

Effects of the North Atlantic Oscillation on growth and phenology of stream insects

Robert A. Briers, John H. R. Gee and Rory Geoghegan

Briers, R. A., Gee, J. H. R. and Geoghegan, R. 2004. Effects of the North Atlantic Oscillation on growth and phenology of stream insects. – *Ecography* 27: 811–817.

Climatic variation associated with the North Atlantic Oscillation (NAO) influences terrestrial and marine ecosystems, but its effects on river and stream ecosystems are less well known. The influence of the NAO on the growth of stream insects was examined using long-term empirical data on the sizes of mayfly and stonefly nymphs and on water temperature data. Models of egg development and nymphal growth in relation to temperature were used to predict the effect of the NAO on phenology. The study was based in two upland streams in mid-Wales UK that varied in the extent of plantation forestry in their catchments. Winter stream temperatures at both sites were positively related to the winter NAO index, being warmer in positive phases and colder in negative phases. The observed mean size and the simulated developmental period of mayfly nymphs were significantly related to the winter NAO index, with nymphs growing faster in positive phases of the NAO, but the growth of stonefly nymphs was not related to the NAO. This may have been due to the semivoltine stonefly lifecycle, but stonefly nymph growth is also generally less dependent on temperature. There were significant differences in growth rates of both species between streams, with nymphs growing more slowly in the forested stream that was consistently cooler than the open stream. Predicted emergence dates for adult mayflies varied by nearly two months between years, depending on the phase of the NAO. Variation in growth and phenology of stream insects associated with the NAO may influence temporal fluctuations in the composition and dynamics of stream communities.

R. A. Briers (r.briers@napier.ac.uk), J. H. R. Gee and R. Geoghegan, Inst. of Biol. Sci., Edward Llwyd Bldg, Univ. of Wales, Aberystwyth, Ceredigion, Wales SY23 4NL (present address of R. A. B.: School of Life Sciences, Napier Univ., 10 Colinton Rd, Edinburgh, UK EH10 5DT).

The North Atlantic Oscillation (NAO) is a cyclical climatic variation resulting from an alternation of differences in atmospheric sea level pressures between the Azores and Iceland (van Loon and Rogers 1976, Hurrell 1995, Hurrell and van Loon 1997). The NAO influences weather patterns across north-west Europe most strongly in winter through changes in the strength of surface westerly winds. Hurrell (1995) provides an index of the NAO, based on the mean of pressure differences between December and March, which is linked with temporal variation in winter climatic conditions. Positive values (>1.0) are associated with mild

warm winters and negative values (<-1.0) with cold, dry winters (Hurrell 1995).

In terrestrial and marine systems, changes in community dynamics and species' phenology and demography are correlated with the NAO index (Forchhammer et al. 1998, Post and Stenseth 1999, Belgrano et al. 1999, Ottersen et al. 2001, Post and Forchhammer 2002, Sanz 2003). In freshwater systems, studies have focused on the relationship between the NAO and plankton dynamics in lakes (George and Harris 1985, George and Hewitt 1999, Gerten and Adrian 2000, Blenckner and Hillebrand 2002). However, stream chemistry, fish

Accepted 5 August 2004

Copyright © ECOGRAPHY 2004
ISSN 0906-7590

phenology and invertebrate community persistence are also correlated with the NAO (Elliott et al. 2000, Monteith et al. 2000, Bradley and Ormerod 2001).

For many stream insects, such as mayflies (Ephemeroptera) and stoneflies (Plecoptera), almost all growth takes place in the nymphal stages. The majority of (terrestrial) adults do not feed and no further growth occurs at this stage. The growth rate of the nymphal stages of stream insects is influenced by water temperature (Vannote and Sweeney 1980, Sweeney 1984, Sweeney et al. 1986, Elliott 1987). Under warmer conditions, individuals grow faster and may reach adult stages earlier (Elliott 1984, 1987, 1996, Hogg and Williams 1996, Gregory et al. 2000). There is however significant variation between groups in temperature effects and the growth of stoneflies is less dependent on temperature than other groups (Elliott 1984, 1987, Weatherley and Ormerod 1990). Other factors such as food availability also have a role in determining growth rates, but models based solely on temperature have successfully predicted the growth of individuals in the field (Elliott 1987, 1988). Given the dependence of growth on water temperature, it is expected that alterations in winter stream temperatures associated with the NAO (Elliott et al. 2000) would influence the growth of stream insects and consequently their phenology, but also that these effects would vary between groups. This paper uses long-term data on annual variation in the size of mayfly (Ephemeroptera) and stonefly (Plecoptera) nymphs and in water temperature in two UK upland streams, coupled with models of nymph growth in relation to temperature, to determine the magnitude of variation in species growth rates and phenology that results from NAO driven alterations in stream thermal regimes.

Materials and methods

Study site

All data relate to two headwater streams of the River Severn, the Afon Hafren (British National Grid reference SN 843 877) and Afon Hore (SN 845 873), on the Plynlimon ridge, Mid-Wales, UK. These streams are similar in terms of size, altitude, discharge and physico-chemical conditions (Hudson et al. 1997), but differ in the vegetation surrounding the stream channel. The Hafren catchment is afforested with mature (40–60 yr old) plantation forestry, mostly Sitka *Picea sitchensis* and Norway spruce *Picea abies* planted up to the stream edge. Similar forestry surrounding the Hore was cleared at the study site between 1985 and 1989 and immediately replanted, with the exception of a tree-less buffer strip of 50–60 m from the edge of the stream channel. The vegetation in the buffer strips consists of a mixture of grasses (mainly *Festuca* sp.), heather *Calluna*

vulgaris, bilberry *Vaccinium myrtillus* and scattered deciduous trees (mainly rowan, *Sorbus aucuparia*). Over 50% of the Hore catchment upstream (the source was ca 2 km upstream of the study site) remained under plantation forestry, some of which was close enough to the channel to result in significant shading and this may have an influence on the temperature regime of the study reaches.

Nymph size data

Data on the annual variation in nymphal size were obtained for two species; *Baetis vernus* Curtis (Ephemeroptera: Baetidae) and *Nemurella picteti* Kapálek (Plecoptera: Nemouridae). These were derived from surveys of the two streams carried out annually in the first week of July between 1985 and 1991 (Gee and Smith 1995, 1997). Samples of the invertebrate fauna were collected at four sites on each stream using timed (2 min) searches of coarse substrata in riffles, with dislodged invertebrates being collected in a 250 µm mesh net (Gee and Smith 1997) and preserved in 70% industrial methylated spirits. Subsequently, individuals of the two species considered (the only species present in samples from both streams in sufficient numbers to be included in the analysis) were separated from the remainder of the sample and their pronotal widths measured to the nearest 0.1 mm using an eyepiece graticule under a light microscope at ×20. Between 33 and 68 individuals were measured for each species in different years and a mean pronotal width calculated for each year of survey. Replicate measurements (n = 3–5) of ten individuals of each species were also taken, in order to quantify the degree of measurement error. The error was consistent between species and not >0.1 mm in any case.

NAO and temperature data

Winter NAO index values (averages of values from December to March) were obtained from the Climatic Research Unit at the Univ. of East Anglia, UK <<http://www.cru.uea.ac.uk/cru/data/nao.htm>>.

Hourly automated measurements of stream temperature in the two streams between January 1992 and September 1999 were used. For further details of the temperature recording see Crisp (1997). Hourly values were converted into daily means for the purposes of analysis and modelling.

Mean stream temperatures were calculated for the period of December to March (the same period as the winter NAO index) and used to examine changes in winter stream temperature in relation to variation in the NAO. Monthly means were also calculated to examine seasonal changes in the differences in water temperatures between streams.

Three gaps (25, 46 and 63 d) in daily mean data for the Afon Hore were replaced by values estimated from a multiple regression of the temperature of the Hore on that of the Hafren ($r^2=0.987$), including months as dummy variables, to allow for between month changes in the relationship (Holtby 1988, Weatherley and Ormerod 1990).

Growth modelling

Models of growth in relation to water temperature obtained from the literature (see Table 1), were used to simulate nymphal growth from stream temperature data. Since a model for *Baetis vernus* was not available, a model for *B. rhodani*, which occurs in similar streams elsewhere in Wales and has a comparable lifecycle in upland streams (Weatherley and Ormerod 1990, Masters pers. comm.), was substituted.

The duration of egg development of the study species in relation to temperature was modelled as a negative power function

$$E = aT^{-b}$$

where E is the number of days (rounded to the nearest day) required for 50% of the eggs to hatch, T is the water temperature (°C) and a and b are constants.

Nymphal growth was initiated after E days had elapsed. Growth in relation to temperature was modelled by the following equation

$$G = c + dT$$

where G is % increase in body length d^{-1} , T is the water temperature (°C) and c and d are constants.

Representative egg fertilisation months and nymph sizes at hatching and emergence were chosen according to the literature (Table 1), with simulations initiated on the first day of the month of fertilisation. For egg development, temperatures varied throughout the development period and hence the mean temperature for the month in which development was initiated was used to determine development time. For nymphs, daily mean temperatures were used to determine daily growth increments. Nymph development times were defined as the number of days between hatching and reaching size at emergence, rounded to the nearest day.

Statistical analysis

Mean nymph pronotal widths, winter (December–March) water temperatures, and the simulated durations of egg and nymph development were related to the winter NAO index using linear least-squares regression. For the semivoltine *N. picteti*, pronotal widths and simulated development times were related both to the annual values of the winter NAO index for the period over which development was occurring and to the mean of the two years' values. Between-stream variation in nymph pronotal widths was examined using a paired t-test. Seasonal variation in the difference in temperature between the two streams was analysed using a one-way ANOVA of monthly mean temperature differences.

Results

For all regression equations, values in parentheses following parameters are standard errors.

Nymph sizes

For *B. vernus*, there was a significant positive relationship between mean nymph pronotal width and winter NAO index in both streams (Hore: $y = 8.93 (\pm 0.54) + 1.25x (\pm 0.38)$, $F_{[1,5]} = 10.71$, $p = 0.022$, adjusted $r^2 = 0.62$; Hafren: $y = 8.59 (\pm 0.61) + 1.29x (\pm 0.43)$, $F_{[1,5]} = 9.29$, $p = 0.028$, adjusted $r^2 = 0.58$, Fig. 1). For *N. picteti* however, there was no relationship between mean nymph pronotal width and winter NAO index in either stream (Hore: $F_{[1,5]} = 2.45$, $p = 0.178$; Hafren: $F_{[1,5]} = 0.38$, $p = 0.852$).

There was a significant difference between streams in the mean nymph pronotal widths (*B. rhodani* $t_{[6]} = 3.24$, $p = 0.018$, *N. picteti* $t_{[6]} = 2.58$, $p = 0.042$), with nymphs from the Hore being consistently larger than those from the Hafren in both species.

Stream temperatures

Mean winter water temperatures were positively related to the winter NAO index in both streams (Hore: $y = 4.05 (\pm 0.26) + 0.34x (\pm 0.16)$, $F_{[1,6]} = 8.39$, $p = 0.027$, adjusted $r^2 = 0.51$; Hafren: $y = 4.02 (\pm 0.24) + 0.32x$

Table 1. Details of species used in growth simulations and literature sources of growth models.

Order	Species	Egg fertilization date	Larval size (mm)		Growth model reference	
			On hatching	On emergence	Eggs	Nymphs
Ephemeroptera	<i>Baetis rhodani</i> (Pictet)	August	0.6	9.0	Elliott (1972)	Elliott et al. (1988)
Plecoptera	<i>Nemurella picteti</i> (Klapalek)	July	0.7	9.5	Elliott (1988)	Elliott (1984)

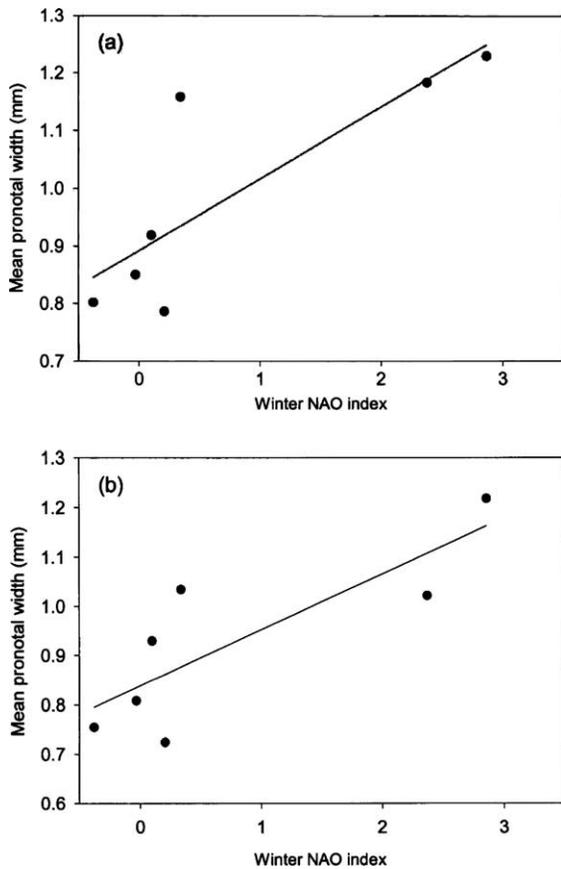


Fig. 1. Relationship between mean pronotal width of *B. vernus* nymphs and winter NAO index between 1985–1991 for a) Hore and b) Hafren streams. See text for details of regression lines.

(± 0.15), $F_{[1,6]}=10.19$, $p=0.019$, adjusted $r^2=0.57$, Fig. 2).

There was significant seasonal variation in the difference in temperature between the two streams ($F_{[1,186]}=7.62$, $p=0.006$). The Hore was consistently warmer than the Hafren in all months, but the difference between streams showed a summer maximum and was lowest in the winter months (Fig. 3).

Simulated growth and development

For both species, simulated egg and nymph development times were longer in the Hafren than the Hore in all years (Table 2) as a result of the consistently cooler water temperatures (Fig. 3).

Simulated egg development time was not related to the winter NAO index for either stream or species (Hore: *B. rhodani* $F_{[1,5]}=0.50$, $p=0.505$, *N. picteti* $F_{[1,4]}=1.74$, $p=0.257$; Hafren: *B. rhodani* $F_{[1,5]}=2.58$, $p=0.169$, *N. picteti* $F_{[1,4]}=0.44$, $p=0.544$).

For *B. rhodani* there was a significant negative relationship between simulated nymph development

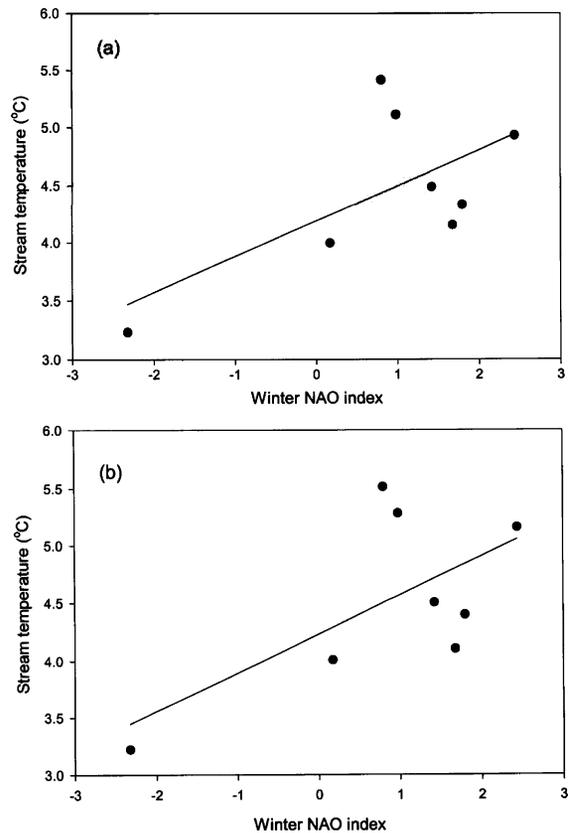


Fig. 2. Relationship between mean winter stream temperature (December–March) and NAO winter index between 1991 and 1998 for a) Hore and b) Hafren streams. See text for details of regression lines.

time (time from egg hatching to emergence) and winter NAO index for both streams (Hore: $y=219.3 (\pm 4.93) - 8.73x (\pm 3.03)$, $F_{[1,5]}=10.47$, $p=0.023$, adjusted $r^2=0.61$; Hafren: $y=229.9 (\pm 5.35) - 8.80x (\pm 2.71)$, $F_{[1,5]}=7.03$, $p=0.045$, adjusted $r^2=0.51$, Fig. 4).

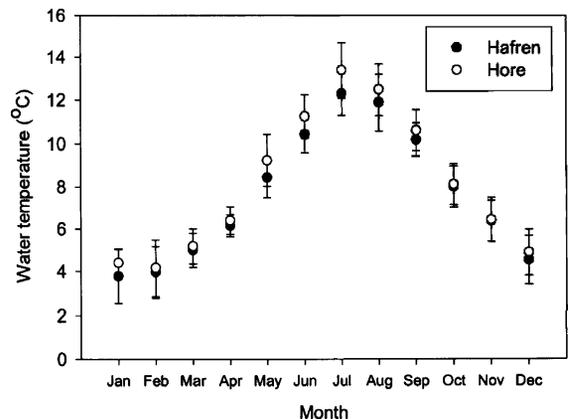


Fig. 3. Seasonal variation in monthly mean water temperatures of the study streams for the period of January 1992–September 1999. Values shown are means ± 1 standard deviation.

Table 2. Simulated egg and nymph development times for *B. rhodani* and *N. picteti* in the study streams. Figures given are means with range in parentheses. See text for definitions of development periods.

Species	Egg development time (d)		Nymph development time (d)	
	Hore	Hafren	Hore	Hafren
<i>B. rhodani</i>	19.0 (14–21)	21.0 (17–25)	213.0 (195–241)	223.3 (202–255)
<i>N. picteti</i>	17.2 (16–20)	19.2 (17–24)	638.5 (630–654)	643.3 (636–666)

In contrast *N. picteti* showed no relationship between simulated nymph development time and the winter NAO index in either year of development, or the average index of the two years (year 1: Hore $F_{[1,4]} = 1.16$, $p = 0.341$, Hafren $F_{[1,4]} = 0.38$, $p = 0.573$; year 2: Hore $F_{[1,4]} = 2.99$, $p = 0.159$, Hafren $F_{[1,4]} = 0.40$, $p = 0.560$; mean of both years: Hore $F_{[1,4]} = 0.10$, $p = 0.771$, Hafren $F_{[1,4]} = 0.94$, $p = 0.387$).

Discussion

Both empirical and modelling approaches demonstrated a significant relationship between the growth and development of *Baetis* mayfly nymphs in the study streams

and the winter NAO index. The mean size of *B. vernus* nymphs was positively related, and simulated development times of *B. rhodani* negatively related, to the winter NAO index. The correspondence between empirical and simulated growth responses suggests strongly that annual variations in mayfly nymph growth rates are influenced by the changes in stream thermal regimes in the winter months associated with regional climatic conditions [Fig. 2 and Elliott et al. (2000)]. In contrast, there was no evidence of a link between the empirical or simulated growth of the stonefly *N. picteti* and the NAO. The two-year lifecycle of this species means that the effects of variation in water temperatures are integrated over a much longer period, and simple relationships between the NAO and growth or development rates would seem less likely. The growth of stonefly species is also less dependent on temperature (Elliott 1984, 1987); the temperature coefficient (d – see Materials and methods) of the *N. picteti* growth model is smaller than that for *B. rhodani*. Therefore it is difficult to separate the effects of differences in development period between the two taxa from those resulting from differences in the dependence of growth on temperature. Other species with semivoltine life histories but different growth characteristics may still show dependence of growth on fluctuations in the NAO.

In common with previous studies using similar methods (Weatherley and Ormerod 1990, Webb and Walling 1993), the results of the simulations assume that nymph growth can be predicted solely from water temperature. Field validation of the models used here (Elliott 1987, 1988), evidence from other laboratory studies (Sweeney and Vannote 1986) and the empirical data on nymph growth rates obtained in this study all suggest that this is reasonable. However, the growth of stream insects in the field may be influenced by other factors, such as the availability of food (Thomsen and Friberg 2002), which have the potential to alter the growth response of nymphs to changes in stream thermal regimes. Nymphal food supply may be influenced by factors such as catchment vegetation (Rundle et al. 1992, Thomsen and Friberg 2002), which may show interactions that cannot be assessed in the present study. It is possible that populations vary in the dependence of growth on temperature and thus in their response to the NAO. However available evidence suggests that such

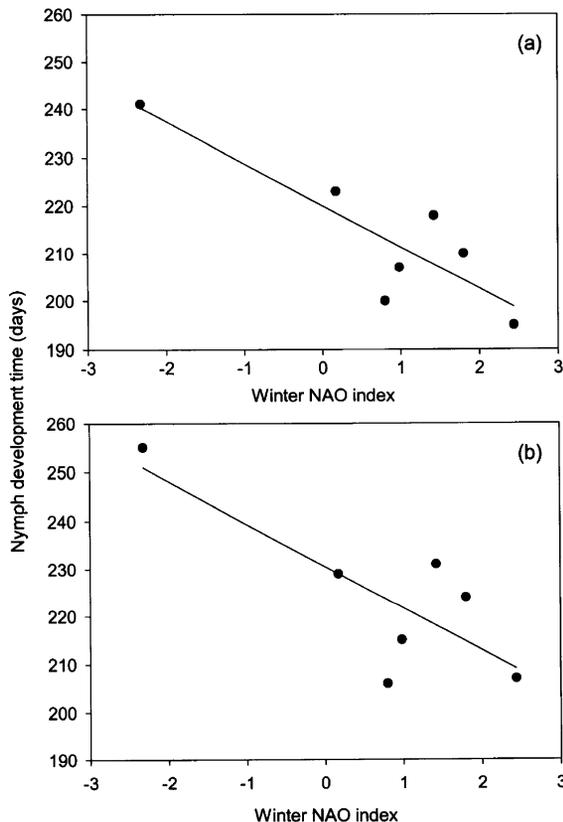


Fig. 4. Relationship between simulated time taken for development of *B. rhodani* nymphs and winter NAO index for a) Hore and b) Hafren streams. See text for details of regression lines.

inter-population differences are small (Humpesch 1980, Elliott 1987).

There was no effect of the NAO on simulated egg development time for either species, although eggs of both species took longer to develop in the forested stream due to the cooler temperatures experienced during the development period [Table 2, Fig. 3, see also Weatherley and Ormerod (1990)]. Given that egg development takes place in the summer, it is not surprising that the winter NAO index did not correlate with egg development periods.

Growth rates of the nymphs of both species also varied significantly between streams, with slower growth in the Hafren. This is likely to be due to the consistently warmer temperatures of the Hore. In contrast with a previous study of similar forested and un-forested streams in Wales (Weatherley and Ormerod 1990), there was no evidence of any amelioration of winter temperature minima in the forested Hafren (see also Crisp 1997), which could mask fluctuations in growth rates associated with the NAO. However the forestry in the catchment of the Hore upstream of the study site may exert an influence on temperature regimes further downstream. Clearly, the effects of factors influencing stream thermal regimes, in this case catchment vegetation, may vary between sites as a result of local differences in catchment characteristics (Weatherley and Ormerod 1990, Webb and Walling 1993, Stott and Marks 2000).

Although the NAO primarily influences stream temperatures in winter, when nymph growth rates are lower than in the summer, the effect on mayfly nymphs is of sufficient magnitude to result in changes in overall nymph growth and development time. The relationships between nymph growth and the NAO index contained significant unexplained variation. This is likely to be a reflection of non-NAO related temperature variations for the remainder of the year, along with factors such as annual differences in the timing of egg laying, in the availability/quality of food for nymphs, or in other physico-chemical parameters (Sweeney et al. 1986, Thomsen and Friberg 2002). There is also strong dependence on the extreme values of the NAO in driving the relationships in Figs 1, 3 and 4. This is expected, as climatic variation is most pronounced when values of the winter NAO index are >1.0 or <-1.0 (Hurrell 1995). Over the period when growth or temperature measurements were taken, the majority of winter NAO index values were between 1.0 and -1.0 and hence the effects of climatic variation on growth rates are likely to be less distinct, resulting in greater scatter.

Predicted time taken for mayfly nymph development, and hence emergence date, varied by nearly two months due to alterations in winter stream thermal regimes resulting from fluctuations in the NAO. Unfortunately, we do not have any data on the emergence of insects from the streams over the same period as the tempera-

ture records with which to validate the model predictions. However, emergence and flight periods of mayflies in Britain vary markedly in different years (Elliott et al. 1988) and it is likely that at least part of this variation is due to the effects of the NAO on nymph development rates. Survival and dispersal of adult aquatic insects is dependent on the weather conditions experienced during adult life (Brindle 1957, Jackson 1988, Waringer 1991, Collier and Smith 2000, Briers et al. 2003). Weather conditions during adult life will vary with emergence date and hence the extent of adult dispersal and reproductive success of adult stages may also be affected by NAO driven phenological changes. Bradley and Ormerod (2001) demonstrated that the persistence of stream communities in terms of the composition and relative abundance of species varies in relation to the NAO. This variation was not related to inter-annual variation in discharge and they suggested that variations in temperature might have played a role in the observed patterns. The effects on insect growth and phenology that we have demonstrated might be one mechanism by which the NAO could influence the persistence of stream communities. However, it is also worth noting that changes in phenology could result in apparent shifts in community composition simply by advancing or retarding normal seasonal changes in relation to a fixed survey date. This effect, which is distinct from longer-term change in community composition, should be accounted for when interpreting long term datasets.

Given the predictions of an increase in the variability of the NAO (Paeth et al. 1999), the effects that we have observed are likely to increase in magnitude. Phenological shifts that result in mismatches between the timing of life history stages and changes in the biotic or physical environment could have important long-term consequences for stream ecosystem function.

Acknowledgements – We would like to thank Trevor Crisp and Bruce Webb for providing the temperature data used in the simulations. Bruce Webb and Iain Barber suggested useful improvements to the manuscript. Dave Bradley is thanked for stimulating discussions about the NAO and freshwater ecosystems. This work was supported by grant GR3/12114 from the UK Natural Environment Research Council.

References

- Belgrano, A., Lindahl, O. and Hemroth, B. 1999. North Atlantic Oscillation primary productivity and toxic phytoplankton in the Gullmar Fjord (1985–1996). – *Proc. R. Soc. Lond. B* 266: 425–430.
- Blenckner, T. and Hillebrand, H. 2002. North Atlantic Oscillation signatures in aquatic and terrestrial ecosystems – a meta-analysis. – *Global Change Biol.* 8: 203–212.
- Bradley, D. C. and Ormerod, S. J. 2001. Community persistence among stream invertebrates tracks the North Atlantic Oscillation. – *J. Anim. Ecol.* 70: 987–996.
- Briers, R. A., Cariss, H. M. and Gee, J. H. R. 2003. Flight activity of adult stoneflies in relation to weather. – *Ecol. Entomol.* 28: 31–40.

- Brindle, A. 1957. The effect of temperature and humidity on the flight of Trichoptera. – *Entomol. Monthly Mag.* 93: 63–66.
- Collier, K. J. and Smith, B. J. 2000. Interactions of adult stoneflies (Plecoptera) with riparian zones I. Effects of air temperature and humidity on longevity. – *Aquat. Insects* 22: 275–284.
- Crisp, D. T. 1997. Water temperature of Plynlimon streams. – *Hydrol. Earth Syst. Sci.* 1: 535–540.
- Elliott, J. M. 1972. Effect of temperature on the time of hatching in *Baetis rhodani* (Ephemeroptera: Baetidae). – *Oecologia* 9: 47–51.
- Elliott, J. M. 1984. Hatching time and growth of *Nemurella pictetii* (Plecoptera: Nemouridae) in the laboratory and a Lake District stream. – *Freshw. Biol.* 14: 491–499.
- Elliott, J. M. 1987. Temperature induced changes in the life cycle of *Leuctra nigra* (Plecoptera, Leuctridae) from a Lake District stream. – *J. Anim. Ecol.* 18: 177–184.
- Elliott, J. M. 1988. Egg hatching and resource partitioning in stoneflies (Plecoptera) – 10 British species in the family Nemouridae. – *J. Anim. Ecol.* 57: 201–215.
- Elliott, J. M. 1996. Temperature-related fluctuations in the timing of emergence and pupation of Windermere alder-flies over 30 years. – *Ecol. Entomol.* 21: 241–247.
- Elliott, J. M., Humpesch, U. H. and Macan, T. T. 1988. Larvae of the British Ephemeroptera: a key with ecological notes. – Scientific Publ. No. 49, Freshwater Biological Association, Ambleside.
- Elliott, J. M., Hurley, M. A. and Maberly, S. C. 2000. The emergence period of sea trout fry in a Lake District stream correlates with the North Atlantic Oscillation. – *J. Fish Biol.* 56: 208–210.
- Forchhammer, M. C., Post, E. and Stenseth, N. C. 1998. Breeding phenology and climate. – *Nature* 391: 29–30.
- Gee, J. H. R. and Smith, B. D. 1995. Impact of forest clear felling on stream invertebrates. – R&D Project Record 270/13/ST, National Rivers Authority, Bristol.
- Gee, J. H. R. and Smith, B. D. 1997. Benthic invertebrates in the headwaters of the Wye and Severn: effects of forestry and clear-felling. – *Hydrol. Earth Syst. Sci.* 1: 549–556.
- George, D. G. and Harris, G. P. 1985. The effect of climate on long-term changes in the crustacean zooplankton biomass of Lake Windermere, UK. – *Nature* 316: 536–539.
- George, D. G. and Hewitt, D. P. 1999. The influence of year-to-year variations in winter weather on the dynamics of *Daphnia* and *Eudiaptomus* in Esthwaite Water, Cumbria. – *Funct. Ecol.* 13: 45–54.
- Gerten, D. and Adrian, R. 2000. Climate-driven changes in spring plankton dynamics and the sensitivity of shallow polymictic lakes to the North Atlantic Oscillation. – *Limnol. Oceanogr.* 45: 1058–1066.
- Gregory, J. S., Beesley, S. S. and Van Kirk, R. W. 2000. Effect of springtime water temperature on the time of emergence and size of *Pteronarcys californica* in the Henry's Fork catchment, Idaho, U.S.A. – *Freshw. Biol.* 45: 75–83.
- Hogg, I. D. and Williams, D. D. 1996. Response of stream invertebrates to a global-warming thermal regime: an ecosystem level manipulations. – *Ecology* 77: 395–407.
- Holtby, L. B. 1988. Effects of logging on stream temperatures in Carnation Creek, British Columbia, and associated impacts on the coho salmon (*Oncorhynchus kisutch*). – *Can. J. Fish. Aquat. Sci.* 45: 502–515.
- Hudson, J. A., Gilman, K. and Calder, I. R. 1997. Land use and water issues in the uplands with reference to the Plynlimon study. – *Hydrol. Earth Syst. Sci.* 1: 389–397.
- Humpesch, U. H. 1980. Effect of temperature on the hatching times of eggs of five *Ecdyonurus* spp. (Ephemeroptera) from Austrian streams and English streams, lakes and rivers. – *J. Anim. Ecol.* 49: 317–333.
- Hurrell, J. W. 1995. Decadal trends in the North Atlantic Oscillation: regional temperatures and precipitation. – *Science* 269: 676–679.
- Hurrell, J. W. and van Loon, H. 1997. Decadal variations in climate associated with the North Atlantic Oscillation. – *Climate Change* 36: 301–326.
- Jackson, J. K. 1988. Diel emergence, swarming and longevity of selected adult aquatic insects from a Sonoran Desert stream. – *Am. Midl. Nat.* 119: 344–352.
- Monteith, D. T., Evans, C. D. and Reynolds, B. 2000. Are temporal variations in the nitrate content of UK upland freshwaters linked to the North Atlantic Oscillation. – *Hydrol. Processes* 14: 1745–1749.
- Ottersen, G. et al. 2001. Ecological effects of the North Atlantic Oscillation. – *Oecologia* 128: 1–14.
- Paeth, H. et al. 1999. The North Atlantic Oscillation as an indicator for greenhouse-gas induced regional climate change. – *Climate Dynamics* 15: 953–960.
- Post, E. and Stenseth, N. C. 1999. Climatic variability, plant phenology and northern ungulates. – *Ecology* 80: 1322–1339.
- Post, E. and Forchhammer, M. C. 2002. Synchronization of animal population dynamics by large-scale climate. – *Nature* 420: 168–171.
- Rundle, S. D., Lloyd, E. C. and Ormerod, S. J. 1992. The effects of riparian management and physicochemistry on macro-invertebrate feeding guilds and community structure in upland British streams. – *Aquat. Conserv.* 2: 309–324.
- Sanz, J. J. 2003. Large-scale effect of climate change on breeding parameters of pied flycatchers in western Europe. – *Ecography* 26: 45–50.
- Stott, T. and Marks, S. 2000. Effects of plantation forestry clearfelling on stream temperatures in the Plynlimon experimental catchments, mid-Wales. – *Hydrol. Earth Syst. Sci.* 4: 95–104.
- Sweeney, B. W. 1984. Factors influencing life-history patterns of aquatic insects. – In: Resh, V. H. and Rosenberg, D. M. (eds), *The ecology of aquatic insects*. Praeger Scientific, pp. 56–100.
- Sweeney, B. W. and Vannote, R. L. 1986. Growth and production of a stream stonefly: influences of diet and temperature. – *Ecology* 67: 1396–1410.
- Sweeney, B. W., Vannote, R. L. and Dodds, P. J. 1986. The relative importance of temperature and diet to larval development and adult size of the winter stonefly, *Soyedina carolinensis*. – *Freshw. Biol.* 16: 39–48.
- Thomsen, A. G. and Friberg, N. 2002. Growth and emergence of the stonefly *Leuctra nigra* in coniferous streams with contrasting pH. – *Freshw. Biol.* 47: 1159–1172.
- van Loon, H. and Rogers, J. C. 1976. The seesaw in winter temperatures between Greenland and northern Europe. Part 1. General description. – *Monthly Weather Rev.* 106: 296–310.
- Vannote, R. L. and Sweeney, B. W. 1980. Geographical analysis of thermal equilibria: a conceptual model for evaluating the effect of natural and modified thermal regimes on aquatic insects communities. – *Am. Nat.* 115: 667–695.
- Waringer, J. A. 1991. Phenology and the influence of meteorological parameters on the catching success of light-trapping for Trichoptera. – *Freshw. Biol.* 25: 307–319.
- Weatherley, N. S. and Ormerod, S. J. 1990. Forests and the temperature of upland streams in Wales: a modelling exploration of the biological effects. – *Freshw. Biol.* 24: 109–122.
- Webb, B. W. and Walling, D. E. 1993. Temporal variability in the impact of river regulation on thermal regime and some biological implications. – *Freshw. Biol.* 29: 167–182.