RESEARCH ARTICLE

Anthropogenic climate change impacts on ponds: a thermal mass perspective

John H. Matthews

University of Texas, Section of Integrative Biology, Austin, U.S.A.

Corresponding author: *John H. Matthews* (johoma@gmail.com)

Abstract

Small freshwater aquatic lentic systems (lakes and ponds) are sensitive to anthropogenic climate change through shifts in ambient air temperatures and patterns of precipitation. Shifts in air temperatures will influence lentic water temperatures through convection and by changing evaporation rates. Shifts in the timing, amount, and intensity of precipitation will alter the thermal mass of lentic systems even in the absence of detectable ambient air temperature changes. These effects are likely to be strongest in ponds (standing water bodies primarily mixed by temperature changes than by wind), for whom precipitation makes up a large component of inflows. Although historical water temperature datasets are patchy for lentic systems, thermal mass effects are likely to outweigh impacts from ambient air temperatures in most locations and may show considerable independence from those trends. Thermal mass-induced changes in water temperature will thereby alter a variety of population- and community-level processes in aquatic macroinvertebrates.

Introduction

Little research has focused on freshwater biological impacts from anthropogenic climate change. Gaps in theoretical and observational perspectives on freshwater ecology stand in high relief in comparison with the amount of climate change impact research on marine and terrestrial systems (e.g., IPCC 2001; Parmesan and Yohe 2003; Root et

al. 2003; Thomas et al. 2004). Worldwide, freshwater aquatic systems account for 15 % of all known animal species even though freshwater covers only about 1.7 % of the world's land surface.

Most of the world's liquid freshwater is located in lakes, here defined as standing water bodies that are mixed primarily by wind. Ponds generally have less surface area than lakes (and thus fetch for wind) and have no more than a few meters of depth. They are here defined as standing water bodies mixed primarily by temperature shifts in the water column. Given their smaller size, ponds are generally more prone to drying than lakes. For the purposes of this chapter, I will divide them into (a) short hydroperiod ponds that are ephemeral and in normal-precipitation years dry up, most often in summer in temperate areas or in dry seasons in tropical zones, and (b) long hydroperiod ponds that persist throughout the annual precipitation cycle and disappear only in dry years. In most instances, ponds of both types require – and are defined by – precipitation patterns (Brönmark and Hansson 2005). And changes in precipitation patterns are likely to have a powerful impact on the inhabitants of ponds.

That said, anthropogenic climate change is probably not seen as the most widespread or pressing issue for lentic systems at the beginning of the 21st century (e.g., Poff et al. 2002). Habitat destruction, increasing withdrawals of surface water for human use, eutrophication, degradation of water quality as a result of industrial and agricultural pollution, acidification and nitrification of precipitation from industrial emissions, the transfer and invasion of exotic species, and many other consequences of human activity have been threatening the biota of freshwater systems for decades and even centuries (Williams 1997; Abell et al. 2000; Brönmark and Hansson 2002; Poff et al. 2002; Williams et al. 2003; Nicolet et al. 2004). Some critics have suggested that biologists studying climate change impacts are alarmists; climate change itself is not a new process, they correctly point out, and regional and global climate patterns shift naturally (e.g., Lomborg 2001). We can infer from the paleontological and paleoecological record that "natural" climate shifts resulting from a variety of nonhuman factors have contributed to the extinction of populations and species over ecological and evolutionary timescales (IPCC 2001). Why is the current period of human-induced change important for species, populations, and communities?

There are good reasons to suspect that the current era of human-induced changes are biologically significant and represent novel challenges to human resource management and ecological resilience and resistance. Past climate changes occurred in the context of relatively intact ecosystems. Species ranges could therefore respond in a plastic manner as the abiotic components of a niche shifted. The current period of human-induced climate change is thus occurring in across heavily modified (and often severely damaged) landscapes, with many fewer acceptable ecological and evolutionary escape paths that might have been open in the past (IPCC 2001; Parmesan and Yohe 2003; Root et al. 2003; Thomas et al. 2004). Perhaps most alarming, climate modeling suggests that global mean temperatures will continue to increase, and the rate of that increase is likely to quicken — perhaps considerably — over coming decades and centuries. At high latitudes and altitudes this era of rapid climate change may already have

begun for terrestrial systems (IPCC 2001; Thomas et al. 2004). Thus, climate change will creep up the list of important influences for most ecosystems; lentic ecosystems should prove no exception (Brönmark and Hansoon 2002).

Since we can expect climate changes to continue and increase in magnitude, the lack of scientific attention to realized lentic impacts from anthropogenic climate change is unfortunate, particularly given their role as important biodiversity reservoirs (Abell et al. 2000, Poff et al. 2002, Williams et al. 2003). I believe that understanding climate impacts on lentic systems will require approaches that will differ in important respects from those used to monitor and untangle terrestrial systems.

Basic to these new approaches is understanding the role of changes in thermal mass occurring as a result of climate shifts. Ambient air temperature is likely to be less important for aquatic biota than terrestrial species since lentic systems buffer aquatic species from air temperature and liquid water is far more difficult to heat/cool than the gases of the atmosphere. The physical properties of aquatic systems will be especially notable in short-hydroperiod ponds, which have small volumes, high variance in volume, and limited inflows; their temperature dynamics respond to water volume and thus thermal mass (Vannote and Sweeney 1980; Brönmark and Hansson 2005). The timing and amount of precipitation inflows for such systems are thus likely to be more important than ambient air temperature in determining seasonal temperature patterns. As a result, water temperatures may follow nonintuitive seasonal trajectories compared to mean air temperatures (Covich et al. 1997), and aquatic biological impacts may be similarly out of sync with surrounding terrestrial systems.

How might these impacts become manifest? Several global analyses have established that recent rises in mean global air temperature are correlated with terrestrial and marine species range and phenology shifts (e.g., IPCC 2001; Parmesan and Yohe 2003). Freshwater biological impacts have received much less attention than terrestrial and marine systems (Brönmark and Hansson 2002; Poff et al. 2002). Small lentic systems are dominated by poikilothermic species such as fish and aquatic macroinvertebrates that are metabolically sensitive to shifts in climate normals. Impacts on several lentic taxa have already been observed even though the realized effects attributable to anthropogenic climate change are small relative to predicted impacts (reviewed in IPCC 2001; Poff et al. 2002). This chapter will focus on the trends in changing precipitation patterns, the role of water volume on temperature shifts in small lentic systems, and (to a lesser extent) how these shifts might alter populations and communities of macroinvertebrates (particularly odonates) and present challenges for future research into climate change impacts on ponds.

Background: Trends in the Seasonality of Precipitation Patterns

Ponds receive inflows from direct precipitation, runoff from their catchment area (including meltwater from snow and ice), connectivity with temporary or permanent streams, and groundwater sources. All four sources will be heavily influenced by pre-

cipitation patterns, although lag times between the latter three and particular precipitation events may be hours, days, weeks, or (in the case of spring meltwater and groundwater sources) months. The major outflow for ponds that are not connected to streams is evapotranspiration.

Specific impacts on precipitation inflows have proven to be more difficult to model than air temperature in global climate models (GCMs), which are the primary basis for predicting climate trends (IPCC 2001; Allen and Ingram 2002; Karl and Trenberth 2003). Nonetheless, some models have shown a close relationship between human forcing and precipitation changes, particularly since 1945 (Lambert et al. 2004). Predictive power for the models may be limited and seems likely to depend on the type of feedback provided by the trajectory of sea-surface temperatures, the influence of atmospheric aerosols and clouds on air temperatures, and the relationship between air temperature and atmospheric humidity at a range of altitudes (Trenberth et al. 2003; Yang et al. 2003; Dore 2005). Much debate also exists about the role of anthropogenic forcing on large storm systems such as hurricane and cyclone frequency/strength and the intensity and periodicity of global or large-scale weather engines such as the North Atlantic Oscillation, El Niño–Southern Oscillation (ENSO) (e.g., Hurrell and Van Loon 1997; Karl and Trenberth 2002; Zahn 2003; Dore 2005). The long-term data to ground GCMs for these major events and cycles is especially limited.

Given these uncertainties, global mean air temperatures are predicted by GCMs to rise between 1.8 and 4.5°C by 2100 . The equivalent range for precipitation by these same models is a global mean increase ranging between 0.6 and 18 % over the same period (Allen and Ingram 2003). Unfortunately, few GCMs examine shifts in intra-annual changes in precipitation patterns. Most of the analyses developed within the IPCC framework span coarse temporal scales that are hard to relate to ecological time-scales, particularly in the context of ephemeral habitats like short-hydroperiod ponds.

Regional predictions from GCMs are also limited. Until the modeling process becomes sufficiently clear to resolve regional processes, the best description of what may happen in particular places is probably observed trend data from the 19th and 20th centuries that has been tempered with short-term modeling outputs. In many cases, historical data is limited, especially in un- and underdeveloped regions of the world. Long-term precipitation data is particularly prone to data quality issues that may exaggerate precipitation patterns (Karl et al. 1995). Nonetheless, several historical and modeling studies have described a handful of both global and regional patterns that are relevant to this discussion. These include:

– Global mean precipitation has increased about 2 % for the 20th century (Karl and Trenberth 2003).

– Precipitation events have risen in their frequency and intensity, particularly with regard to rainfall (Easterling et al. 2000; Allen and Ingram 2002). However, as Dore (2005) summarizes, these changes have not been part of a wholesale shift in the distribution of precipitation intensity but at the cost of both moderate-intensity events and non-rain precipitation. Regionally, these increases have occurred even when total

precipitation has remained steady or fallen. This data is generally interpreted as a sign that the variability of precipitation is itself increasing.

– Regional patterns began developing in the 20th century. In the words of Dore (2005), the "wet areas become wetter, and the dry and arid areas become more so." The northern hemisphere has seen much greater increases (7 to 12 % between 30 and 85°N latitude) than the southern hemisphere (2 % between the equator and 55°S latitude), perhaps as a consequence of having more terrestrial surface area. South Asia appears to show higher amounts of precipitation but not the high central plateau region. East Asia has seen a small decrease in precipitation since the 1950s, and western Canada has declined slightly in contrast to eastern Canada. Australia is divided in a similar pattern. Europe shows a wetter north and a drying south. On these continents, the increases/decreases in precipitation have been as much as several 10s of percent since 1910 (Dore 2005; Milly et al. 2005). A few high-resolution regional precipitation analyses are now being generated (e.g., see Zhang et al. 2000; Schindler 2001).

– The tropics and subtropics seem to follow decadal or multi-decadal cycles that are difficult to correlate with what is seen at mid and high latitudes. The subtropics appear to be generally declining in precipitation. Africa and South America are especially difficult to characterize, particularly northern Africa, which has seen both multi-decade severe droughts and multi-year wet periods and shows few significant large-scale patterns (Mann et al. 1998; Dore 2005).

– Accurate records of snowfall and snow cover extent (SCE) are quite rare worldwide, but SCE has been declining in the northern hemisphere's spring generally while winter SCE seems to be increasing. The spring SCE decrease has been closely correlated with spring ground temperatures in North America. Similar spring/winter patterns appear to be developing in Europe and Asia. Tropical SCE has seen rapid declines. Improved satellite data will improve the resolution of this data over coming decades (Karl et al. 1995; Karl and Trenberth 2003; Dore 2005).

– Pond and lake ice is breaking up two weeks earlier in spring in North America (Magnusson et al. 2000). This trend is likely widespread, but data is generally lacking.

– Comparable drought and flood data are also rare for the 20th century. Several sources believe both categories are becoming more frequent, and if the trend is confirmed it would support the interpretation above that precipitation patterns are becoming more variable. However, clear and widespread data to determine if their intensities have changed over the past century is still scarce. Mixed data also exists about whether trends exist regarding droughts as either a complete absence of rainfall or a decrease in the intensity in rainfall (Allen and Ingram 2002; Klein Tank and Können 2003; Trenberth et al. 2003).

– Evaporation rates are perhaps even more difficult to untangle than precipitation patterns, but they are generally expected to increase with higher air temperatures as the atmosphere becomes a potential larger reservoir for moisture. While mean global air temperatures have increased over the past century, they have not done so evenly, and some areas show little or no rise in air temperatures. Variation also exists in which intra-annual periods increases are occurring. However, within decades the pulse of

climate change is expected to be strong enough to induce air temperature increases worldwide, pulling higher evaporation rates in their wake (Allen and Ingram 2002).

Hydroperiod Impacts from Precipitation and Evaporation Shifts

Large-scale observational and modeling data suggest that seasonal pond volume dynamics (that is, pond hydroperiod) are likely to be shifting in many areas (Milly et al. 2005). For instance, intra-annual variation may result in significant shifts in seasonal precipitation-evaporation deficits. For the Canadian prairie provinces, for example, modeling based on a variety of possible climate impacts to lentic systems in this region suggests that elevated evapotranspiration rates might outweigh higher precipitation amounts in summer and fall (increases up to 10%), effectively shortening hydroperiods (Akinremi and McGinn 1999; Zhang et al. 2000). These increases are on the order of magnitude seen at this latitude in North America (Dore 2005). It has also been suggested that spring precipitation increases could extend short hydroperiods into the summer and fall (Akinremi and McGinn 1999, Schindler 2001). Another study suggested that ponds that were ephemeral only in dry years might desiccate in all years with a doubling of CO_2 levels (Manabe et al. 2004). Effectively, these are shifts in the seasonality of precipitation and evaporation.

Increased precipitation variability exists at two levels: individual precipitation events (more events overall, more intense and heavy events, and fewer moderate events), and in multi-month and multi-year scales in the frequency of droughts and floods. Both types of variability have strong implications for hydroperiod patterns. We begin to enter a more speculative area here since little observational data has been collected on ephemeral ponds over the 20th century (e.g., see Williams 1997), but we can follow the implications from predictions of changes in precipitation variability.

High-intensity rainfall, for instance, tends to increase runoff patterns at the expense of soil moisture; large volumes of runoff are thus likely to enter streams, lakes, and ponds than the groundwater recharge system following such events (Karl et al. 1995; Karl and Trenberth 2003). Likewise, more frequent and more intense droughts will leach out pond volume through evapotranspiration (Akinremi and McGinn 1999).

In both cases, the duration of an ephemeral pond would thereby be altered. What is also interesting to consider is that changing the seasonality, the amount, and the variability of precipitation all have the potential to alter the relative volume of water during its hydroperiod rather than merely extending or attenuating its extremes.

Impacts from Changes in Seasonal Pond Volume Patterns

The amount of water that an ephemeral pond's basin is capable of holding has obvious implications for its hydroperiod, but pond volume also impacts a variety of other biologically relevant variables.

Water Quality: Solubility

One study suggested that relatively small rises in air temperature (1 to 2°C) or declines in precipitation (5 to 10 %) resulted in large impacts on water quality for small prairie pothole ponds (discussed in Covich et al. 1997). Water quality can be variously measured (e.g., see Brönmark and Hansson 2005). Many ponds, for instance, contain a variety of salts from dissolved minerals found in the surrounding in soil, bedrock, or catchment zone. Shifting pond volumes will alter these concentrations through either dilution or concentration; solubility is also a function of temperature. Indeed, human-derived contaminants — fertilizer, animal waste, agricultural herbicides — that wash into the pond will respond in the same way as natural-source substances. Shifts in the concentration of soluble ionic compounds are also likely to alter pond pH. Turbidity changes should result as well since higher rates of precipitation (especially high-intensity events) will trigger higher rates of terrestrial erosion.

Water Quantity: Thermal Mass and Pond Water Volume

Most heat energy enters ponds as solar radiation (Brönmark and Hansson 2005). Increases in precipitation will be associated with increases in water volume and thus pond thermal mass (Brönmark and Hansson 2002). With a relatively constant set of energetic inputs acting on a greater thermal mass, pond temperature should decrease. Calculating the amount of cooling that would occur in a given pond from a particular change in volume is difficult to calculate in the field since many factors modulate temperature. The storm that delivered the precipitation itself, for instance, is likely to alter ambient air and ground temperature, and the storm's cloud cover may reduce solar radiation inputs into the pond for some days. Nonetheless, the pond should be cooler with more water, assuming the same amount of solar inputs. A trend towards a seasonal or annual increase in water volume is thus also a trend towards a cooler pond.

The reverse is also true: the lack of precipitation — either through an absence of rain or runoff or a decrease in the amount or frequency of precipitation events — leaves an unfrozen pond to the mercy of evaporative outflows and a subsequent loss of volume. Evaporation itself is a cooling process (Trenberth et al. 2003), but evaporation is perhaps most importantly a means of reducing pond volume and pond thermal mass (Brönmark and Hansson 2005). Again, given a constant set of solar inputs with a trend of less precipitation, the resulting smaller thermal mass will increase pond temperatures. Indeed, this warming process may proceed in a nonlinear fashion as higher pond temperatures facilitate evaporation (e.g., see modeling discussion in Covich et al. 1997).

Interestingly, these shifts may lead to trends in water temperature that are in opposition to ambient air temperatures. Such patterns may be at work in southern Ontario, Canada (Matthews, unpublished data). Since the late 1960s, spring precipitation amounts have increased several 10s of percent in this area while late-summer precipitation has declined

a corresponding amount. Even though Environment Canada and IPCC (2001) data suggest that air temperatures here have grown 1 to 2°C warmer in spring and remain flat in summer, pond volume trends suggest that water temperatures have declined in spring with increased precipitation and risen in August and September with rainfall declines. As a result, long-hydroperiod ponds may actually be shifting to a short hydroperiod cycle, attenuating regional hydroperiod (Covich et al. 1997; Akrinremi and McGinn 1999). Analogous patterns of regional hydroperiod and volume shifts should become common worldwide. Coming decades may come to prove that pond water temperatures are following trajectories that bear little or no correlation with local air temperatures.

Pond Volume and Thermal Stratification

A far more difficult synergy to predict is the interplay of climate change and thermal turnover processes in ponds. The turnover process is important to a wide range of organisms as it redistributes nutrients and gases within the water column (for a more thorough discussion, see Brönmark and Hansson 2005). Between turnover periods, relatively stable microhabitats are established within two thermal zones (the epilimnion and hypolimnion) separated by a steep temperature gradient in the water column (i.e., a thermocline). By definition, ponds are primarily mixed by thermal processes rather than wind; few ponds could therefore be called meromictic (i.e., of such a depth that there are regions that do not mix). Most ponds are therefore either polymictic (experiencing turnover more than twice a year, a pattern more common in regions without significant pond freezing) or bimictic (with spring and fall turnovers in temperate zones). One study suggests that temperate bimictic ponds can be expected to see a seasonally earlier onset of spring turnover and a later onset of all turnover. In some regions (e.g., ponds currently near the transition between subtropical and temperate latitudes), bimictic ponds may even become polymictic, although Covich et al. (1997) suggest that thermal stratification may prove more stable in spring and summer under elevated temperatures.

Between turnover periods, mixing does occur in the water column but most of this mixing is confined within each thermal zone. In effect, two ponds are formed. During warm seasons, one pond (the epilimnion) is near the surface and contains most of the photosynthetic organisms, high oxygen levels (at least during daytime hours), and higher temperatures. The second pond (or hypolimnion) is cooler and darker; high decomposition rates from detrital rain into this zone fuel aerobic decomposition and deplete oxygen levels. During cool periods, temperature differences are often less extreme within a pond, particularly when surface ice is present. The epilimnion then holds lower temperatures than the hypolimnion, which effectively forms a reservoir or refuge of warmer, denser water.

Climate change is likely to impact these zones in different ways. Increased evapotranspiration rates and higher temperatures will alter the upper thermal zone (Covich et al. 1997). Dissolved oxygen levels (DO) tend to decline as water temperature increases, and these trends may be exacerbated in eutrophic ponds when photosynthesis

ceases at night; in extreme cases, the epilimnetic zone may become hypoxic, killing organisms unable to disperse to more oxygenated regions of the pond (Brönmark and Hansson 2005).

Characterizing the Biota of Ephemeral Ponds

Short hydroperiod ponds frequently lack fish populations, especially large and pis-civorous species (Williams 1997). Given that ephemeral pond are often small (<20 hectares), isolated, and show patchy distributions, fish-free ponds demonstrate both high species richness and high abundance of a wide range of taxa (Williams et al. 2003; Nicolet et al. 2004; Scheffer and van Geest 2006). Comparably sized long-hydroperiod ponds, especially those with fish, tend to lower species richness and abundances for overlapping groups; their community composition is often more typical of lakes in the same region (Williams 1997; Williams et al. 2004). Short-hydroperiod ponds are thus reservoirs of high alpha and beta biodiversity embedded in the terrestrial landscape (Scheffer and van Geest 2006). The short-lived nature and rapid successional cycling of ephemeral ponds suggests these communities may have much in common with other patchy environments with high disturbance rates such as forest treefall gaps or host plant clusters associated with specialist herbivores. Such systems have received much attention in recent decades via metapopulation and metacommunity theoretical approaches (e.g., see Hanski 1999; Holyoak et al. 2005) and by studies of life-history evolution, particularly explorations of the trade-offs associated with residential versus dispersal strategies (Harrison 1980; Roff 1986; Bilton et al. 2001).

Species adapted for patchy, ephemeral habitats generally face a choice between dispersing before a particular patch disappears or using some mechanism to remain in place and await the patch's reappearance (Bilton et al. 2001). Ephemeral ponds are no exception to this pattern. Many aquatic insects, for instance, have terrestrial stages in which dispersal occurs (e.g., most Ephemeroptera and Odonata), or they have be-haviors or life-stages capable of resisting desiccation (a strategy more typical of larvae unable to disperse). Bet-hedging strategies are also common, such as distributing eggs or seeds across a variety of ponds or having offspring with a range of developmental and emergence rates. Similar strategies are also seen in vertebrates, mollusks, and plants adapted to ephemeral ponds (reviewed in Bilton et al. 2001; Bronson and Hansson 2005). Only a few studies have examined odonates in this regard (see Johannsen & Suhling 2004; review in Corbet 1999).

These strategies also imply that the timing (phenology) of major life-history events is critical to understanding the link between hydroperiod, habitat selection, and adap-tational strategy (Jarvenin and Vepsalainen 1975; Hopper 1999). An adult dispersal strategy, for instance, is not effective from an evolutionary perspective if a pond dries up before an aquatic larva metamorphoses into a winged adult form. The birth and death of a water body mark clear and absolute boundaries for the organisms within. From this perspective, a short hydroperiod is useful in so far as it is regular and pre-

dictable. Indeed, Williams has identified the ecological predictability of hydroperiod as a critical and widespread adaptation for species that specialize in short-hydroperiod ponds (1997). A largely unexplored issue in this regard is the relationship between species richness and hydroperiod regularity at large spatial scales. A network of ponds, for instance, differ in their roles as population sources or sinks based solely on hydroperiod.

Biotic Impacts from Changes in Precipitation

Broadly speaking, population and species level effects from anthropogenic climate change have been lumped into shifts in seasonal behavior (phenology) and range shifts. Community-level effects includes changes in relative abundance, richness, and composition (e.g., Parmesan and Yohe 2003). These are coarse, general categories, yet they may be too specific for examining the impacts of changes in precipitation patterns on small ponds given the current small base of knowledge. Too few climate change studies have focused on the particular organisms that specialize in these habitats.

Not all aquatic environments have been so neglected. A handful of studies have explored the thermal constraints of lotic (flowing water) specialists, particularly those of low-order streams (e.g., Sweeney and Vannote 1978; Vannote and Sweeney 1980; Bêche et al. 2006). Some connections have been made between lotic species phenology and large-scale climate cycles (Briers et al. 2004). Experimental manipulations of streams have even been attempted in a number of instances (Hogg et al. 1995; Hogg and Williams 1996; Hogg et al. 2001; Smith and Collier 2005). Some researchers have also begun to examine warming impacts on long-hydroperiod lentic systems such as large lakes (e.g., McKee et al. 2002). Only a handful of studies have examined lentic species-level thermal impacts (Gillooly and Dodson 2000; Van Doorslaer and Stoks 2005a,b). Not all aquatic taxa have been ignored either. A substantial literature devoted to thermal tolerances of fish — particularly commercially important species — long predates the climate change impact literature (for a recent review, see Xenopoulos et al. 2005).

Given the isolation of ephemeral ponds from other water bodies and their relatively small amounts of water volumes, small lentic systems are especially sensitive to changes in precipitation patterns. Fish species are likely to be poor proxies for impacts on most of the invertebrate taxa present in short-hydroperiod ponds. I will focus here on areas I feel that biologists should be aware of as potential impacts or impacts already in progress that merit attention in the field and laboratory, with some highly speculative attention to odonates in particular.

Inter-annual Precipitation Variability

Climate variability stands in direct contrast to the maintenance of hydroperiod regularity (Williams 1997), particularly in the sense of variability in the frequency of droughts

and floods that will dramatically lengthen, delay, or abbreviate hydroperiod. Particularly destructive may be droughts that shift long-hydroperiod periods into short-hydroperiod cycles or extremely wet periods that alter the competitive environment of short-hydroperiod ponds in favor of long-hydroperiod species. Greater rainfall, for instance, may increase pond connectivity and lead to higher rates of pond dispersal by fish, substantially changing pond community composition and structure.

Adjustments to New Thermal Regimes

Regional trends in hydroperiod are likely to have widespread effects on the thermal regime of small ephemeral ponds beyond hydroperiod alone (Covich et al. 1997; Brönmark and Hansson 2002). For aquatic invertebrates, temperature appears to be a major source of community and species level niche differentiation in freshwater systems, whether in a linear context along a stream or river's watershed (Vannote and Sweeney 1980) or within a thermally stratified pond or lake (Sanderson et al. 2005). Poikilothermic invertebrate organisms dominate these systems in richness, abundance, and (in most cases) biomass (Brönmark and Hansson 2005). Given their sensitivity to temperature, such species often show thermal influences on growth rate and size, fecundity, metabolic rate, activity levels, phenology, behavioral strategy, and emergence rates (Vannote and Sweeney 1980; Brönmark and Hansson 2002), which together have second-order effects on range limits, abundance, and interactions with competitors, predators, and conspecifics (Williams 2003; Scheffer and van Geest 2006).

Climate change impacts in all of these areas have been widely documented in terrestrial, marine, and a few freshwater aquatic species. What has not been appreciated previously, however, is that water temperatures in small lentic systems may not correlate with neighboring terrestrial systems very closely. Indeed, given observed shifts in precipitation to date, the temperatures of small bodies of waters may be quite unlikely to track air temperature trends in coming decades. Increases in precipitation may be a global trend, but the result of more rain on small ponds may be decreases in water temperature. For aquatic insects, cooler temperatures tend to result in reductions in growth and development and lower metabolic and activity levels, all of which could alter the phenology of adult dispersal and reproduction. The resulting climate mismatch may be an example of an ecological trap being slowly set and tripped (Battin 2004).

Direct thermal modulation of the traits listed above may be best described as ecological responses to climate change. These are expected to occur over ecological timescales, ranging from one generation to (perhaps) several dozen or hundred generations. Evolutionary responses are also possible to climate change. Evolutionary responses are much harder to characterize or predict than ecological shifts, though a handful of convincing cases have been posited for insects (e.g., Rodríguez-Trelles and Rodríguez 1998; Thomas et al. 2001). In the case of ephemeral ponds, more frequent droughts might shorten pond hydroperiod regionally and provide a source of directional selection to complete development more quickly (Covich et al. 1997).

A microevolutionary response in this context implies that natural selection is sorting through differential and heritable phenotypes based on their relative fitness in a changed environment. While such responses are theoretically possible for all populations and species threatened by deleterious climate change impacts, in fact most populations are highly constrained by such factors as the rate of climate change, by the magnitude of change in environmental factors, by the lack of genetic variation associated with variation in phenotype, or the degree of phenotypic elasticity. A species may thus be unable to complete development in response to shorter hydroperiods because hydroperiod is advancing several weeks per decade and over a large spatial scale, or because the little or no genetically based phenotypic variation in development time exists within the species.

Potential Thermal Impacts on Odonates

Based on the limited work on the subject of thermal mass shifts to date, any speculation applying this perspective to odonates must serve as an example of scientific recklessness. Nonetheless, given the constraints of this volume, I will plunge ahead boldly. Several categories of change particular to odonates seem likely given the impacts described above:

  – So-called "spring" species in temperate and subtropical zones are likely to reflect mismatches between water and air temperatures. Two impacts appear possible. First, in regions with less spring and winter precipitation, the thermal mass of small freshwater systems will decrease, resulting in warmer water and faster rates of development that may outpace observed shifts in the phenology of nearby terrestrial systems. Second, regions with more spring and winter precipitation (especially more winter rain) will see the opposite effect: more thermal mass and slower development, resulting in phenological delays relative to nearby terrestrial systems. Evolutionary impacts resulting from either shift may be driven more by community-level processes, such as food availability for teneral adults.

  – "Summer" species in temperate and subtropical zones may see even more pronounced impacts as widespread warm-season trends of higher air temperatures and evapotranspiration rates, combined with decreased precipitation, reduce the amount and thermal quality of available habitat. Abbreviated hydroperiods will serve as a hard ecological boundary that could serve to limit the ranges of many species, with few evolutionary responses possible. Summer species may be forced to shift range boundaries when possible.

  – Trends towards warmer temperatures are likely to facilitate increases in the number of odonate generations per year in many species. Such shifts have already been observed in North American freshwater plankton (Daniel Schindler, personal communication) and British butterflies (Roy and Sparks 2000) but historical data are limited for comparisons between periods of relative climate stability (roughly 1850 to 1970) and periods of rapid warming (since 1970). Thus, we may have few opportunities to record the occurrence of these shifts in odonates.

– Far more likely to be recorded are changes in the historical range boundaries of long-observed species. These changes have been widely observed in many taxa (e.g., Parmesan and Yohe 2003). Recent reports suggest that "tropical" odonates have entered subtropical zones such as Florida, USA (Paulson 2001) since the late 1960s. There are also intriguing reports that the overwintering larvae of bivoltine species with both slow-developing overwintering larvae and fast-developing summer larvae may have separate ranges that are shifting independently (Catling 2003; Westover 1999). In high-latitude zones such as northern Canada, the combination of rapidly increasing temperatures and ample water supplies could result in dramatic poleward shifts as these regions effectively trade exotic temperate odonates for native Arctic taxa. Similar trends should be occurring in high-altitude areas as well.

Taking these trends in the aggregate, climate trends over the twenty-first century are likely to favor the species most capable of colonizing new habitats (i.e., high-dispersing species and species that specialize in short-hydroperiod systems), species that are tolerant of extreme temperature conditions, and temperate and subtropical species whose range is primarily limited by winter cold.

Research Needs for Ephemeral Pond Species and Communities

Profiles of how small single ponds have changed over long temporal periods are probably the most important gap in how understanding of how ponds may be changing in coming decades. Data linking water volume, water temperature at several depths, ambient air temperature, and the relationship between particular precipitation events and changes in water volume are essential parameters for creating a new generation of models. In essence, we need to develop a thermal life-history of small lakes and ponds.

Closely related is the issue of regional hydroperiod and precipitation trends. Can we make generalizations between a measurable shift in regional precipitation and hydroperiod regularity? Moreover, how does climate variability alter regional hydroperiod?

The biological impacts of changes in water temperature should also be a major research focus. Ephemeral ponds possess high variance in biotic and abiotic qualities seasonally and regionally, requiring substantial tolerance for variation on the part of their specialist denizens. Will future conditions remain within these tolerances, or will new levels of environmental variation extend beyond the limits of resilience and resistance? This area is ripe for species and community level experimental manipulations.

Some impacts on aquatic species can already be associated with a changing climate; indeed, other chapters with this volume provides ample documentation for effects on odonates alone. This research must extend over two levels. First, what large-scale patterns can we observe? What directions do we see in phenology or range shifts, and how are richness and abundance being modified at the community level? This level of detail is descriptive and observational. Second, we need proxy studies that reveal the specific mechanisms of change at population, species, and community levels. Can we

find proxy species for particular habitats and regions that allow us to untangle the complex elements that may be driving climate change impacts? This second approach will help determine why the changes we are observing at large scales are occurring, and it may ultimately assist in developing strategies to mitigate and untangle adverse impacts through policy shifts and more effective resource management.

References

Abell R, Olson DM, Dinerstein E, Hurley P, Diggs JT, Eichbaum W, Walters S, Wettengel W, Allnutt T, Loucks CJ, Hedao P (2000) Freshwater ecoregions of North America: a conservation assesment. Island Press, Washington, D.C., USA.

Akineremi OO, McGinn SM (1999) Precipitation trends on the Canadian prairies. Journal of Climate 12: 2996–3003.

Allen MR, Ingram WJ (2002) Constraints on future changes in climate and the hydrologic cycle. Nature 419: 224–232.

Battin J (2004) When good animals love bad habitats: ecological traps and the conservation of animal populations. Conservation Biology 18(6): 1482–1491.

Bêche LA, McElravy EP, Resh VH (2006) Long-term seasonal variation in the biological traits of benthic-macroinvertebates in two Mediterranean-climate streams in California, USA. Freshwater Biology 51: 56–75.

Bilton DT, Freeland JR, Okamura B (2001) Dispersal in freshwater invertebrates. Annual Review of Ecology and Systematics 32: 159–181.

Briers RA, Gee HR, Geoghegan R (2004) Effects of the North Atlantic Oscillation on growth and phenology of stream insects. Ecography 27: 811–817.

Brönmark C, Hansson L (2002) Environmental issues in lakes and ponds: current state and perspectives. Environmental Conservation 29(3): 290–306.

Brönmark C, Hansson L (2005) The Biology of Lakes and Ponds. Second edition. Oxford University Press, Oxford, UK.

Corbet P (1999) Dragonflies: behavior and ecology of Odonata. Ithaca, NY, USA: Cornell University Press.

Covich AP, Fritz SC, Lamb PJ, Marzolf RD, Matthews WJ, Poiani KA, Prepas EE, Richman MB, Winter TC (1997) Potential effects of climate change on aquatic ecosystems of the great plains of North America. Hydrological Processes 11: 993–1021.

Doorslaer WV, Stoks R (2005) Growth rate plasticity to temperature in two damselfly species differing in latitude: contributions of behavior and physiology. Oikos 111: 599–605.

Doorslaer WV, Stoks R (2005) Thermal reaction norms in two *Coenagrion* damselfly species: contrasting embryonic and larval life-history traits. Freshwater Biology 50: 1982–1990.

Dore, M.H.I. 2005: Climate change and changes in global precipitation patterns: what do we know? Environment International 31: 1167–1181.

Easterling DR, Evans JL, Groisman PYa, Karl TR, Kunkel KE, Ambenje P (2000) Observed variability and trends in extreme climate events: A brief review. Bulletin of the American Meteorological Society 81: 417–425.

Easterling DR, Chagnon S, Karl TR, Meehl J, Parmesan C (2000b) Climate extremes: observations, modeling, and impacts. Science 289: 2068–2074.

Gillooly JF, Dodson SI (2000) The relationship of egg size and incubation temperature to embryonic development time in univoltine and multivoltine aquatic insects. Freshwater Biology 44: 595–604.

Hanski I (1999) Metapopulation ecology. New York: Oxford University Press.

Harrison RG (1980) Dispersal polymorphisms in insects. Annual Review of Ecology and Systematics 11: 95–118.

Hogg ID, Williams DD (1996) Response of stream invertebrates to a global-warming thermal regime: an ecosystem-level manipulation. Ecology 77(2): 395–407.

Hogg ID, Eadie JM, Williams DD, Turner D (2001) Evaluating fluctuating asymmetry in a stream-dwelling insect as an indicator of low-level thermal stress: a large-scale field experiment. Journal of Applied Ecology 38: 1326-1339.

Hogg ID, Williams DD, Eadie JM, Butt SA (1995) The consequences of global warming for stream invertebrates: a field simulation. J. Therm. Biol. 20(1): 199–206.

Holyoak M, Leibold M, Holt RD (2005) Metacommunities: spatial dynamics and ecological communities. University of Chicago Press, Chicago, USA.

Hopper KR (1999) Risk-spreading and bet-hedging in insect population biology. Annual Review of Entomology 44: 535–560.

Hurrell JW, Van Loon H (1997) Decadal variations in climate associated with the North Atlantic Oscillation. Climatic Change 36: 301–326.

Intergovernmental Panel on Climate Change Third Assessment Report (2001a) Climate Change 2001: The Science of Climate Change. Houghton JT, Ding Y, Griggs DJ, Noguer M, van der Linden PJ, Dai X, Maskell K, Johnson CA (Eds) Cambridge University Press, Cambridge, UK.

Intergovernmental Panel on Climate Change Third Assessment Report (2001b) Climate Change 2001: Impacts, Adaptation, and Vulnerability. McCarthy JJ, Canziani OF, Leary NA, Dokken DJ, White KS (Eds) Cambridge University Press, Cambridge, UK.

Jarvinen O, Vepsalainen K (1975) Wing dimorphism as an adaptive strategy in water-striders (*Gerris*). Hereditas 84(1): 61–68.

Johansson F, Suhling F (2004) Behavior and growth of dragonfly larvae along a permanent to temporary water habitat gradient. Ecological Entomology 29: 196–202.

Karl TR, Trenberth KE (2003) Modern global climate change. Science 302: 1719–1723.

Karl TR, Knight RW, Easterling DR, Quayle RG (1996) Indices of climate change for the United States. Bull. Am. Meteor. Soc. 77(2): 279–292.

Klein Tank AMG, Können GP (2003) Trends in indices of daily temperature and precipitation extremes in Europe, 1946–99. Journal of Climate 16: 3665–95.

Knight (1999) Trends in precipitation and snow cover in the United States. Potential Consequences of Climate Variability and Change to Water Resources of the United States, D. B. Adams, Ed., Amer. Water Resourc. Assoc., 89–92.

Lambert FH, Stott PA, Allen MR, Palmer MA (2004) Detection and attribution of changes in 20th century land precipitation. Geophysical Research Letters 31: L10203.

Lomborg B (2001) The skeptical environmentalist. Cambridge University Press, New York.

Magnuson JJ, Robertson DM, Benson BJ, Wynne RH, Livingstone DM, Arai T, Assel RA, Barry RG, Card V, Kuusisto E, Granin NG, Prowse TD, Stewart KM, Vuglinski VS (2000) Historical trends in lake and river ice cover in the northern hemisphere. Science 289: 1743–46.

Manabe A, Wetherwalk RT, Milly PCD, Delworth TL, Stouffer RJ (2004) Century-scale change in water availability: CO_2-quadrupling experiment. Climatic Change 64: 59–76.

Mann ME, Bradley RS, Hughes MK (1998) Global-scale temperature patterns and climate forcing over the past six centuries. Nature 392: 779–787.

McKee D, Atkinson D, Collings S, Eaton J, Harvey I, Heyes T, Hatton K, Wilson D, Moss B (2002) Macro-zooplankter responses to simulated climate warming in experimental freshwater microcosms. Freshwater Biology 47: 1557–1570.

Milly PCD, Dunne KA, Vecchia AV (2005) Global patterns of trends in streamflow and water availability in a changing climate. Nature 438: 347–350.

Nicolet P, Biggs J, Fox G, Hodson MJ, Reynolds C, Whitfield M, Williams P (2004) The wetland plant and macroinvertebrate assemblages of temporary ponds in England and Wales. –Biological Conservation 120: 261–278.

Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts in natural systems. -Nature 421: 37–42.

Parmesan C, Root TL, Willig MR (2000) Impacts of extreme weather and climate on terrestrial biota. Bull. Am. Meteor. Soc. 81: 443–450.

Paulson DR (2001) Recent Odonata records from southern Florida: effects of global warming? International Journal of Odonatology 4(1): 57–69.

Poff NL, Brinson MM, Day JW (2002) Aquatic Ecosystems and Global Climate Change: Potential impacts on Inland Freshwater and Coastal Wetland Ecosystems in the United States. Pew Center on Global Climate Change, Arlington, VA, USA.

Rodríguez-Trelles F, Rodríguez MA (1998) Rapid micro-evolution and loss of chromosomal diversity in Drosophila in response to climate warming. Evolutionary Ecology 12(7): 829–838.

Roff DA (1986) The evolution of wing dimorphism in insects. Evolution 40(5): 1009–1020.

Root TL, Price JT, Hall KR, Schneider SH, Rosenzweig C, Pounds JA (2003) Fingerprints of global warming on wild animals and plants. Nature 421: 57–60.

Roy DB, Sparks TH (2000) Phenology of British butterflies and climate change. –Global Change Biology 6(4): 407–416.

Sanderson RA, Eyre MD, Rushton SP (2005) Distribution of selected macroinvertebrates in a mosaic of temporary and permanent freshwater ponds as explained by autologistic models. Ecography 28: 355–362.

Scheffer M, van Geest GJ (2006) Small habitat size and isolation can promote species richness: second-order effects on biodiversity in shallow lakes and ponds. Oikos 112: 227–231.

Schindler DW (2001) The cumulative effects of climate warming and other human stresses on Canadian freshwaters in the new millennium. Can. J. Aquat. Sci. 58: 15–29.

Smith BJ, Collier KJ (2005) Tolerances to diurnally varying temperature for three species of aquatic insects from New Zealand. Environmental Entomology 34(4): 748–754.

Sweeney BW, Vannote RL (1978) Size variation and the distribution of hemimetabolous aquatic insects: two thermal equilirium hypotheses. Science 200(4340): 444–446.

Thomas CD, Bodsworth EJ, Wilson WJ, Simmons AD, Davies ZG, Musche M, Conradt L (2001) Ecological and evolutionary processes at expanding range margins. Nature 411: 577–581.

Thomas CD, Cameron A, Green RE, Bakkenes M, Beaumont LJ, Collingham YC, Erasmus BFN, de Siqueira MF, Grainger A, Hannah L, Hughes L, Huntley B, van Jaarsveld AS, Midgley GF, Miles L, Ortega-Huerta MA, Peterson AT, Phillips OL, Williams SE (2004) Extinction risk from climate change. Nature 427: 145–148.

Trenberth KE, Dai AD, Parsons DB (2003) The changing character of precipitation. Bulletin of the American Meteorological Society (September): 1205–1217.

Vannote RL, Sweeney BW (1980) Geographic analysis of thermal equilibria: a conceptual model for evaluating the effect of natural and modified thermal regimes on aquatic insect communities. –The American Naturalist 115(5): 667–695.

Westover D (1999) Observations on the possibility of overwintering larvae of *Anax junius* in Wisconsin. Argia 11(1): 15–16.

Williams DD (1997) Temporary ponds and their invertebrate communities. –Aquatic Conservation: Marine and Freshwater Ecosystems 7: 105–117.

Williams P, Whitfield M, Biggs J, Bray S, Fox G, Nicolet P, Sear D (2003) Comparative biodiversity of rivers, streams, ditches, and ponds in an agricultural landscape in southern England. Biological Conservation 115: 329–341.

Xenopoulos MA, Lodge DM, Alcamo J, Märker M, Schulze K, Van Vuuren DP (2005) Scenarios of freshwater fish extinctions from climate change and water withdrawal. Global Change Biology 11: 1557–1564.

Zahn R (2003) Monsoon linkages. Nature 421: 324–25.

Zera AJ, Harshman LG (2001) The physiology of life-history trade-offs in animals. Annu. Rev. Ecol. Syst. 32: 95–126.

Zhang X, Vincent LA, Hogg WD, Niitsoo A (2000) Temperature and precipitation trends in Canada during the 20th century. Atmosphere-Ocean 38(3): 395–429.