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Evidence for the role of climate in the local extinction of a cool-water triclad

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Abstract. Climate change is expected to alter freshwater communities and accelerate extinction, but the exact processes are poorly known. Here, we appraise interannual variation between 2 sympatric planarians (*Crenobia alpina* and *Phagocata vitta*) in upland Welsh streams over 25 y during which 1 of this pair (*C. alpina*) disappeared. We tested 3 nonexclusive hypotheses involving: 1) long-term changes in stream chemistry, 2) interspecific competition, and 3) climatic variation or directional change to explain this apparent local extinction. Several lines of evidence revealed potential exploitation competition between *C. alpina* and *P. vitta*. Coexistence was confined to conditions with high prey abundance (recorded as the abundance of Ephemeroptera, Plecoptera, and Trichoptera) and summer temperatures <12.5°C, whereas *P. vitta* dominated at sites with higher temperature, greater discharge, and lower prey abundance. The loss of *C. alpina* in the Llyn Brianne experimental catchments coincided with the largest-ever positive amplification of the North Atlantic Oscillation (NAO) in 1989 to 1994, accompanied by increased stream temperature, increased winter discharge, 2 summer droughts, and markedly reduced prey abundance. We suggest that interspecific competition and this prolonged climatic event acted in concert to favor *P. vitta* over *C. alpina*. Since its local loss, summer stream temperatures have generally exceeded the favorable range for *C. alpina* and, coupled with weak dispersal ability, probably explain its continued absence. Our data are consistent with the prediction that extreme climatic events will affect small, fluctuating populations. Nevertheless, this case study demonstrates clear difficulties in identifying unequivocally the exact climatic processes causing extinction where: 1) evidence is confined to weak inference, 2) responses to complex climatic events are nonlinear, 3) interactions occur among species or between climate and ecological processes, and 4) assessments are made retrospectively following extinctions.

Key words: climate change, freshwater, planarians, streams, temperature, NAO, Wales.

Extinction risk in freshwaters is now greater than in almost all other ecosystems (Revenga et al. 2005, Heino 2009). In North America, for example, the projected loss of freshwater fauna is estimated to be 5× faster than for terrestrial fauna (Ricciardi and Rasmussen 1999, Ricketts et al. 2005), and rates are liable to increase in the future (Duncan and Lockwood 2001, Stuart 2004, Revenga et al. 2005). Habitat degradation, pollution, invasive species, disease and species exploitation have been implicated in these effects (Malmqvist and Rundle 2002), but climate change is considered a growing threat because altered temperature and discharge affect organisms directly, exacerbate existing stressors (Xenopoulos et al. 2005, Ormerod and Durance 2009), and will affect catchment use and management (Sala et al. 2000, Ormerod 2009, Kaushal et al. 2010). Evidence already suggests that effects on freshwater species distribution and composition are large and widespread, particularly for rivers (Daufresne et al. 2004, Bêche and Resh 2007, Durance and Ormerod 2007, Chessman 2009). However, the exact mechanisms are poorly known, and case studies that describe how climate change might contribute to local or global extinctions in freshwaters are extremely scarce.

Identifying the exact causes of extinction is challenging (Korkeamaki and Suhonen 2002, McLaughlin et al. 2002, Munday 2004). Difficulties include anticipating where losses are likely to occur, collecting appropriate data over a sufficient period, differentiating environmental effects clearly among multiple stressors, and identifying the biological processes involved. Existing analyses suggest that biological risk factors include small body size, small geographical range or ecological niche, small population size,

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poor dispersal capacity, and limited phenotypic or genetic plasticity (McKinney 1997, Gaston 1998, Belovsky et al. 1999, Olden et al. 2007). However, biological and environmental factors are liable to interact to cause extinction, and demographic and environmental variations might sometimes combine stochastically to eliminate small populations (Dennis et al. 1991, Lande 1993). These circumstances are relevant to climatic change, where progressive shifts, coupled with extreme events, such as floods, droughts, and heat waves, could drive conditions beyond the ranges normally experienced by many species in their existing locations.

Our studies on replicate, upland streams in central Wales (UK) over >25 y show how climate change and variation can have large effects on stream organisms. Examples include negative effects on salmonids in hot, dry years (Weatherley et al. 1991, Clews et al. 2010), reductions in community stability and species' persistence during a large amplification of the North Atlantic Oscillation (NAO; Bradley and Ormerod 2001), and retarded recovery from acidification under warmer, wetter conditions (Ormerod and Durance 2009). Long-term warming also has been accompanied by reductions in invertebrate abundance and altered species composition (Durance and Ormerod 2007). Two related triclads, *Crenobia alpina* (Dana 1766) and *Phagocata vitta* (Duges 1830), are particularly interesting in that these cool-water stenotherms made up the entire triclad fauna at our study sites for around a decade, but *C. alpina* disappeared in the late 1980s and early 1990s. We use this paper as an opportunity to investigate this local extinction and attempt to identify retrospectively the processes that might have been involved.

The biology and ecology of *C. alpina* and *P. vitta* are well known from classical studies during the 1970s and 1980s. Both species should be relatively common in upland Britain, although *C. alpina* is scarcer in some regions (Wallace 1991, Chadd and Extence 2004). Both occur in lowland streams or springs only where year-round temperatures are <13 to 15°C (Reynoldson and Young 2000). Both species are predators found predominantly within the stream benthos or sometimes in ground waters (Wright 1974). Direct observations and serological investigations reveal overlap in their prey spectra, which include oligochaetes and larval Plecoptera, Ephemeroptera, and Trichoptera (Wright 1968, Lock and Reynoldson 1976, Armitage and Young 1990). Potential predators also overlap, and include larval dysticids, megalopterans, odonates (e.g., *Cordulegaster boltonii*), some Plecoptera (e.g., *Isoperla grammatica*, *Perlodes microcephala*), and some Trichoptera (e.g., *Rhyacophila* spp.) (Ball and Reynoldson 1981). Both triclads are hermaphrodites characterized in summer by asexual fission and in winter by sexual reproduction (Reynoldson 1978). Both occur under similar stream ionic composition, although older data suggest they avoid low pH or low Ca concentrations (Carpenter 1928, Wright 1974).

These observations provide the basis for hypotheses tested here about interactions between climate and the ecology of *C. alpina* and *P. vitta*. First, we used a combination of long-term data (1981–2005) on replicate streams and regional surveys across upland Wales (1984 and 1995) to illustrate when and where *C. alpina* appears to have been lost. Next, we used observations over a range of temporal and spatial scales to examine possible effects on the occurrence of *C. alpina* of: 1) variations in stream chemistry, 2) possible competition between *P. vitta* and *C. alpina*, and 3) climate and, in particular, the NAO because of its large shift over the period during which *C. alpina* progressively disappeared from Llyn Brianne. We stress that none of our hypotheses is tested by experimental manipulation but by observations about species' co-occurrence over varying spatiotemporal scales (months to years, site to region).

Methods

Field sites and sampling

Our study combined regional (Wales-wide) and catchment-specific data from the Llyn Brianne experimental catchments, where 14 perennial streams drain individual catchments of 15 to 264 ha (215–410 m altitude, lat 52°8′N, long 3°45′W). The underlying rocks are mostly base-poor and overlain by brown podzolic soils, stagnopodzols, and peats that yield soft-water (mean total hardness 3.9–7.9 mg $CaCO_3$/L) except where local calcite veins buffer some streams at circumneutral pH and 15 to 19 mg $CaCO_3$/L. Streams are categorized as acid grassland (CI1–CI6), acid conifer (LI1–LI5, LI8), and circumneutral moorland (LI6, LI7) (see Durance and Ormerod 2007, Ormerod and Durance 2009 for a map and further description). The sites are ~35 km from the nearest coast, so the climate is maritime and temperate with mean annual precipitation ~1900 mm. Monthly mean temperatures are invariably within the range 0 to 15°C, although these temperatures have increased over the last 25 y (Durance and Ormerod 2007).

The regional data were derived from 74 headwater streams that were used in 2 invertebrate surveys of upland Wales in 1984 and 1995 (Welsh acid waters survey [WAWS]). Geology, soils, altitudes (45–440 m), and land uses are broadly similar to those at Llyn Brianne and give rise to similar stream chemistry

(mean total hardness ~4–25 mg $CaCO_3$/L), although some streams in this set drained larger catchments (20–5700 ha; see Wade et al. 1989, Ormerod and Durance 2009 for a map and further details).

Streams at Llyn Brianne were sampled in 1981 to 1982 by Stoner et al. (1984) and from 1985 to present (except 1991) by personnel from Cardiff University. Sampling was done with identical procedures in April each year. Exact sampling coverage has varied among years so that data span 8 to 22 y/location. At the WAWS sites, samples were collected in April in both 1984 and 1995. In all cases, kick-samples of 3-min duration were collected from riffles (2 min) and margins (1 min) with a standard net (0.9-mm mesh, 230 × 255-mm frame). This sampling strategy collects >66% of all taxa present and >80% of all but the rarest taxa in any one stream in each year (Weatherley and Ormerod 1987, Bradley and Ormerod 2002). Samples were preserved on-site in 70% ethanol, and later sorted and identified to species. Preservation by ethanol or formaldehyde (see below) distorted the shape of the 2 planarians, but each was still detectable and distinguishable (validated against preserved specimens of known identity).

In addition to annual kick-samples, monthly (summer) to bimonthly (winter) quantitative samples were collected from 6 of the Llyn Brianne streams (LI1, LI2, LI6, CI3, CI4, CI6) over the period April 1985 to December 1986 with a cylinder sampler (0.05-m^2 diameter, 440-μm mesh aperture; after Neill 1938). At each site on each occasion, 5 replicates were taken from riffles disturbed to a depth of ~10 cm and preserved in 4% formaldehyde prior to sorting and identification in the laboratory (Weatherley et al. 1989).

In total, available data to assess the occurrence of *C. alpina* and *P. vitta* consisted of 260 kick-samples on up to 14 headwater streams over 22 different years (1981–2005), 148 samples from 74 headwater streams sampled in 2 different years during the WAWS (1984, 1995), and 450 individual Surber samples taken from 6 streams in 15 different months over a 2-y period (1985–1986).

The annual invertebrate collections were accompanied by full ionic analyses for each site. Analyses were done using standard methods on samples taken at least monthly. We used mean values of pH, Al, and Ca over the winter preceding the April sampling to illustrate typical conditions under which each triclad occurred. These variables describe acid–base status effectively but also incorporate features liable to change during long-term recovery from the effects of acid rain with possible consequences on invertebrate occurrence (Ormerod and Durance 2009).

Measured stream temperatures were not available throughout the study, but long and continuous runs of air and stream temperatures were available from which we could model long-term variations with methods described previously (Durance and Ormerod 2007). For the entire study period, we downloaded air temperatures recorded at 15-min intervals by the UK Meteorological Office at nearby Aberporth (National Grid Reference SN 241521, lat 52°07′55″N, long 4°32′44″W, altitude 133 m). We adjusted these data with the environmental lapse rate (0.0069°C/m) to account for the difference in altitude between Aberporth and the streams at Llyn Brianne. At a monthly time-step, we verified that these altitude-adjusted data reflected actual air temperatures recorded continuously at Llyn Brianne by an automatic weather station deployed from March 1985 to April 1989 ($r^2 = 0.93$, slope = 0.87, $n = 50$; National Grid Reference SN 825497, lat 52°7′59″N, long 3°43′5″W, altitude 340 m). Next, we used regressions to calibrate stream temperature at Llyn Brianne against lapse-adjusted air temperature from Aberporth using 16 mo of continuously logged (15-min intervals) data from LI1 (forest, 1985–1986), 25 mo from CI6 (moorland, 1985–1987), and 59 mo from the upper Afon Tywi above Llyn Brianne (AT; mixed forest/moorland, 1980–1984) (Weatherley and Ormerod 1990). Monthly air temperature explained 85 to 95% of the variation in monthly stream temperature over these periods (slopes = 0.94–0.97, intercepts = 0.5–0.67°C in CI6 and AT, respectively; see Durance and Ormerod 2007 for details). A lower slope (0.78) and greater intercept (1.6°C) in the afforested LI1 reflected well-known shading effects under forest (Weatherley and Ormerod 1990). Last, we used these regressions of stream temperature on lapse-adjusted air temperature from Aberporth to calculate mean winter (December–February) and mean summer (July–September) stream temperature for 1981 to 2005. We also identified maximum summer values in view of the probable sensitivity of *C. alpina* to temperatures >13–15°C (Wright 1974, Lock and Reynoldson 1976).

Although characterized by a high degree of fit, this modeling approach would be subject to error if relationships between air and stream temperature changed through time, e.g., because of varying discharge or periods of ice cover. However, calibration periods for air–stream temperature relationships already reflected wide discharge variations between months and seasons, and the streams at Llyn Brianne have never frozen throughout the study. Observations elsewhere show that calibrations of this type persist through time (Durance and Ormerod 2009), and

modeled stream temperatures at Llyn Brianne have a relationship with long-term variations in air temperature caused by the NAO that is identical to the relationships at other western British locations (Durance and Ormerod 2007 vs Elliott et al. 2000).

Hydrological data also were unavailable at the Llyn Brianne sites, but they were available from the Hafren flume, 37 km to the north of Llyn Brianne catchment (National Grid Reference SN 853872, lat 52°27′26″N, long 3°47′46″, altitude 331 m, mean discharge 0.53 m^3/s; http://www.nwl.ac.uk/ih/nrfa). Hafren flume was in a catchment of plantation conifer, but on a monthly basis between 1970–2005, discharge there was highly correlated ($r^2 = 0.96$, slope = 1.26) with discharge at an adjacent gauged site in grassland (National Grid Reference SN 829838, altitude 334 m, mean discharge 0.7 m^3/s) between 1970 and 2005. Discharge in the Hafren flume also was strongly and significantly correlated with discharge at a gauged site on the Afon Cothi (lat 51°51′37″N, long 41°11′00″W), also in the Tywi system ($r^2 = 0.89$, $n = 289$ monthly mean values, $p < 0.0001$). For these reasons, we followed earlier precedents (Bradley and Ormerod 2001, Durance and Ormerod 2007) and used the Hafren data to indicate relative fluctuations in mean winter (October–March) or mean summer (April–September) discharge at Llyn Brianne.

The NAO affects the winter climate in western Britain and has marked consequences on river discharge, temperature, and stream biota (Bradley and Ormerod 2001). We downloaded values of the winter NAO index (December–February), calculated from pressure differences between the Azores and Iceland, for the period before biological sampling in April (http://www.cgd.ucar.edu/cas/jhurrell/indices.html). We also calculated a smoothed NAO index, corresponding to the mean of winter index values over the 3 preceding years.

Data analysis

Care is needed with the analysis of data spanning multiple years from the same streams because of possible correlation between observations (nonindependence). We attempted to reduce these problems in our study by: 1) calculating mean values with years as replicate samples across streams, 2) calculating means or frequencies with streams as replicate values across years, and 3) where appropriate, using mixed-effects models based on general linear modeling (GLM) to identify sources of variability correctly.

We assessed the chemical conditions under which *C. alpina* and *P. vitta* occurred at Llyn Brianne and across the Welsh region by calculating the mean, standard deviation, and range for pH, Al, and Ca concentrations in occupied streams. At Llyn Brianne, we also used long-term data to assess whether chemical conditions have remained in the range of conditions at sites typically occupied by each species (see Ormerod and Durance 2009).

We could not measure competition directly, but several aspects of our data allowed us to make an indirect assessment of habitat overlap, potential competition, and possible mutual exclusion between the 2 triclads. These aspects included: 1) appraising the water-quality ranges occupied by each species as indicated above, 2) calculating the mean abundance (after $\log[x + 1]$-transformation) of each species across all years in the period when both species co-occurred (1981–1993) for the 14 streams at Llyn Brianne and measuring intercorrelation between these average abundances as a measure of association with similar streams (i.e., with years as replicate units), 3) plotting the year-specific mean logarithmic abundance of the 2 species against each other across all replicate streams at Llyn Brianne and in each stream category (acid grassland, circumneutral grassland, acid forest), 4) appraising their seasonal pattern of occurrence and density across months as averaged across streams (i.e., with streams as replicate units), 5) assessing associations within sites for riffle or margin habitats across all sites (regional and Llyn Brianne) using Wilcoxon signed ranks tests after correcting for differences in sampling effort, and 6) categorizing the annual Llyn Brianne samples from 1981 to 1993 into 3 groups representing site–year combinations when only *P. vitta* was present, only *C. alpina* was present, and both species coexisted. In the latter case, we used mixed-effects models and GLM procedures to determine whether mean prey or mean predator abundances varied among samples in each group to account for any significant effects of streams or years simultaneously. The abundance of prey for the 2 triclads was estimated as the total abundance of nymphal Ephemeroptera, nymphal Plecoptera, and larval Trichoptera (EPT) because these groups contribute most to macroinvertebrate benthos in our streams.

To assess potential climatic effects at Llyn Brianne, we examined linear correlations between the occurrence or mean abundance of the 2 triclads and summer discharge, winter discharge, winter temperature, summer temperature, maximum summer temperature, and the NAO index. Our previous work showed how some of these climatic variables affected abundance of potential invertebrate prey for predatory triclads, so we investigated whether linear correlations existed between triclad occurrence and the

mean abundance of prey measured as combined EPT across streams (Bradley and Ormerod 2001, Durance and Ormerod 2007).

We also considered the possibility that the loss of *C. alpina* might have reflected a nonlinear response to the large positive amplification of the NAO during the late 1980s and early 1990s and plotted time series of the NAO index and EPT prey abundance across the Llyn Brianne streams. We categorized Llyn Brianne samples from 1981 to 1993 into groups 1) representing *P. vitta* alone, 2) *C. alpina* alone, and 3) both species in coexistence before using mixed-effects models with GLM procedures to appraise variations in summer temperature and discharge among these 3 groups.

Results

Local and regional occurrence of Crenobia alpina

Long-term annual data on the abundance and frequency of occurrence of *C. alpina* ($r_s = 0.98$, $p < 0.001$, $p = 22$ y) and *P. vitta* ($r_s = 0.97$, $p < 0.001$, $n = 22$ y) were consistent in indicating population variations through time. Both species fluctuated at ~1 to 10 individuals/sample in each stream throughout the 1980s but with marked variability among locations (Fig. 1A, B). However, in ~1989 to 1990, both species became sporadic. *Crenobia alpina* was absent in 1990 and was not found after 1992. *Phagocata vitta* was absent from all 14 streams at Llyn Brianne in 5 of 9 y during the 1990s before returning more consistently after 1999. These general patterns were repeated across Wales, where *C. alpina* occurred in 15% of the WAWS sites sampled in 1984, but was not recorded when the same sites were surveyed in 1995. *Phagocata vitta* occurred in 56% of the WAWS sites in 1984 and 44% in 1995, and its frequency of occurrence had not fallen significantly ($\chi^2_{1\ \mathrm{df}} = 1.72$, $p > 0.05$).

Crenobia alpina and *P. vitta* both occurred under near-identical pH, Al, and Ca concentrations and over the wider range of acid–base conditions typical of base-poor hill streams in Wales (Table 1). During 1993 to 2005, mean pH, Al, and Ca concentrations in several Llyn Brianne streams changed as the streams recovered from the effects of acid deposition but remained well within the ranges typically occupied by both *P. vitta* and *C. alpina* (Table 1).

Habitat overlap and possible competition

During the period when both species occurred at Llyn Brianne, both reached their highest abundances in nearly the same streams (Fig. 2). However, they seldom reached high numbers in the same year (Fig. 3) or same streams simultaneously, except in circumneutral LI6 and LI7 (Fig. 4). As further evidence of how dominance could change between the 2 species, quasimonthly quantitative samples revealed a marked switch from *C. alpina* to *P. vitta* between 1985 and 1986 that corroborated findings from the annual sampling data (cf. Figs 4, 5).

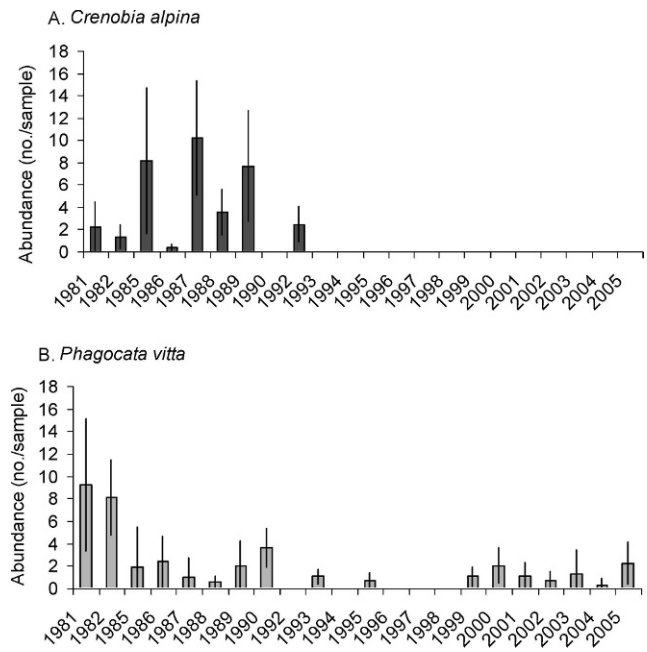

FIG. 1. Annual mean (±1 SD) abundance/sample of *Crenobia alpina* (A) and *Phagocata vitta* (B) from 1981 to 2005 in the Llyn Brianne experimental catchments, Wales (UK).

Some habitat separation existed where the 2 species co-occurred at Llyn Brianne. *Phagocata vitta* occupied margins and riffles with equal frequency, whereas *C. alpina* apparently had a preference for riffles (Wilcoxon signed ranks test, $W = 21$, $p < 0.05$, $n = 7$ y). Evidence of competition mediated by EPT prey abundance also was found. Both species occurred together only in year/site combinations with elevated EPT prey abundance (GLM, $F_{2,85} = 4.2$, $p < 0.02$; Fig. 6A), whereas the lowest prey abundances probably favored *P. vitta* alone.

Climate

Climate fluctuated markedly over the 25-y study period. Fluctuations were linked to the NAO and to directional trends through time. As shown more fully elsewhere (Durance and Ormerod 2007), winter temperatures ranged from 1.5 to 4.5°C, increased by 2 to 2.4°C as the NAO shifted from negative to positive, and increased significantly by 1.4 to 1.7°C between 1981 and 2005 after accounting for NAO effects. Mean summer temperature ranged from 10.1

TABLE 1. Ranges of mean pH, Al, and Ca (with SD) in streams occupied by *Crenobia alpina* and *Phagocata vitta* in the catchment (Llyn Brianne) and regional data sets (Welsh acid waters survey [WAWS]). Also shown are the range of mean conditions recorded across unmanipulated Llyn Brianne streams from 1993 to 2005.

Location	pH	Al (mg/L)	Ca (mg/L)
Llyn Brianne			
Crenobia alpina	4.6 ± 0.2–7.2 ± 0.4	0.04 ± 0.02–0.53 ± 0.16	0.11 ± 0.05–5.12 ± 1.32
Phagocata vitta	4.6 ± 0.4–6.6 ± 0.4	0.04 ± 0.02–0.51 ± 0.21	0.81 ± 0.24–6.67 ± 1.53
All sites	4.6 ± 0.2–7.2 ± 0.4	0.03 ± 0.01–0.63 ± 0.2	0.11 ± 0.05–6.67 ± 1.53
WAWS			
Crenobia alpina	5.9–6.8	0.01–0.07	0.94–4.44
Phagocata vitta	4.8–6.8	0.01–0.19	0.76–4.75
All sites	4.8–6.9	0.01–0.19	0.76–4.75
Llyn Brianne 1993–2005	4.6–7.1	0.03–0.59	0.8–4.7

to 14.6°C and increased weakly by 1.2°C between 1981 and 2005 ($r = 0.36$, $p < 0.1$, $n = 25$). Mean summer (0.42–1.47 m^3/s) and winter (1.14–3.87 m^3/s) discharge varied 340 to 350% at the gauged site. No linear trends through time were detected, but particularly dry summers occurred in 1983, 1985, 1990, 1991, and 1996, whereas winter discharge tended to be greater in years with strongly positive NAO (NAO > 1) than at other times (2.33 ± 0.62 m^3/s vs 2.82 ± 0.65 m^3/s, $F_{1,23} = 3.62$, $p = 0.07$)

Despite these climatic variations, few linear correlations were found between the abundance of either *C. alpina* or *P. vitta* and any single measure of winter or summer temperature or discharge. One exception was that *P. vitta* increased in frequency of occurrence in wetter years with greater discharge ($r = 0.46$, $p < 0.05$). Nevertheless, 3 climatically related results appeared to be of particular importance. First, *C. alpina* and *P. vitta* co-occurred only in year/site

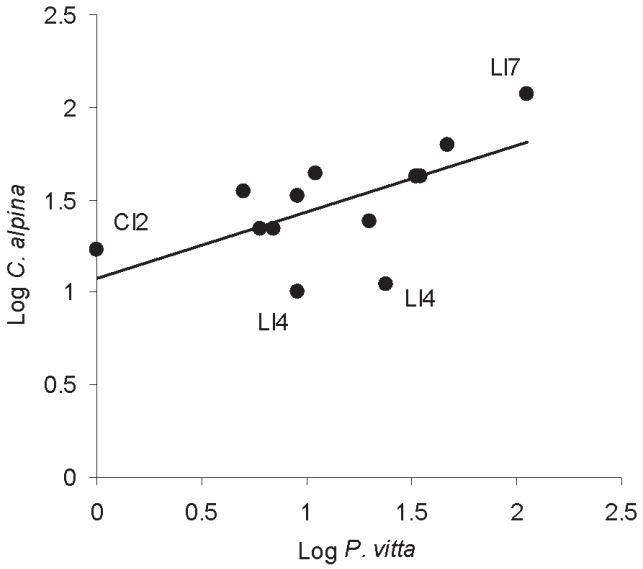

FIG. 2. Relative abundances per site during 1981 to 1993 of 2 cool-water triclads in streams around Llyn Brianne, Wales (UK). The fitted regression is defined by the equation $y = 1.08 + 0.36x$, $R^2 = 0.39$, $F_{1,13} = 7.8$, and $p < 0.05$.

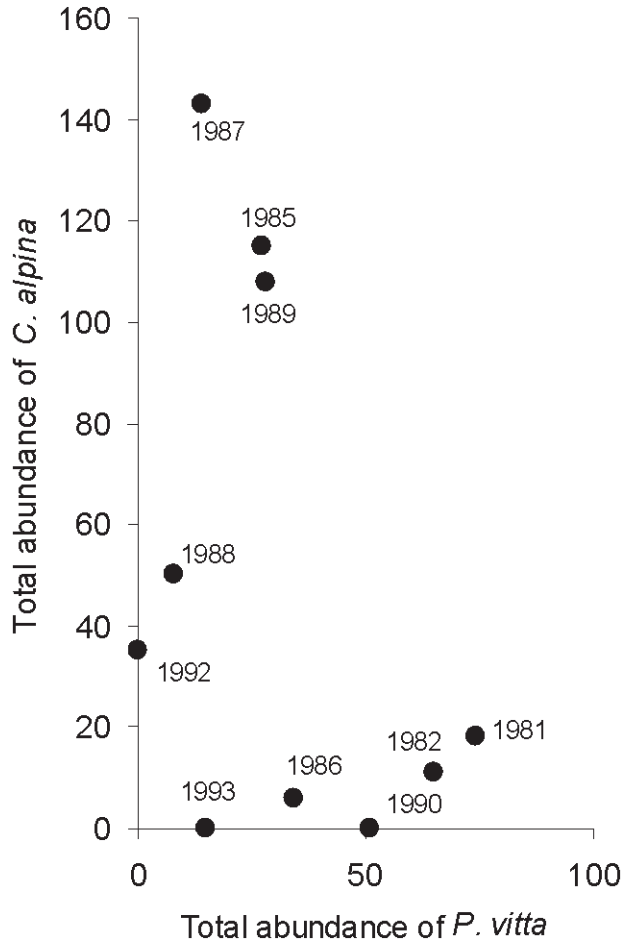

FIG. 3. Relative abundances of 2 cool-water triclads in all streams at Llyn Brianne, Wales (UK) during the years in which both species occurred.

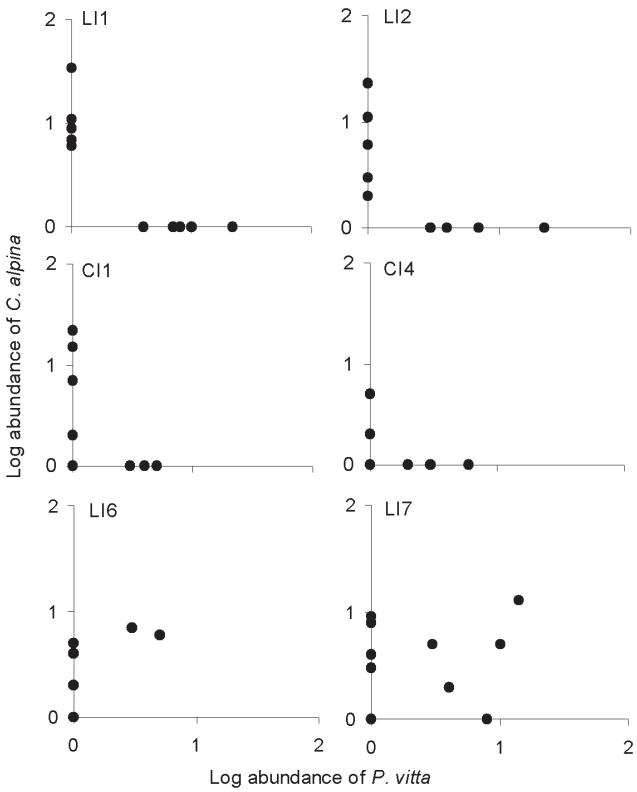

FIG. 4. Relative abundances of 2 cool-water triclads in 2 acid forest (LI1, LI2), acid moorland (CI1, CI4), and circumneutral streams (LI6, LI7) at Llyn Brianne, Wales (UK). Each data point represents 1 y.

combinations with the lowest mean summer temperatures (on average <12.5°C; Fig. 6B) (GLM $F_{2,85}$ = 3.04, $p < 0.05$). Second, *C. alpina* (but not *P. vitta*) declined to 0 in its frequency of occurrence when the NAO became increasingly positive for prolonged periods ($r = 0.64$, $p < 0.05$, 8 df; Fig. 7). Third, prolonged and markedly increased positive values of the NAO from 1989 to 1994 were accompanied by the

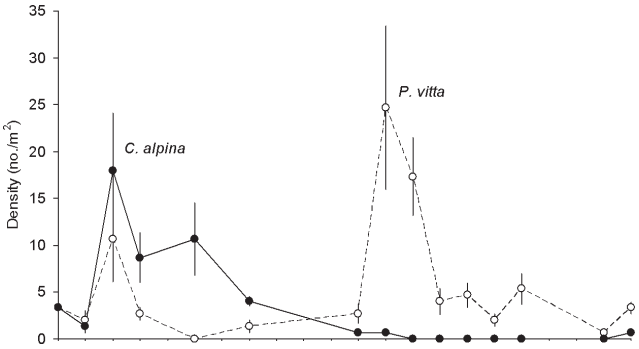

FIG. 5. Mean (±1 SE) monthly density of *Crenobia alpina* and *Phagocata vitta* between April 1985 and December 1986 in 6 streams around Llyn Brianne, Wales (UK).

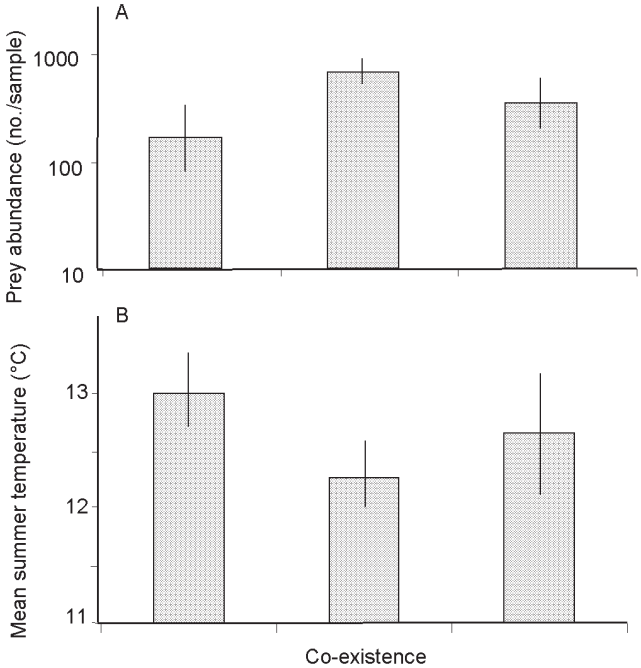

FIG. 6. Mean (±1 SD) total prey abundance (Ephemeroptera, Plecoptera, and Trichoptera) per sample (A) and stream temperature (B) for stream/sample combinations where *Phagocata vitta* occurred alone, *P. vitta* and *Crenobia alpina* occurred together, and *C. alpina* occurred alone. Both temperature and prey abundance differed significantly among patterns of species co-occurrence (see text).

lowest EPT abundances ever recorded across all the Llyn Brianne streams, particularly in 1993 and 1994 (Fig. 8A). This result was reflected in reductions in EPT abundance with increasing values of the smoothed NAO in all Llyn Brianne streams combined ($r = 0.42$, $p = 0.05$, $n = 22$ y; Fig. 8B), in acid moorland streams alone ($r = 0.54$, $p < 0.05$, $n = 20$ y), and in circumneutral moorland streams ($r = 0.41$, $p < 0.1$, $n = 22$ y). In other words, a marked break in the occurrence of *P. vitta* at Llyn Brianne up to 1999 and the apparent disappearance of *C. alpina* occurred during a 6-y positive phase of the NAO when prey abundances declined across streams to the lowest levels recorded.

Discussion

These data, collected over 25 y, illustrate how populations of *P. vitta* and *C. alpina* fluctuated before one of them disappeared from the Llyn Brianne experimental catchments over the period 1989 to 1992. Among the possible explanations, changes in acid–base status caused by recovery from acidification can be ruled out because current chemical conditions remain well within both species' optimal

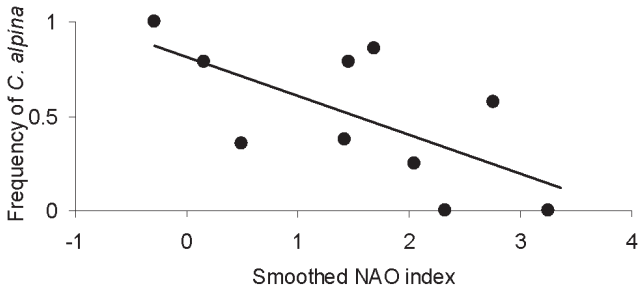

FIG. 7. Relationship between the frequency of occurrence of *Crenobia alpina* across streams at Llyn Brianne and a smoothed North Atlantic Oscillation (NAO) index (3-y running mean) from 1981 to 1993. The fitted regression follows the equation $y = 0.81 - 0.21x$, $R^2 = 0.43$, $F_{1,9} = 6.1$, $p < 0.05$.

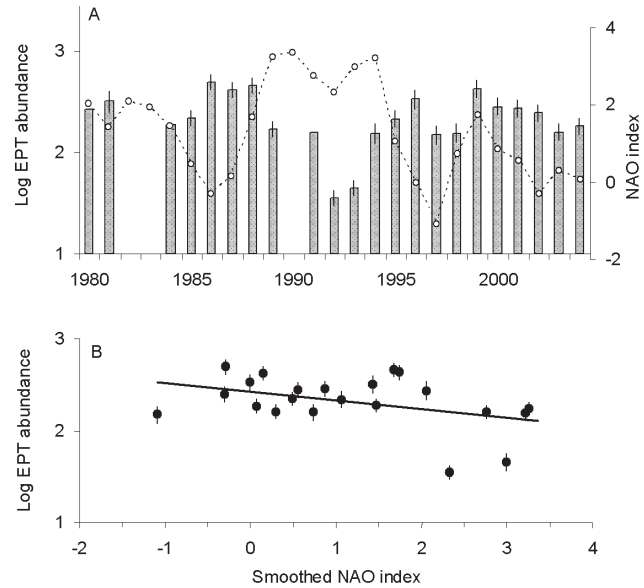

FIG. 8. Mean (±1 SD) prey abundance (combined Ephemeroptera, Plecoptera, Trichoptera; histograms) across streams at Llyn Brianne and the smoothed (3-y running mean) North Atlantic Oscillation index (NAO; open symbols with dotted line) through time (A) and the relationship between prey abundance and the smoothed NAO index (B). See text for statistical analysis.

ranges (Ormerod and Durance 2009). Other potential drivers, such as landuse change, have not been sufficiently large, consistent, or synchronous across all the catchments involved to explain such a rapid change. Salmonid fish, potential vertebrate predators, are relatively abundant only in the 2 circumneutral sites, and therefore, cannot explain such widespread losses. Instead, the most plausible explanation from the available data is that an unusually large, positive amplification of the NAO from 1989 to 1994 led to warmer, wetter conditions that markedly reduced prey abundance in ways that disrupted both species and favored *P. vitta* over *C. alpina* in a relationship already characterized by interspecific exploitation competition. Regional data suggested a similar and coincident reduction in the occurrence of *C. alpina* more widely across Wales, but too few years' data were available from these other sites to identify whether apparent losses were sustained. Samples from other British headwaters show that *Crenobia alpina* still persists elsewhere (Furse 2002). We stress again that our interpretation of trends inevitably relies on correlation and observation rather than experimentation because of the spatiotemporal scales involved. Nevertheless, other studies support the suggestions that *P. vitta* and *C. alpina* are competitors (Pattee 1965, Wright 1974), that these species are differentially affected by climatic effects on stream conditions (Beauchamp 1933, Lock 1972, Wright 1974), and that NAO fluctuations off western Europe in the late 1980s and early 1990s had large and pronounced effects on streams (Briers et al. 2004, Durance and Ormerod 2007).

Evidence for niche overlap and potential competition between *P. vitta* and *C. alpina* and sometimes another cool-water triclad, *Polycelis felina*, comes from previous laboratory and field studies (Lock 1972, Reynoldson 1978, Roca et al. 1992, Wallace 1991). For example, Lock and Reynoldson (1976) concluded that these species were close competitors on the basis of overlapping prey spectra, reach-to-reach vicariance, the effects of experimental food supplementation, and apparent competitive release when the other species declined. In laboratory experiments, Armitage and Young (1991) showed that differential avoidance of predation had only a limited role in mediating competition. In contrast, *P. vitta* out-competed *C. alpina* when feeding on either of 2 prey types except when *P. vitta* became so abundant that intraspecific competition occurred. In our case, strong circumstantial evidence indicated that *P. vitta* and *C. alpina* competed in the same streams and reaches where they rarely co-existed on an annual basis. The 2 species replaced each other through time in monthly or annual time series, and they occurred together only at the highest EPT prey abundances, e.g., in circumneutral streams. Small-scale local spatial partitioning between margins and riffles, where *C. alpina* sometimes dominated, also indicated possible local exclusion. This latter observation is consistent with laboratory experiments showing that *C. alpina* tolerates greater current velocity than *P. vitta* (Lock 1972, Roca et al. 1992).

Most interesting of all with respect to *C. alpina* and *P. vitta* was that the switch from fluctuating coexis-

tence to the occurrence of *P. vitta* alone occurred when EPT prey abundances declined substantially during a major positive phase of the NAO. An interesting parallel in the English Lake District (but not attributed to the NAO) occurred when marked reductions in prey abundance between 1981 and 1990 led to substantial changes in the relative abundances of populations of 2 competing triclads in which *Polycelis tenuis* increased while *Dugesia polychroa* numbers declined (Martin et al. 1994).

Contemporary observation and retrospective analyses have shown how variations in the NAO during the 1980s and early 1990s had large, synchronous effects on terrestrial, marine, and freshwater ecosystems across the northern hemisphere (Ottersen et al. 2001, Beaugrand and Reid 2003, Alheit et al. 2005). Effects on western European rivers included changes in the concentrations of nutrients, acidity, and other solutes (Monteith et al. 2000, Ness et al. 2004), consistently large increases in winter temperatures over extensive areas (Elliott et al. 2000, Briers et al. 2004, Durance and Ormerod 2007, Webb and Nobilis 2007), and increased winter discharge (Peterson et al. 2002). Marked drought over the period 1990 to 1991 also might have been driven by processes linked to the NAO that were generated from the same anomalies in Atlantic sea-surface temperatures (Sutton and Hodson 2005). In several of these cases, changes in the phenology, composition, and abundance of river organisms occurred as the winter NAO became strongly positive. At Llyn Brianne, the interannual stability of invertebrate assemblages was markedly reduced, a pattern indicative of a regime shift (Bradley and Ormerod 2001). The reductions in invertebrate abundance detected here echo this effect and contributed to the longer-term trends explored by Durance and Ormerod (2007).

The exact mechanisms of how the NAO might affect stream organisms are not well understood, but changes described here are consistent with the notion that the NAO represents a synoptic index of multiple climate processes that in combination have large, widespread ecological effects (Ottersen et al. 2001). The most likely factors in our case were direct thermal, chemical, or discharge effects on *C. alpina* or their prey abundance in summer or winter. The loss of *C. alpina* following increased winter temperatures of 2 to 2.5°C would be consistent with the sensitivity of this cool-water stenotherm to higher water temperatures, although winter temperatures remained well within its tolerance range (Wright 1974, Roca et al. 1992). Effects of progressively increased summer temperatures coupled with low flow in 1990 to 1992 are more likely to have been detrimental to *C. alpina* than to *P. vitta*. Beauchamp (1933) demonstrated in the 1930s that *C. alpina* responded to warming with upstream range contraction. This behavior and the facultative hyporheic distribution of *C. alpina* might have protected it from short-term extreme temperatures, but experiments by Wright (1974) showed that *C. alpina* cannot withstand temperatures >14°C for long periods, a result that matches its field distribution (Pattee 1965, Wright 1974). In our case, *P. vitta* and *C. alpina* coexisted most often when average stream temperatures were <12.5°C. During our study, elevated discharge appeared to have an adverse effect on *C. alpina*, in contrast to *P. vitta*, which appeared to benefit from high discharge. In alpine regions, experimental floods led to a large and sustained reduction in *C. alpina*, which accompanied substantial reductions in associated invertebrate densities (Robinson and Uehlinger 2008).

If the loss of *C. alpina* from the Llyn Brianne streams resulted from prey reduction and competition with *P. vitta* during NAO amplification during 1989 to 1994, one intriguing question is: why has it not returned in the ensuing 15 y? One possibility involves dispersal ability, and genetic evidence shows that *C. alpina* is a particularly poor disperser, even between adjacent headwaters (Brändle et al. 2005, 2007). A potentially more important factor is that summer temperatures at Llyn Brianne have remained in the range in which *C. alpina* would be excluded or out-competed by *P. vitta* (Fig. 6B). Mean summer stream temperatures >13°C occurred in 0 of 8 y before 1990 but 6 of 15 y between 1991 and 2005, and mean temperatures have exceeded this value in the single hottest month each summer in all but 2 y since 1991.

Wider issues and conclusions

Overall, our data are consistent with the view that extreme events generated by climate can be detrimental to small, fluctuating populations, particularly where species have a narrow thermal tolerance, limited geographical range, and limited dispersal capability. In this case, the extreme events involved probably were generated by the NAO rather than directional climate change. Nevertheless, the warmer, wetter winters and hotter, drier summers caused by positive NAO values are potentially an analog of future climate-change predictions for western Britain. The extent to which intensification of the NAO itself reflects greenhouse-gas forcing is still unclear (Hurrell and Deser 2009). Our data support the expectation that headwater or alpine species like *C. alpina* will be particularly at risk (Parmesan 2006). In Britain, this

species already is considered a glacial relict with reduced genetic diversity (Reynoldson 1966, Roca et al. 1992, Brandle et al. 2005). The loss we describe appears at present to be local, but the processes involved might provide insight into effects that could occur over larger spatial extents (Angermeier 1995).

At the same time, however, our study demonstrates the many difficulties in ascribing changes in species occurrence or extinction unequivocally to specific climate-change processes, particularly where data are examined retrospectively. First, in many cases, interpretation of occurrence or loss in relation to climate will depend on correlation and weak inference because extinctions are not always foreseeable. Second, climatic effects on streams and rivers involve complex combinations of discharge and thermal effects that can vary among seasons with different consequences for organisms. Third, effects from directional climate change can be augmented or confounded by factors like fluctuations in the NAOs, to which ecological responses can be large and nonlinear. Fourth, climatic effects might well interact with poorly understood processes or ecological interactions, such as competition, food limitation, and dispersal. Last, as demonstrated elsewhere, climate change interacts with other stressors, such as abstraction, pollution, and habitat degradation, to affect organisms (Ormerod and Durance 2009, Durance and Ormerod 2009). In resolving these challenges, long-term studies like ours will be most valuable when coupled with broader geographical assessments and with experiments and detailed studies of the effects of climate on both abiotic and biotic processes in running-water systems.

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