Macrobrachium carcinus* (Linnaeus) and *Macrobrachium crenulatum* Holthuis did not. Severe hurricanes have a return interval of 50–60 years for this area (Scatena & Larsen, 1991), while droughts occur every 5–10 years (Covich *et al.*, 2003). Thus, contrary to the popular view of the tropics as a temporally stable environ-

ment, macroinvertebrate communities in tropical streams are dynamic, reflecting not only seasonal and annual variation in environmental conditions and biological interactions (e.g. Flecker & Feifarek, 1994), but also the effects of severe disturbances that are infrequent.

Examples of complex relationships

Studies of biological interactions or the relationships among consumers, food resources and abiotic conditions have been undertaken extensively for freshwater macroinvertebrates. However, most of these studies represented relatively short-term experiments and isolated observations. Long-term data have provided additional insights into relationships that are often complex. For example, long-term, large-scale studies of a grazing caddisfly, food resources and other invertebrate consumers confirmed the direction of relationships observed in short-term experiments. The long-term studies also found that the extent and magnitude of the impact of the grazing caddisfly was underestimated in short-term, small-scale experiments (Kohler & Wiley, 1997). These same studies led to the discovery of a significant interaction between microsporidium pathogens and their caddisfly hosts (e.g. Kohler & Wiley, 1997; Kohler & Hoiland, 2001). In both species studied, cyclical population dynamics appear to be driven by pathogens. Although the potential importance of these pathogens has been known for over a decade, studies of pathogens and freshwater macroinvertebrate populations remain rare.

A recently published 16-year study of the Kuparuk River in Alaska (Slavik *et al.*, 2004) is another example of how experimental outcome can depend on study duration. This phosphorus addition study found that macroinvertebrate responses observed after 4 years differed markedly from responses observed after 16 years. Initially, fertilisation increased production at all trophic levels, but there was little change in macroinvertebrate community structure. However, bryophytes replaced epilithic algae 8–10 years into the experiment and this appeared to contribute to significant changes in macroinvertebrate community structure. Thus, there was a delayed ecosystem response to nutrient enrichment in the Kuparuk River that could only be observed with a long-term study.

Another example of how long-term data have helped resolve complex relationships involves the interactions between food, climate and habitat for the amphipod *Monoporeia affinis* (Lindström) in Swedish lakes (Johnson & Wiederholm, 1992; Goedkoop & Johnson, 2001). The longer temporal scale provided significant insight into the impact of climatic factors (i.e. total solar irradiance) in structuring these freshwater communities and showed how the relative importance of concurrent mechanisms (e.g. food resources, nutrient availability, hypolimnetic temperature, hypoxia) can vary seasonally and interannually. For example, increases in total solar irradiance as part of the multi-year solar cycle resulted in greater spring diatom production and greater amphipod densities 1 year later in Lake Vänern.

Examples of anthropogenic disturbance and recovery

Many long-term data sets have been used to provide an essential temporal/historical perspective in studies of anthropogenic disturbance. Some of these data reflect general monitoring efforts, while others resulted from planned experiments looking at specific management or remediation practices. Because it is in this arena that long-term science most frequently interfaces with environmental planning and management, we believe that in the future this connection will produce many long-term data sets, just as the economic implications of agricultural and forest pests have resulted in many of the long-term studies of terrestrial insects that exist today.

Freshwater macroinvertebrates are a cost-effective, commonly used and widely accepted tool in water quality monitoring (Rosenberg & Resh, 1993) and they have provided water quality assessment programmes with valuable insight for more than 100 years (Hella-well, 1986; Cairns & Pratt, 1993). In the last 30 years, legal mandates or regional concerns have resulted in numerous large-scale monitoring programmes that use freshwater macroinvertebrates to assess water quality. These programmes generate data vital to the evaluation and validation of regulatory efforts. Much of this information remains generally unavailable in paper and electronic files and reports with limited circulations (e.g. Davies *et al.*, 1999; Bode *et al.*, 2004). However, some results from these programmes are now beginning to appear in the peer-reviewed literature, adding to our understanding of both impaired

and natural conditions in freshwater ecosystems. For example, the long-term study with the greatest combination of temporal (29 years) and spatial (a peak of 50 000 km of rivers) scale that we found in the recent literature resulted from the Onchocerciasis Control Programme in 11 West African countries (Yaméogo *et al.*, 2001; Resh, Lévêque & Statzner, 2004). The unmatched temporal and spatial scale of this project reflects the medical, social and economic significance of river blindness in West Africa. While only a fraction of the data has been published, the study provides insights into the resilience of freshwater macroinvertebrate assemblages, the confounding influences of natural environmental variation and the benefit of additional short-term descriptive and experimental projects to supplement the long-term study.

Scarsbrook *et al.* (2000) recently examined data collected over 8 years from 30 reference streams and 36 impaired streams in New Zealand. Conditions at reference sites (and to a lesser degree impaired sites) improved significantly throughout the study. They suggested that this multi-year, regional improvement reflects changes in regional climatic conditions, rather than river management practices. Thus, this study illustrates how climatic conditions may mask responses (improvement or degradation) to management practices and the potential importance of revisiting site classification criteria as more data become available. It also provided a measure of natural variation that may affect other studies of freshwater organisms in the region (Elliott, 1990).

Marten (2001) exploited a long history of macroinvertebrate studies when combining data from several sources to illustrate the disturbance and recovery of macroinvertebrates in the river Rhine between 1903 and 1998. This was the longest study identified in our literature search. During this 96-year period, species richness was observed to decline dramatically and then to return to early 20th century conditions. While the increase in total species richness suggests a remarkable recovery for the Rhine, many of the original species were never collected again. Instead, much of the increase represents species not previously found in the river. A primary source of these introduced species may be the Danube, which is connected to the Rhine by the Rhein-Main-Donau canal. Thus, recovery to date has not resulted in a return to the earlier condition but rather the establishment of a new state that includes many introduced species. Without

the older data, the continued absence of many native species could not have been documented.

Marten (2001) is a rare example illustrating the process of biotic homogenisation for freshwater macroinvertebrates. Biotic homogenisation is the changing community structure through habitat modification, loss of native species and introduction of non-native species (Rahel, 2002). This phenomenon challenges efforts to conserve, restore and manage native freshwater fish faunas throughout the world (Rahel, 2002). While most introductions of non-native macroinvertebrates occur without notice, impacts that resulted from the introductions of the zebra mussel (*Dreissena polymorpha* (Pallas); Strayer, Hattala & Kahnle, 2004), New Zealand mud snail (*Potamopyrgus antipodarum* (Gray); Hall, Tank & Dybdahl, 2003), various crayfish (Cambaridae; Lodge *et al.*, 2000) and opossum shrimp (*Mysis relicta* Lovén; Stafford *et al.*, 2002) illustrate the potentially negative effect of non-native macroinvertebrates on freshwater ecosystems. Long-term studies (especially those that look at ecosystem function as well as structure) will have an important role in interpreting the impact of these species introductions.

Long-term studies put a time frame on acid rain (e.g. Likens & Bormann, 1974) and they are now being used to examine recovery (e.g. Soulsby *et al.*, 1995; Johnson, 2000; Bradley & Ormerod, 2002). These studies have demonstrated that remediation efforts (source reduction and/or lime applications) are effective at some sites but not others. They also suggest that early conclusions may not agree with the long-term perspective (cf. Slavik *et al.*, 2004 above). For example, rapid improvement in the first years after lime application may be followed by a period with little additional improvement. Conversely, early improvements may appear limited because more than a few years are needed for dispersal if certain taxa are to 'recover'.

The potential for additional insights into freshwater ecosystems is great as other programmes for monitoring and/or managing anthropogenic disturbance generate their own data and analyse it. These efforts will not only describe current conditions, but also make possible a historical perspective against which future change (natural or anthropogenic) can be judged. This historical perspective is sorely missing in current monitoring and management efforts. The challenge for all these programmes and for future

analyses based on their data, will be to ensure that historical data are comparable. This challenge actually applies to all long-term studies and it increases with time as researchers change, methods evolve and new questions arise.

Future contributions from long-term studies of freshwater macroinvertebrates

Although long-term data are not common, a long-term perspective is inherent in many of the general topics addressed (e.g. hydrologic regimes, disturbance, succession, biological monitoring, river continuum) in the most widely cited papers in freshwater benthic science (Resh & Kobzina, 2003). The above examples illustrate the many ways that long-term studies of macroinvertebrates have contributed to our knowledge of freshwater ecosystems. They have quantified natural variation in freshwater ecosystems and shown that it reflects abiotic and biotic cycles as well as rare, episodic events. They have demonstrated anthropogenic changes in freshwater ecosystems and helped to evaluate efforts to mitigate these changes. They have also shown the temporal limitations (and strengths) of short-term experiments. Overall, long-term studies have led to new discoveries and unexpected insights for freshwater macroinvertebrates and ecosystems that could not have been evident from more temporally limited studies.

Future increases in our understanding of the theoretical foundation of and practical issues for, freshwater ecosystems will depend on a combination of short- and long-term studies. Freshwater macroinvertebrates will no doubt have an important role in many of these studies because of their ecological importance and scientific attraction: they are numerous, often dominant, consumers that can be collected quantitatively and manipulated experimentally. The duration of studies on freshwater macroinvertebrates will continue to be limited by availability of funds, changes in personal or institutional research directions and the brevity of professional careers (e.g. Statzner *et al.*, 1994). However, it seems clear that the temporal perspective of ecological studies can and should be expanded relative to the perspective presented in most recently published papers.

We have three suggestions that should help expand the temporal scale in studies of freshwater macroinvertebrates. First, researchers need to look to

both continuous and discontinuous approaches to generate long-term studies. Both can measure change over time, but in different ways and with different investments. Second, ongoing studies with long-term potential need to be transferred to colleagues dedicated to continuing the effort. For example, the long-term study of stream insect emergence from the Breitenbach started by Joachim Illies in 1969 (e.g. Illies, 1975, 1979) generated 12 years of data before his sudden death in early 1982. Colleagues continued the study, which allowed Obach *et al.* (2001) to examine 30 years of data. Without being transferred to colleagues, long-term studies will rarely last more than 30 years. While 30 years is long relative to the temporal perspective in most published papers we examined (Fig. 2), it is still temporally limited relative to ecological phenomena such as 50- or 100-year floods or droughts, climate change, forest or soil maturation, or major changes in anthropogenic activities or land use. Third, after papers are published and researchers retire or move to new projects, options are needed to archive raw data with essential annotation and in some cases voucher specimens so they can be retrieved later.

Peer-reviewed publications are valuable sources of information and insight, but they are often not a good source of data for generating a long-term perspective because the data are generally not presented with that purpose in mind. This can greatly limit future use of the data. Some journal publications are currently linked to electronic data archives (e.g. publications of the Ecological Society of America), but most are not. Government agencies and programmes involved in environmental monitoring have taken significant steps to address the need to transfer studies among colleagues and to archive data. The U.S. Long Term Ecological Research (LTER) Network has more than 2000 ecological datasets in a network-wide information system designed to facilitate data exchange and integration. Unfortunately, most research data and peer-reviewed publications are products of academic research programmes that do not have the necessary space, background and/or resources to archive data. Long-term electronic storage of data has many advantages over paper records, but it has costs and challenges that make it virtually impossible to keep data from all projects.

Because it is difficult to anticipate future research needs or directions, any success in transferring

studies or archiving data with appropriate annotation and vouchers will increase the potential for a longer temporal perspective in studies of freshwater macroinvertebrates. Our challenge is to keep in mind that temporal variation is inherent in our science such that, no matter how long our run of data, it is only a snapshot of the natural pattern. The type, magnitude and sometimes even the direction of responses or signals we see can depend on our temporal perspective as defined by the duration of our data.

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