UV-B radiation, climate change and frogs — the importance of phenology

Clive P. Cummins

Centre for Ecology & Hydrology, Monks Wood, Huntingdon PE28 2LS, UK

Received 20 May 2002, revised version received 12 July 2002, accepted 12 July 2002

Cummins, C. P. 2003: UV-B radiation, climate change and frogs — the importance of phenology. — *Ann. Zool. Fennici* 40: 61–67.

The authors of a recent commentary challenged a "traditional view" that organisms living at high latitudes are normally exposed to lower doses of potentially damaging UV-B radiation than those living at lower latitudes. Taking as their main example the European common frog (*Rana temporaria* L.) in Scandinavia, they suggested that global warming might be masking adverse biological effects of ozone depletion, which allows a greater percentage of solar UV-B to reach the Earth's surface, by altering species' phenology. Here, I expand the scope of that study to include phenology and potential exposure to UV-B radiation across a larger part of the common frog's geographic range, including populations from oceanic and alpine climates. The results highlight both the importance of phenology in limiting exposure to UV-B radiation and the need for a mechanistic understanding of phenological variation. The results also illustrate some important limitations of a commonly used field experiment, at least in terms of its utility for comparing sensitivities to UV-B or predicting effects of ozone depletion.

Introduction

In middle- and high latitudes, many organisms have highly seasonal life cycles in which key events such as breeding are tied closely to seasonality of weather. It is widely anticipated that the timing of such key events (phenology) will change in concert with changes in seasonal patterns of weather (climate change) resulting from ongoing global warming, which in turn is being influenced by human activities (IPCC 2001a). Because of the annual cycle of variation in angle of solar elevation, a species' phenology may determine the potential exposure of particular life stages to solar UV radiation. In a recent commentary, Merilä *et al.* (2000c) challenged a

"traditional view" that organisms living at high latitudes are normally exposed to lower doses of potentially damaging UV-B radiation (hereafter, UV-B) than those living at lower latitudes. They considered embryonic and larval amphibians developing in pools, taking as their primary example the European common frog, Rana temporaria L. On the basis of several outdoor and laboratory studies, hatchability and incidence of abnormality among embryonic R. temporaria appear to be little affected by exposure to ambient levels of UV-B radiation in Scandinavia (Langhelle et al. 1999, Merilä et al. 2000b, Pahkala et al. 2000, Hakkinen et al. 2001). Even increasing exposure to UV-B by 81%-113% above ambient levels did not affect hatchability or incidence of abnormalities in outdoor experiments in the UK (Cummins *et al.* 1999). However, in a recent laboratory study, Pahkala *et al.* (2001) found that tadpoles that had been exposed to UV-B during embryonic development reached metamorphosis later, at a smaller size and with greater incidence of abnormality than tadpoles raised without exposure to UV-B, so there is cause for concern about potential effects of ozone depletion upon this species, via increasing levels of UV-B.

Merilä et al. (2000c) noted that in Sweden the common frog breeds progressively later in the year with increasing latitude, from early April at 56°N to early June at 69°N, following the latitudinal cline in the time of onset of the spring thaw. Although the potential maximum intensity of UV-B is greater at 56°N than it is at 69°N at any particular time of year, Merilä et al. (2000c) calculated that the maximum, biologically effective daily dose that might be received at 69°N in June is approximately twice the maximum daily dose that might be received at 56°N in April. Thus, they argued, embryonic and larval frogs at higher latitudes are likely to be exposed to higher daily doses of UV-B than those at lower latitudes. Merilä et al. (2000c) also argued that development would take longer with increasing latitude, owing to lower ambient temperature, and that the total exposure to UV-B during embryonic and larval stages would consequently increase further with increasing latitude. More generally, they suggested that field experiments may be failing to detect adverse biological effects of ozone depletion because the appearance of such effects is being masked or delayed by a concurrent effect of global warming on the phenology of the species concerned.

Here, I compare the data from Sweden given by Merilä *et al.* (2000c) with data from earlyand late-breeding populations of *R. temporaria* in other parts of the species' range, and I evaluate their hypothesis that lower temperature at higher latitudes enhances a "reversed" latitudinal cline in exposure to UV-B. Finally, I suggest that the utility of field experiments for detecting adverse effects of ozone depletion is less likely to be undermined by global warming than by a failure to recognise inherent limitations of the most commonly used experimental design, and/ or a failure to measure UV-B.

Latitude, phenology and UV-B

Within the geographical context of their examples, Merilä et al. (2000c) showed that later spawning at high latitudes could generate a cline of increasing exposure to UV-B with increasing latitude. However, a latitudinal cline in time of breeding does not extend throughout the common frog's range. Like many other species, common frogs are found at higher altitudes near their lower-latitudinal limit. Indeed, the latest records of breeding reported in the literature concern populations of the common frog near the southern limit of its range in Europe, in the Alps (Miaud et al. 1999). There, at altitudes of 2000–2300 m, spawning may occur at the beginning of July and the animals are active for only 3 months of the year (Guyétant et al. 1988). Spawn laid near the time of the summer solstice, at such high altitude and relatively low latitude (ca. 46°N), is likely to be exposed to much higher doses of UV-B than spawn laid at any time in the northern part of the species' range. To illustrate the scale of the potential variation in maximum daily dose of UV-B at spawning time, I estimated daily doses of UV-B, weighted for biological effectiveness (UV-B_{BE}), for a subset of the examples listed by Merilä et al. (2000c) and for two further examples (Fig. 1). The doses were calculated using the same algorithms as used by Merilä et al. (2000c), but as implemented in the model "UVB" (revision 3.02) by E. L. Fiscus and F. L. Booker (E. L. Fiscus, U.S.D.A.-A.R.S., North Carolina State University, 1509 Varsity Drive, Raleigh, NC 27606, U.S.A.). One of the additional examples is a breeding site in Devon, S.W. England (50.8°N), where common frogs usually begin spawning in mid-January (Tyson & Smith 1999). There, the potential for exposure to solar UV-B is extremely small (Fig. 1) and actual exposures are frequently even lower because of cloud cover; in the period 1971-2000, the mean monthly percentage cloud cover (± S.D.) for January for the 5 km UK grid square containing the site was $74.5\% \pm 6.2\%$. At the other extreme is an estimate of the potential daily dose of UV-B_{BE} at an altitude of 2000 m at 46°N on 1 July, approximating the circumstances of a latebreeding population in the Alps. Note that the length of the "UV-B day" at spawning time in the far North of the common frog's range differs very little from that in the Alps - it is mainly the amplitude that differs (Fig. 1). There may be 24 hours of "daylight" in the far North, but for much of that time the Sun is low in the sky and little solar UV-B reaches the ground. Thus, late-breeding common frogs at high latitude may experience higher levels of UV-B than earlier breeders at lower latitude in Sweden, as shown by Merilä et al. (2000c), but the cline along 13° of latitude within Sweden is rather small (Fig. 1). In fact, the highest potential for exposure exists in lower-latitude, high-altitude populations, whereas the lowest potential exists among populations in oceanic climates where spawning occurs about the time of the winter solstice. If intraspecific variation in tolerance/resistance to UV-B has evolved, the best chance of detecting such differences probably lies in a comparison of populations from the latter two regions.

Latitude, phenology and temperature

Merilä et al. (2000c) postulated that the cumulative exposure of frogs to UV-B during embryonic development at high latitude might exceed that at lower latitudes by an even greater margin than is suggested by the two-fold difference in potential daily dose (Fig. 1: Lund vs. Kilpisjärvi). Their hypothesis was based on a supposition that frog embryos at high latitude experience lower ambient temperatures, and therefore develop more slowly than embryos at lower latitudes. However, just as later breeding at higher latitude may expose embryos to seasonally higher levels of UV-B, so it may also expose them to seasonally higher ambient temperature. Figure 2 shows annual patterns of monthly means of temperature and documented dates of spawning by R. temporaria at nine locations, from N. France to N. Sweden. It is important to note that the temperature curves represent one aspect of the *climate* at the respective sites, and not necessarily the weather at the time of spawning in any particular year. The date of spawning may be influenced by weather; for example, adults may defer spawning during very cold weather and thereby reduce the risk of exposing their offspring to unfavour-



Fig. 1. The diel profile of potential intensity and potential daily dose of biologically effective UV-B radiation (UV-B_{BE}) at the times of year when common frogs (*Rana temporaria* L.) spawn in five places: Kilpisjärvi (69.0°N, 485 m); Umeå (63.8°N, 7 m); Lund (55.6°N, 72 m); North Wyke (50.8°N, 177 m); Alps (46.0°N, 2000 m). See Fig. 2 for spawning times. UV-B_{BE} profiles were generated using an algorithm by Björn and Murphy (1985), as implemented in the model "UVB" (revision 3.02) by E.L. Fiscus (U.S.D.A.-A.R.S., North Carolina State University, Raleigh, NC 27606, U.S.A.) and F.L. Booker. UV-B was weighted for biological effectiveness using an action spectrum for damage to DNA (Setlow 1974), normalised to unity at 300 nm.

ably low temperatures. However, the conditions experienced by the embryos after spawning are beyond the control of the parents. Thus, Fig. 2 provides a somewhat crude, statistical summary of the thermal conditions likely to prevail during embryonic development in the respective locations. This analysis is necessarily imprecise, for various reasons such as variable quality of the climate data, year-to-year variation in date of spawning, variable length of spawning season, etc. Nevertheless, across the nine locations considered here, no correlation between date of spawning and mean temperature at that time of year is apparent. If there is any trend in the Scandinavian data, it is for embryonic development to occur in somewhat warmer conditions with increasing latitude (Fig. 2: sites 6-9). If that trend extends to water temperatures, as well as air temperatures, it might result in shorter periods of embryonic development with increasing latitude, and hence lower-than-predicted total exposure to UV-B. Furthermore, several studies have suggested that embryos and/or tadpoles of



Fig. 2. Annual trends in temperature and the spawning times of common frogs (*Rana temporaria* L.): the symbols show monthly means of daily mean temperature over an 8–10 year period at each location. Spawning times at the respective location are indicated by numbered ovals, for which corresponding comments and data sources (spawning; climate) are as follows: 1: Mean dates of first spawning and last spawning, 1986–1994 (Le Garff 1998; Rennes, France 1981–1990^a). 2: Mean date of first spawning 1990–1999 (Tyson & Smith 1999; North Wyke, England 1990–98^b). 3 and 4: Published and unpublished observations by the author, 1983–1989 (Cummins 1986; 3 = Monks Wood, England 1981–1990^b; 4 = Donna Nook, England 1981–1990^b). 5: Spawning date for 1976 (Beattie 1985; Moor House, England 1970–1979^b). 6–9: Spawning dates after Merilä *et al.* (2000) (6 = Lund, Sweden 1981–1990^a; 7 = Stockholm, Sweden 1981–1990^a; 8 = Umeå, Sweden 1981–1990^a; 9 = Kiruna, Sweden 1981–1990^a). Sources of climate data: ^a = Global Historical Climatology Network, version 1; ^b = UK Meteorological Office.

frogs from high-altitude or high-latitude populations undergo more rapid ontogenetic development than those from lower altitude or lower latitude, at a given temperature (*see* Table 5 of Miaud *et al.* 1999, Merilä *et al.* 2000b, Laurila *et al.* 2001, Stahlberg *et al.* 2001, Laurila *et al.* 2002). Such a tendency would also offset any latitudinal increase in cumulative exposure to UV-B resulting from a phenological cline.

Is climate change masking effects of ozone depletion?

Merilä *et al.* (2000c) argued that "the negative effects of ozone depletion in nature may go undetected for long periods of time" if concurrent warming leads to frogs (and other organisms) breeding earlier and thereby experiencing seasonally lower levels of UV-B. In this context, it is important to distinguish between a *potential* for adverse effects of ozone depletion and a *realisation* of that potential. In the scenario described

by Merilä *et al.* (2000c) there may simply be no negative effect of ozone depletion on frogs to detect if, albeit fortuitously, concurrent warming induces frogs to breed earlier in the year. Such a lack of effect should not be confused with an undetected effect.

Certainly, it is possible for certain types of field experiment to fail to identify a potential for adverse effects of a relative deficit of ozone. This could happen if the highest experimental exposures to UV-B fall short of the highest potential exposures. Relatively early breeding in the year(s) of study is but one possible cause of such a shortfall. A commonly used experimental design is one in which the exposure of amphibian embryos to solar UV-B is manipulated using filters that transmit ambient UV-B to various degrees (Blaustein et al. 1998): typically, the fate of embryos exposed to unobstructed solar UV-B is compared with that of embryos under filters that block solar radiation in the UV-B waveband $(\lambda \leq 320 \text{ nm})$. Referring to Fig. 1, it is evident that an experiment of this type carried out during the breeding season of R. temporaria in S.W. England, in January, could not effect very different exposures of frog embryos to UV-B, simply because ambient, biologically effective doses of UV-B cannot be very high at that location and time of year. Consequently, if blocking ambient UV-B in such an experiment had no effect, one would still have no basis for predicting effects of exposure to ambient UV-B anywhere else in the species' range where UV-B intensity and daily dose may be much higher (Fig. 1). Even if the filtration experiment were carried out in the Alps in July, if it happened to take place during a period with heavy cloud cover, when ambient UV-B intensity was below its potential value, the outcome might not be indicative of what could occur under conditions of maximal exposure. Thus, the location and time of year at which experiments based on filtration of ambient solar radiation are carried out impose fundamental limitations on one's ability to generalise from their outcomes, and the vagaries of the weather may impose further restrictions. It is mainly for those reasons that Merilä et al. (2000c) were right to recommend experimental supplementation of UV-B. Of course, filtration experiments can yield useful information if the exposures to UV-B are measured. The data could help to define a "doseresponse" relationship that could be used to make testable predictions of the effects of exposure to UV-B for particular scenarios of location, time of year, atmospheric conditions and intraspecific variation in sensitivity. Regrettably, measurements of UV-B are relatively scarce among studies on amphibians published to date.

Conclusions

Ultimately, the extent to which any potential for adverse effects of ozone depletion on frogs is realised, via increased exposure to UV-B, may depend on the durations and rates of change of ozone depletion and climate, the rate and extent to which frogs can keep advancing their date of spawning, and the rate of evolution of protective mechanisms or avoidance behaviours. During the past two decades, which have shown pronounced warming on a global scale (IPCC 2001b), *R. temporaria* showed no significant tendency towards earlier breeding in a 16-year series of observations (1979–1994) in S. England (Beebee 1995) or in a 10-year series (1990-1999) in S.W. England (Tyson & Smith 1999). However, preliminary analysis of 16 series of dates of first spawning from Great Britain, varying in length from seven to 25 years, suggests an average advancement of 11 days over the past 30 years (T. H. Sparks, pers. comm.). Long-term monitoring of the dates of first spawning by R. temporaria in large parts of Finland suggested an advancement of 2-13 days between 1846 and 1986 (Terhivuo 1988). On a broad, geographic scale there is a very large variation in time of year at which R. temporaria breeds (Fig. 2). Such variation might be interpreted as evidence of flexibility (relative to photoperiod, for example) or inflexibility (e.g. relative to prevailing temperatures; Fig. 2). So far, the underlying system controlling the time of breeding has not been established, and so the scope for breeding earlier within any particular population remains unknown. The alpine populations of *R. temporaria* are evidence of the species' capacity to persist in environments where potential exposure to UV-B far exceeds any level likely to occur in the northernmost part of its range, even under extreme scenarios of ozone depletion. Hofer and Mokri (2000) described a UV-absorbing substance in the skin of R. temporaria tadpoles from the Alps that may confer protection. However, the nature and degree of intraspecific variation in resistance, tolerance or avoidance of UV-B also remain unknown.

On the basis of some predictions, ozone depletion by man-made chemicals should be declining already (Staehelin et al. 2001), whereas global warming is set to continue for many decades (IPCC 2001b). Any threat posed by ozone depletion to spring-breeding amphibians might, therefore, be expected to decline on both counts, i.e. declining penetration of solar UV-B owing to higher ozone amounts and lower exposure owing to earlier breeding. However, the expected reversal of the recent decline in mid-latitude stratospheric ozone content has not yet materialised, and it may be that changes in global atmospheric circulation, driven by global warming, play a greater part in such changes than was previously recognised (Egorova et al. 2001, Harris & Bishop 2001, Staehelin et al. 2001). Thus, it seems that recent ozone depletion may persist. If there is a broad tendency for potential, adverse effects of ozone depletion to be offset by concurrent changes in climate, as suggested by Merilä *et al.* (2000c), then that might be regarded as a cause for relief, rather than concern, at least in the short term. However, the importance of phenology is evident and the need to understand its controlling mechanisms is more urgent than ever.

Acknowledgements

I am grateful to Juha Merilä and Trevor Beebee, for helpful and interesting comments on an earlier draft of the manuscript, Tim Sparks of CEH Monks Wood, for a preview of his analyses of spawning dates from historical records and the ongoing Phenology Network (www.phenology.org.uk), the Met Office, for climate data from the UK Climate Impacts Programme, the British Atmospheric Data Centre, which provided access to the Met Office Land Surface Observation Stations Data, and Ed Fiscus, who kindly provided a copy of the programme "UVB".

References

- Beattie, R. C. 1985: The date of spawning in populations of the common frog (*Rana temporaria*) from different altitudes in northern England. — *Journal of Zoology* 205: 137–154.
- Beebee, T. J. C. 1995: Amphibian breeding and climate. — *Nature* 374: 219–220.
- Björn, L. O. & Murphy, T. M. 1985: Computer calculation of daylight ultraviolet radiation at ground level. — *Physiologie Végétale* 23: 555–561.
- Blaustein, A. R., Kiesecker, J. M., Chivers, D. P., Hokit, D. G., Marco, A., Belden, L. K. & Hatch, A. 1998: Effects of ultraviolet radiation on amphibians: field experiments. — Am. Zool. 38: 799–812.
- Cummins, C. P. 1986: Temporal and spatial variation in egg size and fecundity in *Rana temporaria*. — J. Anim. Ecol. 55: 303–316.
- Cummins, C. P., Greenslade, P. D. & McLeod, A. R. 1999: A test of the effect of supplemental UV-B radiation on the common frog, *Rana temporaria* L., during embryonic development. — *Global Change Biology* 5: 471–479.
- Egorova, T. A., Rozanov, E. V., Schlesinger, M. E., Andronova, N. G., Malyshev, S. L., Karol, I. L. & Zubov, V. A. 2001: Assessment of the effect of the Montreal Protocol on atmospheric ozone. — *Geophysical Research Letters* 28: 2389–2392.
- Guyétant, R., Brosse, S., Hérold, J. P. & Pinston, H. 1988: Étude de la croissance et du développement de grenouilles rousses *Rana temporaria* L. en altitude (Alpes

du nord). — Comptes Rendus des Séances de la Société de Biologie 182: 301–307.

- Hakkinen, J., Pasanen, S. & Kukkonen, J. V. K. 2001: The effects of solar UV-B radiation on embryonic mortality and development in three boreal anurans (*Rana temporaria*, *Rana arvalis* and *Bufo bufo*). — *Chemosphere* 44: 441–446.
- Harris, N. R. P. & Bishop, L. 2001: Changes in global stratospheric ozone. — Ozone-Science and Engineering 23: 437–443.
- Hofer, R. & Mokri, C. 2000: Photoprotection in tadpoles of the common frog, *Rana temporaria*. — *Journal of Photochemistry and Photobiology B* 59: 48–53.
- IPCC 2001a: McCarthy, J. J., Canziani, O. F., Leary, N. A., Dokken, D. J. & White, K. S. (eds.), *Climate change* 2001: impacts, adaptation and vulnerability. — Cambridge University Press. 1000 pp.
- IPCC 2001b: Houghton, J. T., Ding, Y., Griggs, D. J., Noguer, M., van der Linden, P. J. & Xiaosu, D. (eds.), *Climate change 2001: the scientific basis.* — Cambridge University Press. 944 pp.
- Langhelle, A., Lindell, M. J. & Nyström, P. 1999: Effects of ultraviolet radiation on amphibian embryonic and larval development. — *Journal of Herpetology* 33: 449–456.
- Laurila, A., Karttunen, S. & Merilä, J. 2002: Adaptive phenotypic plasticity and genetics of larval life histories in two *Rana temporaria* populations. — *Evolution* 56: 617–627.
- Laurila, A., Pakkasmaa, S. & Merilä, J. 2001: Influence of seasonal time constraints on growth and development of common frog tadpoles: a photoperiod experiment. — *Oikos* 95: 451–460.
- Le Garff, B. 1998: Relations between meteorological factors and laying in the common frog *Rana temporaria* L. (Amphibia, Anura, Ranidae), in West of France (Forest of Rennes). — *Bulletin de la Société zoologique de France* 123: 61–71.
- Merilä, J., Laurila, A., Laugen, A. T., Rasanen, K. & Pahkala, M. 2000a: Plasticity in age and size at metamorphosis in *Rana temporaria* — comparison of high and low latitude populations. — *Ecography* 23: 457–465.
- Merilä, J., Laurila, A. & Pahkala, M. 2000b: Effects of ambient UV-B radiation on early development of the common frog (*Rana temporaria*) embryos in the subarctic. — Ann. Zool. Fennici 37: 51–58.
- Merilä, J., Pahkala, M. & Johanson, U. 2000c: Increased ultraviolet-B radiation, climate change and latitudinal adaptation — a frog perspective. — Ann. Zool. Fennici 37: 129–134.
- Miaud, C., Guyétant, R. & Elmberg, J. 1999: Variations in life-history traits in the common frog *Rana temporaria* (Amphibia: Anura): a literature review and new data from the French Alps. – J. Zool. 249: 61–73.
- Pahkala, M., Laurila, A. & Merilä, J. 2000: Ambient ultraviolet-B radiation reduces hatchling size in the common frog *Rana temporaria*. — *Ecography* 23: 531–538.
- Pahkala, M., Laurila, A. & Merilä, J. 2001: Carry-over effects of ultraviolet-B radiation on larval fitness in *Rana temporaria. — Proceedings of the Royal Society of London* B 268: 1699–1706.

- Setlow, R. B. 1974: The wavelengths in sunlight effective in producing skin cancer: a theoretical analysis. — Proceedings of the National Academy of Sciences of the United States of America 71: 3363–3366.
- Staehelin, J., Harris, N. R. P., Appenzeller, C. & Eberhard, J. 2001: Ozone trends: A review. — *Reviews of Geophysics* 39: 231–290.
- Stahlberg, F., Olsson, M. & Uller, T. 2001: Population diver-

gence of developmental thermal optima in Swedish common frogs, *Rana temporaria. – J. Evol. Biol.* 14: 755–762.

- Terhivuo, J. 1988: Phenology of spawning for the common frog (*Rana temporaria* L.) in Finland from 1846 to 1986. — Ann. Zool. Fennici 25: 165–175.
- Tyson, K. & Smith, R. 1999: Predicting the date of frog emergence in Devon. — British Wildlife June 1999: 310.