MAYFLIES, BIODIVERSITY AND CLIMATE CHANGE

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Abstract

Mayflies (Ephemeroptera) are an ancient order of insects that are globally distributed in both northern and southern hemispheres and have survived major environmental shifts. Despite the problems associated with selection processes operating in both terrestrial and aquatic environments, mayflies have successfully colonized a wide range of freshwater habitats from the tropics to the arctic, a somewhat greater range than other hemimetabolic aquatic insects such as the Plecoptera and Odonata. While many species of Ephemeroptera require specific environmental cues, others display considerable flexibility in life cycle length and timing in relation to environmental changes. This is particularly apparent in arctic and alpine species. Climate change scenarios predict rapid shifts across many environmental gradients, including temperature and the frequency and magnitude of floods and droughts. Changes in the mayfly fauna are hypothesized in the light of the environmental tolerances, life cycle plasticity and the dispersal mechanisms of present day mayflies. During periods of rapid environmental transition certain species traits will be beneficial. Generalists will do better; specialists with strict environmental limits and poor powers of dispersal may become extinct.

Key words: mayflies; Ephemeroptera; climate change; life cycles; alpine; streams; lakes; temperature; ice cover; floods; dispersal; species traits.

Introduction

Mayflies (Ephemeroptera) are an ancient order of insects, first appearing in the fossil record in the Upper Carboniferous in excess of 250 million years ago (Brittain 1980). Mayflies have a complex life cycle, involving both aquatic and terrestrial phases. Such life cycles create evolutionary dichotomy with selection pressures operating in two, more or less, independent environments (Wilbur 1980). In theory, this dichotomy will lead to the reduction of one of these phases. This is clearly seen in the extremely short-lived adult stages of the Ephemeroptera, whose sole, but crucial roles are reproduction and dispersal.

The Ephemeroptera are a small order of insects, numbering about 3000 described species within 37 families (Brittain and Sartori 2003). Despite the problems associated with selection processes operating in both terrestrial and aquatic environments, mayflies have survived many climatic shifts and have successfully colonized a wide range of freshwater habitats from the tropics to the Arctic and from large rivers to small ponds. In comparison with the stoneflies (Plecoptera), they have made a greater intrusion into the tropics, both in terms of diversity and abundance, at the same time as they are more abundant and diverse than the dragonflies (Odonata) in Arctic and alpine regions (Brittain 1990, Fig. 1). In this paper, future trends in the mayfly fauna as a result of climate change are hypothesized in the light of the environmental tolerances, life cycle plasticity and the dispersal mechanisms of present day mayflies.

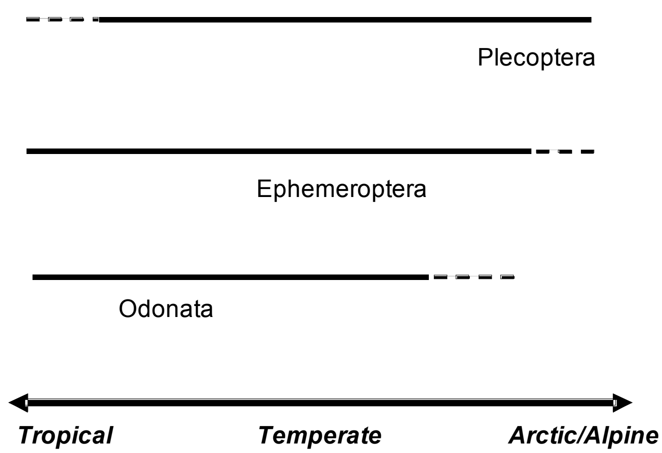

Figure 1. Optimal and suboptimal geographic and climatic regions for the aquatic insects orders, Plecoptera, Ephemeroptera and Odonata.

Climate Change

Climate has changed many times over the course of the Earth's history. Over the past two million years there have been numerous Ice Ages, but at present we are in a warm interglacial period. The geological record reveals that past climate change has not always been gradual, rather there have been many changes that were very rapid; over periods as short as centuries or decades (Bonan 2002). Beginning around 1550 A.D. and lasting until 1850 was a period of cold temperatures, known as the "Little Ice Age" (Lamb 1995). Temperatures warmed by over 0.5°C between the mid 1800s and the 1940s, but cooled again over the next 25 years. Since then temperatures have been rising and current predictions indicate increases of annual mean air temperatures as much as 8°C by the end of the century in some regions (IPCC 2001).

These changes are predicted to be greater in arctic and alpine regions and thus emphasis in this paper is given to aquatic ecosystems in these areas.

Response to Temperate Changes

Aquatic organisms and ecosystems respond to climate change in a variety of different ways. There are four main consequences of climate change at the species or population level: simple adaptation, demographic change, emigration/immigration and extinction. Adaptation can involve inherent plasticity in response to environmental change or be accomplished by longer-term evolutionary change. Demographic effects include changes in recruitment, mortality and growth, while emigration and immigration will produce changes in species' distributions. These processes, including extinction, can give rise to changes, both in ecosystem structure and function. At the ecosystem level, the primary effects of temperature and runoff changes will give rise to a number of secondary effects, affecting physico-chemical aspects such as length of the ice-free season, decomposition, weathering and water residence time, as well as affecting levels of primary and secondary production (Hauer et al. 1997, Rouse et al. 1997).

Water temperature steers many of the physiological processes in aquatic insects and all life cycle stages respond to changes in temperature (e.g., Brittain 1980, Ward and Stanford 1982, Sweeney 1984). This is particularly apparent in the egg stage, and in many mayflies there is a clear relationship between water temperature and the length of egg development, as well as distinct temperature limits for successful development (Elliott and Humpesch 1980). The effect of such limitations on distribution can be illustrated in the Australian mayfly genus, *Coloburiscoides*. This genus is widespread in the higher regions of mainland southeastern Australia, but is absent from apparently suitable habitats in Tasmania. Laboratory studies demonstrated that despite its assumed adaptation to cooler environments, the eggs only hatch successfully between 15 and 25°C (Brittain and Campbell 1991). It is, therefore, likely that this genus became extinct in Tasmania during a recent glacial period as water temperatures were too low for successful egg development.

Adult body size in many hemimetabolous insects depends largely on thermal conditions during development, while adult size in mayflies is closely correlated with fecundity (Brittain 1980, Elliott and Humpesch 1980). It therefore follows that smaller adults and lowered fecundity result when temperatures are suboptimal (Sweeney and Vannote 1978). Thus, a species' distribution both locally and regionally is limited, at least in part, by lowered fecundity as adult size gradually diminishes in streams that are either too warm or too cold. Such relationships will lead to changed mayfly distributions under global warming.

Many mayfly species, especially among the Baetidae, display considerable life cycle plasticity, being able to change the number of generations per year in response to changes in temperature. For example, the widespread western Palaearctic species, *Baetis rhodani*, that has several generations a year in warmer lowland habitats, is univoltine in cooler streams and even displays a two-year semivoltine life cycle in alpine areas (Sand 1997). In a warmer climate, such species will be able to shorten generation time and increase the number of generations per year.

The timing of mayfly emergence also frequently depends on temperature (Brittain 1980) and earlier emergence is likely in many mayfly species in a warmer climate. Relatively small shifts in temperature in warmer years or at lower altitudes have been shown to cause significant changes in the timing of the onset of mayfly emergence (Brittain 1976, 1978, 1980), although not always (Langford 1975). In laboratory studies, emergence has been advanced by several months by artificially increasing temperatures (Nebeker 1971). A shift in emergence as a result of rising temperatures has already been reported by fly fishermen who are especially focused on the "mayfly hatch" in an English river (The European Times 1992).

In arctic and alpine areas, the balance of water sources between glacial or kryal, spring-fed or krenal and snowmelt/precipitation or rhithral is crucial in determining biological communities (Ward 1994, Füreder 1999). This interplay of these different water sources operates via two main pathways, fluvial processes and water quality (Fig. 2). The important role of water source was clearly demonstrated in a study of the benthic macroinvertebrate fauna of two contrasting alpine catchments, the one glacier-fed and the other dominated by groundwater inputs (Füreder et al. 2003). Mayflies were much more abundant in the nonglacial system, although the wider food niche of species inhabiting glacial rivers was much broader than in the spring-fed system, demonstrating the adaptive nature of certain mayfly species faced by paucity of food resources.

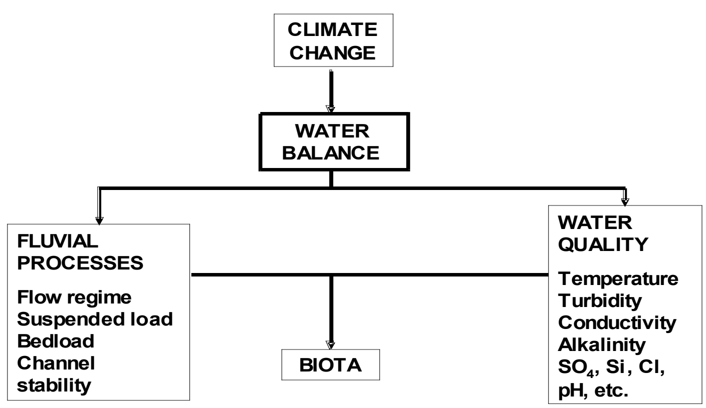

Figure 2. The conceptual relationship between stream biota and climate change in Arctic and Alpine ecosystems.

Climate change, by altering the water balance in arctic and alpine regions, will cause changes in mayfly species' distribution and abundance. In general, an increase in diversity of mayflies in temperate and arctic regions, as well as expansion further up into alpine areas is to be expected as a result of global warming (Lillehammer and Brittain 1978, Hauer et al. 1997). However, this could be confounded by the upward and northward movement of the tree line and a concomitant decrease in primary production as a result of increased shading. This may negatively affect the mayflies, which are predominantly grazers. In addition, there will be the increase, at least in the short-term, of cold adapted species in watercourses affected by glacial runoff (Melack et al. 1997). Increased discharge in glacier-fed watercourses as a result of warmer summers will cause reduction in water temperatures, increased turbidity and greater channel instability, which in turn will result in changes in benthic composition and abundance (McGregor et al. 1995, Milner et al. 2001a). Among the changes predicted downstream is an expansion of cold-adapted species such as the Diamesinae at the expense of other invertebrate taxa such as the mayflies. Primary production would also be reduced, again making the environment less favourable for most mayflies. However, in the southern hemisphere leptophlebiid mayflies occur close to glacial margins and such species are unlikely to be adversely affected by increased glacial runoff (Milner et al. 2001a). These include the mayfly genera *Deleatidium* in New Zealand (Milner et al. 2001b) and *Meridialaris* in Patagonia (Wais and Bonetto 1988).

There may be other unexpected effects of global warming on the balance of water sources. In the cold regions of the world, permafrost limits the availability of groundwater to lakes and rivers. However, under polythermal glaciers, temperatures at parts of the glacier base along with a steep hydraulic gradient may permit groundwater intrusion. However, the retreat of the front position of many glaciers as a result of global warming can expose new areas to permafrost, thereby cutting off groundwater sources (Haldorsen et al. 2002). In fact, under a rapidly changing climate regime, such as predicted for future anthropogenic global warming, groundwater influxes will be crucial in maintaining spatial and temporal heterogeneity in freshwater systems (Malard et al. 1999, Ward and Uehlinger 2003) and will provide refugia for mayfly species affected by climate change and other human impacts. Groundwater influenced systems are characterised by stability in environmental characteristics and will in general be less affected by changing air temperatures, although changes in runoff will undoubtedly affect water table levels.

Response to Other Effects of Climate Change

Climate change scenarios predict rapid shifts in environmental conditions, not only air temperatures, but also in precipitation and runoff. This will change the frequency and magnitude of floods and droughts. Precipitation will also affect the extent and duration of ice cover in cold regions.

Air pressures in the Atlantic Ocean affect ocean currents, temperature and precipitation in the North Atlantic, northern Europe and even further a field (Straile et al. 2003). A high winter North Atlantic Oscillation (NAO) index, based on the difference in sea-level air pressure measured close to the centre of the Azores High and that measured at a station in Iceland, results in mild, moist air currents over northern Europe. An increase in the NAO index is predicted in climate change scenarios and is already taking place, giving a deeper snow pack in the mountains of western Norway. A deeper snow pack delays ice break resulting in a shorter ice-free season in mountain lakes (Borgstrøm 2001). In the lakes of southern Norway, the number of mayfly species has been shown to be highly correlated with the length of the ice-free season (Brittain 1974). A shorter ice-free season is likely to give rise to lower summer water temperatures and lower primary production, both disadvantageous for mayfly diversity, while a longer ice-free season will have the opposite effect. It is predicted that in mountains areas, especially in the high precipitation areas of western Norway, the winter snowpack and the length of the period of ice cover will increase. However, in lowland areas the extent of ice cover will decrease and winter floods will become more frequent. The absence of ice cover during winter permits some degree of primary production and it has been shown that mayfly densities and growth rates can be significantly higher in ice-free sections of alpine rivers (Schütz et al. 2001).

Floods have a major structuring effect on aquatic communities, triggering species replacement and succession. Certain climate scenarios predict an increase in the frequency and magnitude of floods. Floods, especially those with a long return time, can have a catastrophic effect on mayfly communities (Pupilli and Puig 2003). In less catastrophic floods, there may be a shift in dominance in benthic communities as a result of high discharge (e.g., Anderson and Lehmkuhl 1968, Fjellheim and Raddum 1993). In alpine streams in central southern Norway, an unusually high spring flood significantly decreased densities of the mayfly, *Baetis rhodani*, which was present as nymphs at that time. In contrast, densities of the summer species, *Acentrella lapponica*, present in the egg stage down in the substrate, increased in the two years after the flood (Sand and Brittain 1997). Floods are also important in terms of dispersal, opening up waterways and establishing connectivity between watercourse elements and permitting the establishment of new populations.

While runoff will increase in some regions as a result of climate change, it will decrease in others. Droughts and low flows will also impact mayfly communities. In rivers regulated for hydropower, flows are frequently reduced for all or part of the year. Such flow reductions favor genera characteristic of lentic habitats, such as *Cloeon, Paraleptophlebia* and *Siphlonurus* at the expense of the typical lotic genera such as *Baetis, Rhithrogena* and *Epeorus* (Brittain and Saltveit 1989). A similar shift may take place as a result of climate change.

Dispersal and Gene Flow

In a changing environment brought on by climate change, dispersal ability will be crucial to species survival. If a species is unable to adapt physiologically to a changed climate regime in its present habitat, then it must be able to reach a suitable environment by dispersal. If not, extinction will result and it has recently been predicted that on the basis of climate scenarios for 2050, that between 18% and 35% of all plant and animal species on the Earth are committed to extinction (Thomas et al. 2004).

Mayflies, particularly Baetidae, often dominate stream drift (Brittain and Eikeland 1988), providing an efficient mechanism for downstream dispersal of lotic species. However, upstream movement and colonization of adjacent watercourses and lakes occurs primarily through adult flight (e.g., Peckarsky et al. 2000).

Mayflies have winged adults, but they are small, fragile and short-lived (Brittain 1980). This limits their powers of dispersal. Mountain ranges, deserts and oceans present major barriers to dispersal. Climate change can also have impacts on the mayfly fauna of islands, especially those far away from continental landmasses. In this respect, the time frame and the rapidity of climatic changes are critical. The mayfly fauna of Madagascar displays a high degree of endemism, although showing strong affinities with the African fauna, while Oriental and Oceanian elements are negligible (Gattolliat and Sartori 2003). This contradicts with the separation sequence of Gondwanaland and suggests the dispersal powers of the Baetidae are greatly underestimated. Three mayfly families, Leptophlebiidae, Baetidae and Prosopistomatidae are present on the Comoros Islands, young volcanic islands at least 300 km from Madagascar and Africa (Starmühlner 1979). In the Arctic, there is already evidence of the migration of insects over large distances by the help of favorable winds generated by a changing climate (Coulson et al. 2002).

Colonization of new habitats by mayflies can take place fairly rapidly, although this depends on a supply of colonizers and environmental conditions being suitable. After the commencement of liming of a Norwegian river affected by acidification, the mayfly *Baetis rhodani* returned within two years (Raddum and Fjellheim 2003). In Canada, the mayflies *Stenonema femoratum* and *Stenacron interpuctatum* recolonized acid-damaged lakes from nearby refugia less than 4–8 years after pH reached threshold levels (Snucins 2003). However, initial small populations are very vulnerable to stochastic and Alle effects, such as low encounter rates for fertile adults (Frank and Brickman 2000, Yan et al. 2003). In an Alaskan glacial river, created in the 1960s as a result of glacial retreat, it was not until the mid 1980s that Baetidae were first recorded (Milner 1994). However, this delay was more a result of low water temperatures than the species' inability to colonize from nearby streams. Apart from the abiotic factors such as temperature affecting the ability of a species to colonize new habitats, species interactions may also be important, and the debate on the relative importance of biotic versus abiotic factors in determining the distribution and abundance of animals continues in the context of global warming (Hodkinson 1999).

Although it is possible to mark insects using stable isotopes for example (Hershey et al. 1993), the degree of dispersal can also be estimated indirectly by studying the genetic structure of a population. If dispersal is high, little genetic variation is to be expected, and vice versa (Slatkin 1985). However, Bunn and Hughes (1997) in a study of a subtropical stream in northern Australia found that genetic variation in *Baetis* was low at larger spatial scales indicating that there was considerable dispersal by winged adults. However, at the reach scale genetic variation was high, suggesting that recruitment was the result of oviposition by only a few females, a conclusion supported by work on populations of *Baetis alpinus* (Monaghan et al. 2001, 2002). The presence of greater genetic diversity at large spatial scales may be evidence of nonequilibrium between gene flow and genetic drift, resulting from historical gene flow that continues to mask reduced dispersal (Monaghan et al. 2002). In contrast, *Rhithrogena loyolaea* exhibited little genetic differentiation within and among streams but significant differentiation among drainages, suggesting that dispersal occurs readily among stream reaches and between adjacent valleys and that equilibrium has been reached between gene flow and genetic drift (Monaghan et al. 2002). Clearly there are differences in the dispersal ability of mayfly taxa and under climate change those species with greater powers of dispersal will have a better chance of survival.

As a result of their manipulation study of the effects of global warming on a first-order stream, Hogg and Williams (1996) concluded that the level of gene flow among habitats may be critical to the degree of impact as a result of global warming. Fragmentation, both natural and anthropogenic, represents a potential barrier to gene flow and dispersal (Zwick 1992). However, Sweeney et al. (1986) observed no genetic differentiation between populations of two mayflies, *Ephemerella subvaria* and *Euryophella verisimilis*, above and below reservoirs of the Delaware River, USA. In a study of populations of *Baetis alpinus* in alpine streams, where populations were fragmented either by natural lakes or by reservoirs, Monaghan et al. (2001) concluded that lentic water bodies act as barriers to gene flow in *B. alpinus*, but that the low divergence between fragments separated by reservoirs did not indicate high levels of gene flow, but rather showed that genetic differentiation is not detectable within the first 100–1000 years of habitat fragmentation.

Species Traits

During periods of rapid environmental transition certain species traits will be beneficial (Brittain 1991, Table 1). Mayfly eggs are frequently located down in the substrate where they are protected at least in part from environmental vicissitudes. A relatively long egg development period will increase the chance of the species' survival. This was clearly seen in a Norwegian alpine area in connection with an extreme spring flood. The summer species that were still in the egg stage survived and in fact increased in numbers at the expense of species that were present as nymphs during the spring (Sand and Brittain 1997). The "hedging of bets" associated with asynchronous egg hatching as well as variation in nymphal growth rates is also clearly advantageous in a changing environment (e.g., Bretschko 1990). A smaller size and a more cylindrical body shape enable nymphs to move down into the substrate during periods of high discharge and other unfavourable environmental conditions.

Table 1. Aquatic insect life history attributes generally advantageous or disadvantageous in disturbed habitats or in rapidly changing environments (modified from Brittain 1991).

Species Trait	Advantageous	Disadvantageous
Egg development	Long	Short
Egg hatching	Asynchronous	Synchronous
Nymphal development	Asynchronous	Synchronous
Nymphal size and shape	Small and cylindrical	Large
Temperature relationships	Eurytherm; temperature independent	Stenotherm; temperature dependent
Life cycle	Flexible; multivoltine	Fixed; univoltine

Strict temperature limits or specific temperature cues will be disadvantageous, as will growth relationships that show a strong dependence on temperature. The ability to shift life cycle duration, for example from univoltine to multivoltine in a warmer climatic regime will increase a species' annual production, while species with a fixed voltinism are likely to be disadvantaged or even become extinct. Although hatching success may be lower, parthenogenesis, both facultative and obligatory, is advantageous for dispersal of mayflies to new and more suitable habitats as it does not require mating and fertilization before oviposition (Sweeney and Vannote 1987). As a rule, it is envisaged that generalists will do better in a rapidly changing environment, while specialists with strict environmental limits and poor powers of dispersal may face extinction.

Temporal and Spatial Differences

There will be both temporal and spatial differences in the effects of climate change. Short-term and long-term changes are likely to differ as secondary and tertiary effects come into play. There will also be major regional differences, depending on the extent and nature of climatic changes (see Cushing 1997). For example, temperature increases are predicted to be greater in northern and Arctic regions and less in the southern hemisphere. In some areas precipitation will increase while in others it will remain stable or decrease. The effects of increased precipitation will also differ in mountain areas compared to lowlands. However, the accuracy of climate change predictions becomes lower when downscaled to smaller regional and national scales (Hauer et al. 1997). Nevertheless, the small order of aquatic insects, the mayflies, by virtue of their worldwide distribution and response to environmental cues, have the potential to function as sensitive indicators of present and future climate change.

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