



OVERVIEW

Rising water temperature in rivers: Ecological impacts and future resilience

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Abstract

Rising water temperatures in rivers due to climate change are already having observable impacts on river ecosystems. Warming water has both direct and indirect impacts on aquatic life, and further aggravates pervasive issues such as eutrophication, pollution, and the spread of disease. Animals can survive higher temperatures through physiological and/or genetic acclimation, behavioral and phenological change, and range shifts to more suitable locations. As such, those animals that are adapted to cool-water regions typically found in high altitudes and latitudes where there are fewer dispersal opportunities are most at risk of future extinction. However, sub-lethal impacts on animal physiology and phenology, body-size, and trophic interactions could have significant population-level effects elsewhere. Rivers are vulnerable to warming because historic management has typically left them exposed to solar radiation through

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the removal of riparian shade, and hydrologically disconnected longitudinally, laterally, and vertically. The resilience of riverine ecosystems is also limited by anthropogenic simplification of habitats, with implications for the dispersal and resource use of resident organisms. Due to the complex indirect impacts of warming on ecosystems, and the species-specific physiological and behavioral response of organisms to warming, predicting how river ecosystems will change in the future is challenging. Restoring rivers to provide connectivity and heterogeneity of conditions would provide resilience to a range of expected co-occurring pressures, including warming, and should be considered a priority as part of global strategies for climate adaptation and mitigation.

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Science of Water > Water and Environmental Change

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climate change, thermal ecology, thermal regime, water temperature

1 | INTRODUCTION

Globally, rivers are undergoing warming due to changes in climate, land-use, and water usage, with severe implications for aquatic life. River water temperature (T_w) is expected to rise with climate change (van Vliet et al., 2013; Wanders et al., 2019)—a trend that is already being observed across large swathes of Europe, North America, and Asia (Baranov et al., 2020; Chen et al., 2016; Hannah & Garner, 2015; Isaak et al., 2012). This is concerning because rivers are disproportionately biodiverse compared to other habitats (Reid et al., 2019) and are also some of the most threatened (Dudgeon, 2019). Human alterations to river channels, land-use, and patterns of water resource utilization have left rivers vulnerable to thermal change, and pervasive pressures, including eutrophication, are amplified by rising water temperatures (Reid et al., 2019; Woodward et al., 2010). Freshwater environments and the organisms that inhabit them are therefore vulnerable to warming, with important but complex potential outcomes for ecological communities and their functioning (IPCC, 2022), which forms the focus of this review. While much research has addressed river temperature and its impacts on particular taxa, there has been less attention to ecosystem-level river resilience under current and future warming. In this review, we evaluate knowledge of the direct and indirect impacts of elevated T_w on riverine fauna, particularly ectothermic (i.e., cold-blooded) animals. We then discuss factors affecting the resilience of ecological communities and river environments to future thermal change. We concentrate mainly on chronic rises in T_w associated with ongoing climate change, but acknowledge that altered frequencies and extremes of T_w can also be detrimental to ectotherms (e.g., Vasseur et al., 2014).

River T_w is largely controlled by incoming solar radiation (Caissie, 2006; Evans et al., 1998) and, as such, varies diurnally, seasonally, and with latitude, but tends to correlate to air temperature (Figure 1). T_w is also dependent on water volume and local controls on solar exposure, related to the geometry and condition of river channels, topographic shading, and riparian (bankside) vegetation (see Garner et al., 2015). For example, removal of riparian vegetation through felling, herbivore grazing, or wildfires can reduce the shading of river channels and thereby contribute to warming (Dunham et al., 2007; Fuller et al., 2022; Moore et al., 2005). Catchment hydrology also influences thermal regimes. For example, warmer runoff from urban impervious surfaces can raise temperatures, and altered snowmelt timing and extent can significantly alter seasonal T_w (Tonkin et al., 2019). Thermally modified effluent from power stations, industrial units, and wastewater treatment plants can also impact thermal regimes (Madden et al., 2013). As such, the thermal regimes of rivers vary greatly within and between systems, over short distances (<kms; e.g., Johnson et al., 2014; Figure 1), and with diurnal, seasonal, and inter-annual cycles that reflect prevailing climate (e.g., seasonality will be less in tropical regions than temperate regions) and local conditions (e.g., buffering by groundwater and other water inputs; Figure 1). Warming due to climate change is also projected to differ globally (see van Vliet et al., 2013), with T_w

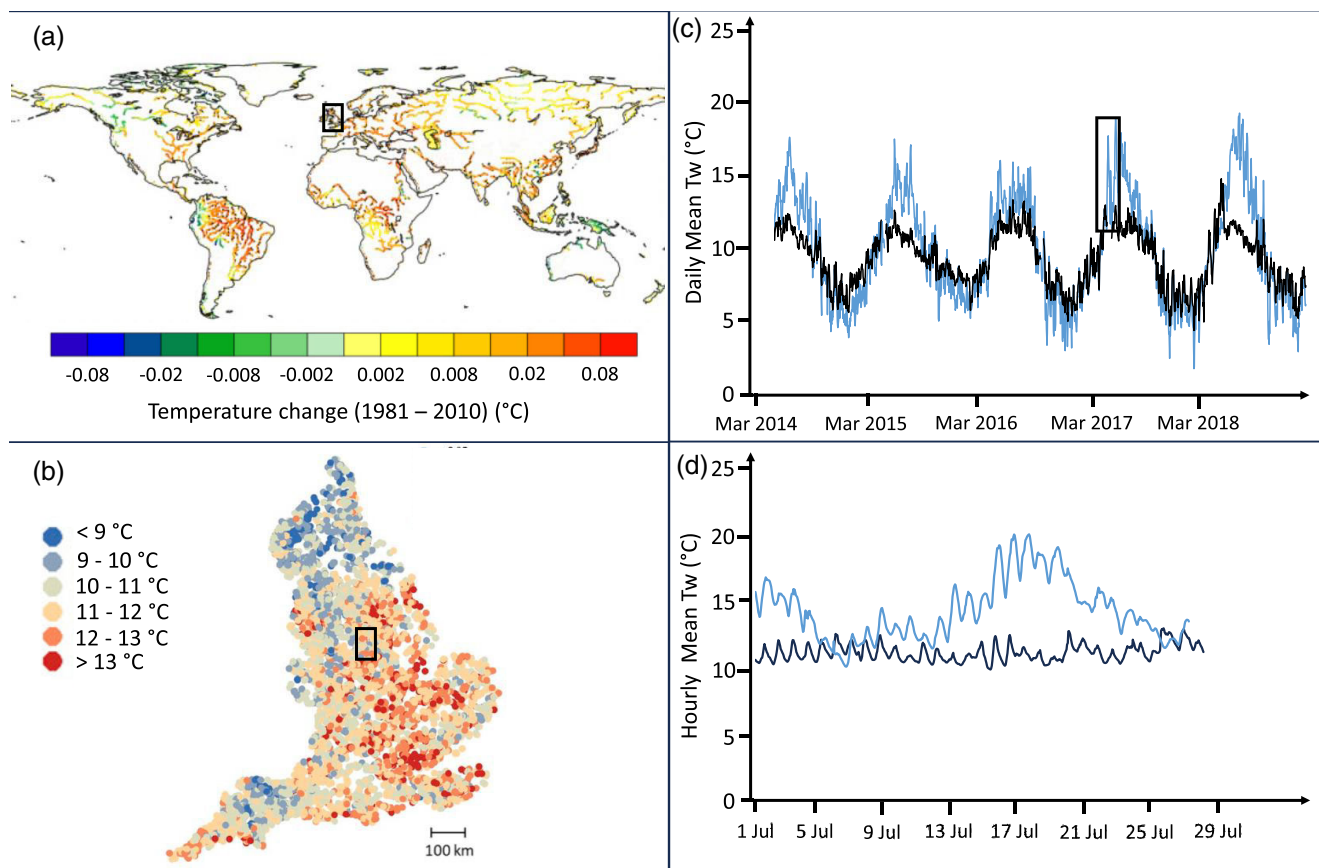


FIGURE 1 (a) Thirty-year trends (1981–2010) of global river temperature change. *Source:* Liu et al. (2020). (b) Annual average river temperature in England. *Source:* Wilby and Johnson (2021). (c) Interannual temperature at sites on the River Dove, England, separated by 1.2 km but one being surface water driven (blue line) and the other groundwater driven (black line); (d) diurnal cycles in temperature at the same two sites on the Dove.

increasing by 0.03°C per year in the UK (Orr et al., 2014), $0.001\text{--}0.08^{\circ}\text{C}$ per year in the USA (Kaushal et al., 2010), and $0.03\text{--}0.05^{\circ}\text{C}$ per year in China (Chen et al., 2016). While predicted and measured Tw changes associated with climate change are typically small relative to the natural diurnal, seasonal, and inter-annual thermal variability recorded in many temperate rivers, the chronic nature of these changes can have significant ecological impacts. A particular concern relates to tropical regions, where fish species may already be living close to their upper thermal tolerance limits (Nati et al., 2021). Many climate-related thermal and ecological changes are now evident in river systems, and these are addressed in this review.

Rivers have been altered globally over centuries, with major implications for warming, including through disconnection of channels laterally to terrestrial environments, vertically to groundwater, and longitudinally to up- and downstream river reaches through hydrological alterations. For example, disconnection of rivers longitudinally due to dams and weirs is widespread (Grill et al., 2019), resulting in reduced flow velocities (and mixing) upstream of structures and increasing exposure time of surface water to solar radiation which both lead to warming (Olden & Naiman, 2009). Where reservoir depth is sufficient to cause thermal stratification, dams can also release cooler water downstream, depending on where it is drawn from; these dynamics are, however, changing as reservoir levels decline in many regions due to climate change and water usage (Bruckerhoff et al., 2022). River channels have also been enlarged over centuries to convey higher flows and increase navigability. Anthropogenically widened channels are particularly abundant in urban areas (e.g., Walsh et al., 2005; Walter & Merritts, 2008), resulting in greater ratios of surface area to volume and shallower channel slopes, increasing the area and time of exposure to solar radiation (Caissie, 2006; White et al., 2017). Similarly, low flows associated with abstraction, regulation, droughts, and/or climate change can reduce thermal buffering, leading to more rapid warming of freshwaters (Booker & Whitehead, 2022; White et al., 2023).

Hence, globally many rivers are vulnerable to thermal change due to historic and contemporary alterations of their physical form and flow regimes.

Rivers will continue to respond to climate and land use changes plus other anthropogenic alterations. As such, future river ecosystems are likely to differ from those today, many of which are already distinct from undisturbed, pristine systems (Brown et al., 2018; Johnson et al., 2019). However, the magnitude of change and types of human impact will differ between locations. In general, freshwater ecosystems are adapted to highly variable abiotic (including thermal) conditions due to the natural heterogeneity that rivers provide (e.g., Biggs et al., 2005). Nonetheless, variability outside of the range of “natural” conditions, such as at unusual times of year; changes happening rapidly or over large stretches of river; or where natural resilience has been undermined through other anthropogenic pressures, may lead to significant detrimental effects on river ecosystems.

2 | DIRECT THERMAL IMPACTS ON RIVERINE ANIMALS

2.1 | Thermal maxima and thermal performance

Fish and aquatic invertebrates are ectotherms so changes in T_w can have a direct impact on their physiology (e.g., Bonacina et al., 2022). Organisms have critical thermal minimum and maximum temperatures, beyond which activities essential for survival cannot be sustained (Huey & Kingsolver, 1989). The response of an organism between these limits is typically represented by a thermal performance curve (review in Sinclair et al., 2016), where activity increases with temperature from the minimum value to an optimum, and then, characteristically, declines rapidly toward the maximum survivable temperature (Figure 2). Thermal maxima have been determined for some freshwater animals and relate to temperature controls on oxygen consumption (Box 1). The GlobTherm database includes 92 records of freshwater fish with thermal maxima spanning 20–43°C, with an average of 33.5°C (Bennett et al., 2018). Dallas and Rivers-Moore (2012) identify thermal maxima for multiple families of aquatic insect larvae in South Africa, and review past measurements from other studies; they cite maxima ranging between 25°C and 45°C. Thermal maxima and minima for when specific activities (e.g., feeding, growth, burrowing, and reproduction) cease or commence have also been reported. For example, a review of Atlantic salmon (*Salmo salar*) suggests an upper thermal limit of 22.5°C for growth (Elliott & Elliot, 2010). However, these fish can still feed at higher temperatures (Forseth et al., 2009) and the interactions between temperature, feeding behavior, and food availability are thus complex (Huey & Kingsolver, 2019). Such discussions also assume that body temperatures match water temperature, which is contentious because body temperatures of many terrestrial cold-blooded animals can exceed air temperatures due to incoming solar radiation (e.g., basking behavior of reptiles; Seebacher & Franklin, 2005). Coastal fish are known to bask (Nordahl et al., 2018), but little is known about the basking of freshwater fish and invertebrates.

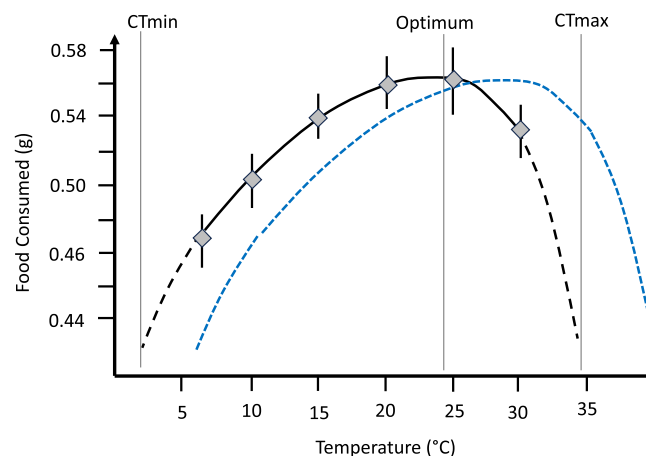


FIGURE 2 An examples of a thermal performance curve for feeding activity in Signal Crayfish (*Pacifastacus leniusculus*). Means and standard errors are from 12 replications. Critical minimum (CTmin) and maximum (CTmax) temperatures are shown, as well as the optimum temperature for feeding. The dashed blue line indicates how a thermal performance curve may change with acclimation to higher temperatures. In this case, the optimum, CTmax, and CTmin have shifted to higher temperatures. Modified from Rodrigues Valido et al. (2020).

BOX 1 Oxygen- and capacity-limited thermal tolerance

Although elevated T_w can have a range of indirect effects (see Section 3), the mechanism that directly links rising T_w to altered animal behavior and survival is not fully understood but is encapsulated by the oxygen- and capacity-limited thermal tolerance (OCLTT) concept. The OCLTT relates to how T_w can constrain the ability of animals to meet their oxygen demand (review in Pörtner et al., 2017). Oxygen is poorly soluble in water, but this solubility is inversely related to T_w and pressure. For example, freshwater at 0°C and 100% oxygen saturation will have an oxygen concentration of 14.6 mg L⁻¹ whereas at 20°C the concentration will approximate 9 mg L⁻¹, and at 30°C it will approximate 7 mg L⁻¹. The reduction in oxygen delivery relative to oxygen demand as T_w rises is generally believed to determine the upper thermal tolerance of aquatic organisms. For example, stonefly larvae increase their respiration rate when exposed to relatively warm T_w (Maison et al., 2022; Verbeck & Bilton, 2011). This also means that organisms can acclimate to different T_w through adjustment of respiration rates and other physiological processes, and through reductions in body size, as discussed in the main text (Audzijonyte et al., 2018; Verberk et al., 2021).

Despite thermal maxima being reported for some species, there is still limited information about thermal preferences and behaviors for the vast majority of freshwater species. Most research has been performed under controlled laboratory conditions and excludes factors such as food availability (discussed below), that can modify thermal performance (Railsback, 2022). Caution should therefore, be exercised when comparing temperature metrics because they can vary depending on the performance trait (e.g., feeding vs burrowing; Rodrigues Valido et al., 2020; locomotion vs. feeding; Iacarella et al. 2015) and by geographic location, acclimation, and life history (see below). Published research is also dominated by a few species (e.g., Salmonid fish) and regions (e.g., temperate zone rivers). Research also tends to focus on upper thermal thresholds, with less work on other important metrics of thermal performance, including changes in mobility, behavior, trophic interactions, and phenology (for which see below). Altered temperatures below thermal maxima can impact thermal performance too. For example, many species prefer temperatures significantly below thermal maxima, although the two values have been found to correlate across fish species (Payne et al., 2015; Richardson et al., 1994). Warming autumn and winter temperatures, well below thermal maxima, have also been shown to influence the survival and performance of aquatic animals, including diapause (Nielsen et al., 2022), phenology (e.g., Overall et al., 2014), and reproduction (Firkus et al., 2017).

Critical thresholds above 30°C, which represent the majority of records in meta-analyses of freshwater fish (Bennett et al., 2018) and insects (Dallas & Rivers-Moore, 2012), are only expected to be exceeded for short periods (<days). This is because T_w does not increase linearly with air temperature as, at high temperatures, cooling from outgoing evaporative (and to a lesser extent sensible and longwave) heat fluxes limits further rises (Mohseni et al., 1999). Hence, T_w much above 30°C is rarely observed even in tropical regions (Liu et al., 2020; van Vliet et al., 2011) and represents extreme conditions typically associated with anthropogenic alterations (such as by dams; Figure 3). However, it should be noted that a combination of anthropogenic alterations to river systems (e.g., reservoirs), coupled with climate change, and climate variability (La Nina, El Nino) can create >30°C conditions for more extended periods (weeks). For instance, the maximum daily T_w of the Amazon River exceeded 30+ for several days in August 2023, leading to mass fish and mammal deaths (Reuters, 2023). Given the rarity of such events, at least over monitored periods, critical thermal maxima are likely to be of more significance to organisms adapted to cooler environments with relatively low thermal maxima. This includes organisms that live near the source of rivers, at high altitudes, or higher latitudes, because their thermal limits could be substantially exceeded (>1°C) by future warming scenarios for extended periods (weeks, months). Also, organisms that live in regions where temperatures are more stable (e.g., tropical rivers range between 22 and 34°C; Wanders et al., 2019), may have evolved to live close to their thermal maxima and be susceptible to T_w change outside of experienced conditions (<1°C) for extended periods (>weeks).

2.2 | Importance of thermal acclimation and life stage to thermal performance

Critical thermal maxima (CT_{max}) can be highly variable within species and even between individuals, based on thermal acclimation and animal response to other pressures. For example, the CT_{max} reported by Dallas and Rivers-Moore

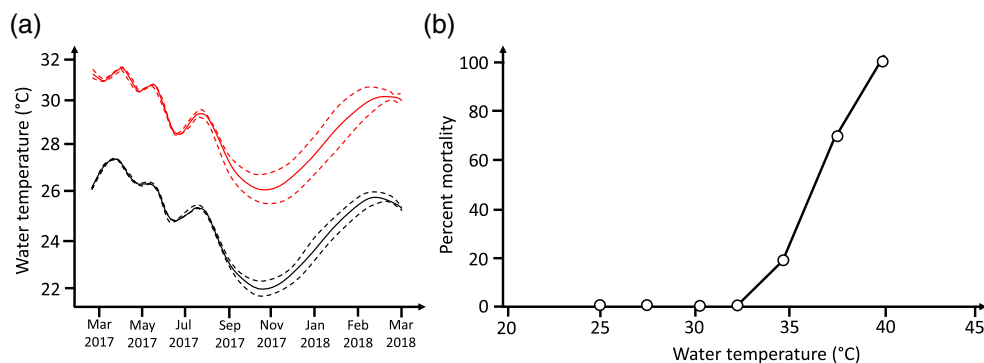


FIGURE 3 (a) Tw in the Semenyih River, Malaysia, 0.5 km upstream (green) and 0.5 km downstream (red) of a dam, showing warming. (b) Mortality of *Platybaetis* (Ephemeroptera) from the Semenyih River, Selangor, Malaysia, exposed to different Tw. Lines on (a) are GAM smoothers fitted to 30-min interval temperature values obtained from loggers. Dotted lines are 95% CI. For (b) 10 different individuals were used for each temperature exposure of 5 min. Experiments were conducted in March 2018 by the authors (CG) in the laboratory on the same day as the collection of animals from the field. They were returned to the lab with stream water maintained at the same temperature as the river, and allowed to acclimate to laboratory conditions for 1 h before treatments commenced.

(2012) depended on acclimation temperature, with median thermal maxima always being lower when insects were acclimated for at least 48 h in 10°C water in comparison to 17°C. Similarly, Moulton et al. (2011) observed a significant relationship between CTmax and acclimation temperature for caddisfly (*Chiamarra obscura*; *Hydropsyche simulans*). Huff et al. (2005) reported different upper thermal limits for rainbow trout (*Oncorhynchus mykiss*) dependent on the ecoregion they reside in. Semsar-Kazerouni and Verbeck (2018) found that the metabolism of amphipod shrimp (*Gammarus fossarum*) rose with temperature, but the increase was much greater in cold-acclimated individuals compared with warm-acclimated ones. Therefore, the thermal limits of individuals within the same species can vary depending on their environmental and thermal context (e.g., Verhille et al., 2023). There are, however, exceptions to this observation; for example, in experiments with the invasive freshwater snail *Potamopyrgus antipodarum*, taken from sites across a thermal gradient, individuals grew quicker and reproduced earlier in warmer water than colder water, but changes were consistent between snails from all sites, that is, acclimation did not alter the response to changed temperature (Dybdahl & Kane, 2005).

The ability to thermally acclimate is partly dependent on experienced temperatures, at least for some species, including absolute temperature, timing and duration of exposure, and rates of change (Nyamukondiwa et al., 2018; Smith & Lancaster, 2020). As such, organisms that live in rivers with stable thermal regimes over long periods (>100 years), such as those residing at high altitudes, high latitudes, tropical zones, or areas with significant groundwater inputs, may be less able to acclimate to future changes due to the consistency in their multi-generational experienced temperatures (González-Tokman et al., 2020; Lagerspetz & Vainio, 2006). Relatively little research has investigated the thermal regimes of tropical rivers or the thermal performance of resident animals. However, data downstream of a dam on the Semenyih River, Malaysia, shows Tw is already close to the lethal limits for some aquatic insects (Figure 3).

Thermal maxima can depend on life stage, body size, and ecological interactions. For instance, Garten and Gentry (1976) found that larval dragonflies (*Libellula auripennis* and *Macromia illinoensis*) with longer bodies displayed higher thermal maxima than smaller individuals of the same species. Stage-specific impacts can influence later stages in animals with complex life cycles. For example, Gray (2013) noted that thermal acclimation in the aquatic larval stage of mosquitoes (*Culex pipiens*) influenced the thermal tolerance of the aerial adult stage. Juvenile Atlantic salmon (*Salmo salar*) are also known to be more thermally tolerant than adults due to their different surface area:body mass ratio (Breau et al., 2011). Consequently, predicting the response of ecological communities to warming is challenging and will be nonlinear if species are able to acclimate.

2.3 | Evolutionary adaptation of thermal maxima

Tolerance to warming in a population can be achieved through local adaptation, where genetic polymorphism (i.e., multiple variants in a gene within a population) leads to phenotypes with different environment tolerances, which

are then selected by environmental drivers (Somero, 2010). For instance, Garvin et al. (2015) compared the gene expression associated with respiration in individual rainbow trout (*Oncorhynchus mykiss gairdneri*) and their progeny, from desert and montane streams. Heat stress in an environment common to both sets of fish elicited changes in gene expression patterns in the desert fish but not the montane group. This was interpreted as evidence of a genetic basis for heat tolerance (Garvin et al., 2015). Similar intraspecific adaptation to particular riverine thermal regimes has also been shown in Atlantic salmon (e.g., Dionne et al., 2008).

Proteins are highly temperature-sensitive components of organisms and Somero (2010) notes that where species are adapted to different temperatures, the structure and function of proteins is different. The ability of a species to genetically adapt (i.e., the pace of protein changes relative to the rate of climate change) could be an important indicator of species' resilience to future warming (Somero, 2010). Populations that have evolved in areas where T_w is relatively constant (such as near poles and the equator), may have lost the genetic variability that allows plasticity in the regulation of temperature (termed DNA decay), making them more vulnerable to future change (Somero, 2010). Morgan et al. (2020) suggested that while evolutionary adaptation to temperature occurs, there is a ceiling to upper thermal limits. They raised zebrafish (*Danio rerio*) over six generations by selecting for higher thermal maxima in one population and lower thermal maxima in another. The fish selected for increased thermal limits evolved towards a higher thermal limit by $0.22 \pm 0.05^\circ\text{C}$ and the rate of change decreased with each successive generation. In contrast, fish selected for lower thermal limits decreased in thermal tolerance by $0.74 \pm 0.05^\circ\text{C}$ with more consistent differences between generations (Morgan et al., 2020). Variations in genetic adaptation may also relate to connectivity of populations. Pilakouta et al. (2020) compared stickleback (*Gasterosteus aculeatus*) from geothermally heated and ambient T_w areas, including sites where populations can interact and sites where populations are separated. Stickleback metabolic rate was similar in populations when exposed to naturally experienced temperatures. Divergence in metabolic rate when experiencing the same temperature was greater in the separated populations (allopatry) than in the connected population (sympatry). Pilakouta et al. (2020) interpret the findings as evidence of lowered metabolic rates in warming rivers, but that gene flow could constrain such physiological adaptations, given the greater acclimation (i.e., metabolic rate changes) observed in the isolated population when compared to the connected population.

Therefore, thermal maxima are, theoretically, important in predicting future impacts of warming on populations but these predictions are complicated by the plasticity of thermal maxima within- and between life stages, individuals, and populations (Clusella-Trullas et al., 2021; Corey et al., 2020; Huff et al., 2005). It does however remain an important concept as anthropogenic activity is more likely to raise T_w (with a few notable exceptions including some dam release strategies) and so thermal maxima of some animal behaviors are increasingly likely to be exceeded in the future. It also suggests that species with higher thermal maxima, or that can rapidly increase their thermal maxima through phenotypic adaptation or gene expression, are likely to be more resilient to climate warming than those with narrow or low thermal maxima, or less plasticity (e.g., see Nukazawa et al., 2023).

2.4 | Changes in physiology, behavior, and phenology

Changes in T_w well below thermal maxima can have significant sub-lethal, behavioral impacts on organisms. Some organisms are likely to benefit from warming through faster growth and raised metabolism. For example, the survival rates of thermally-generalist, juvenile cyprinid fish (Chub, *Leuciscus cephalus*; Dace, *Leuciscus leuciscus*; Roach, *Rutilus rutilus*) in the Yorkshire River Ouse, UK, increased over a 15-year period as waters warmed (Nunn et al., 2003). Similarly, striped bass (*Morone saxatilis*) could benefit from warming in the Lower Saint John River, Canada, due in part to a longer juvenile growth season (Dugdale et al., 2018). While some organisms may benefit from warming (importantly, including some invasive species; e.g., Rahel & Olden, 2008; Coulter et al., 2014; Penk & Williams, 2019) others suffer. This could modify communities, most likely favoring more thermally generalist taxa at the expense of those with narrower thermal tolerances (e.g., Nelson et al., 2017a, 2017b). Numerous studies suggest aquatic insects of the order Plecoptera (stoneflies) are particularly sensitive to rising T_w (Pritchard et al., 1996; Tierno de Figueroa et al., 2010), and European data show that Plecoptera consistently decreased in relative abundance as T_w increased (Jourdan et al., 2018). Conversely, caddisflies (Trichoptera) are considered thermal generalists that typically benefit from rising T_w (Hering et al., 2009). Thermal pollution associated with, for example, wastewater effluent, power-station cooling water discharge, and surface dam releases, may provide analogues for the changes that global warming could bring. Habitats exposed to thermal discharges typically have lower species richness and abundance relative to nonexposed reference sites (Langford, 1990; Worthington et al., 2015). In particular, significant declines were observed in

Chironomidae and Simuliidae in places warmed by thermal effluent, hypothesized to be partially associated with competitive advantages of more thermally generalist taxa (O’Gorman et al., 2012; Quevado et al., 2018; West et al., 2021).

Changes in T_w can also impact the phenology of organisms, that is, the timing of life events. Temperature influences all aspects of fish reproduction, including the gamete development, fertilization, and larval hatching, due to dependency on photothermal cues, aerobic scope, and metabolic rates (see review in Whitney et al., 2014). As such, fish spawning is likely to occur earlier in the year as T_w rises (Gillet & Quetin, 2006; Jonsson & Jonsson, 2009), and embryo development will be faster (Greig et al., 2007). Otero et al. (2013) report that Atlantic salmon (*Salmo salar*) migrate from rivers to the ocean earlier when T_w is higher and, on average, has occurred 2.5 days earlier per decade in North America since the 1960s. Fish eggs also develop quicker in warmer water; for example, Crisp (1981) found *Salmo salar* hatch after 63 days following fertilization at 8°C and 38 days at 12°C, and Lugowksa and Witeska (2018) found that barbel (*Barbus barbus*) eggs developed quicker at higher T_w but suffered an increased rate of embryonic body malformations. In contrast, Marsh et al. (2021) show how Atlantic salmon recruitment was negatively affected in the River Frome, UK, between 2015 and 2020 due to warm spring seasons followed by cool emergence temperatures. Phenological cues are complex and not solely reliant on temperature, so interactions with other disturbances, such as changes to the timing of flow events, may further disrupt life history events such as spawning (Acre et al., 2022).

The phenology of aquatic insects is an understudied topic (see Woods et al., 2022) and changes of only 10ths of a degree Celsius can meaningfully impact the timing of life cycle events through altering the accumulation of degree days over the lifespan of organisms (Figure 4). Warmer water generally leads to earlier emergence of the aerial adult stage because individuals will reach maturity quicker (Anderson et al., 2019; Harper & Peckarsky, 2006). For instance, Baranov et al. (2020) found that peak emergence advanced by 13.4 days between 1969 and 2010 in Breitenbach (1.88°C warming), Germany, with 55% of species showing shifts in peak emergence. Warming in spring when emergence is cued may have different impacts compared to warming in summer when eggs and/or larvae contend with higher temperatures (Anderson et al., 2019). Altered phenology has implications for aquatic communities such as earlier emerging insects having smaller body sizes than would otherwise be expected because maturity is reached quicker (Chown & Gaston, 2010; Everall et al., 2014; Harper & Peckarsky, 2006; Walther et al., 2002). Smaller body size can impact both dispersal ability (Nijhout & Callier, 2015) and fecundity (i.e., number of eggs laid; Kingsolver & Huey, 2008), with potential population-level impacts. The implications of altered phenology when aggregated across ecosystems may be significant if food availability, predator–prey interactions, and/or habitat availability are disrupted (Knight et al., 2005); however, empirical evidence of such effects remains rare (Kharouba & Wolkovich, 2020). In tropical regions where strong phenological seasonality is lacking for many animals, the implications of thermal change may be different, but data are limited and should be a priority for further work.

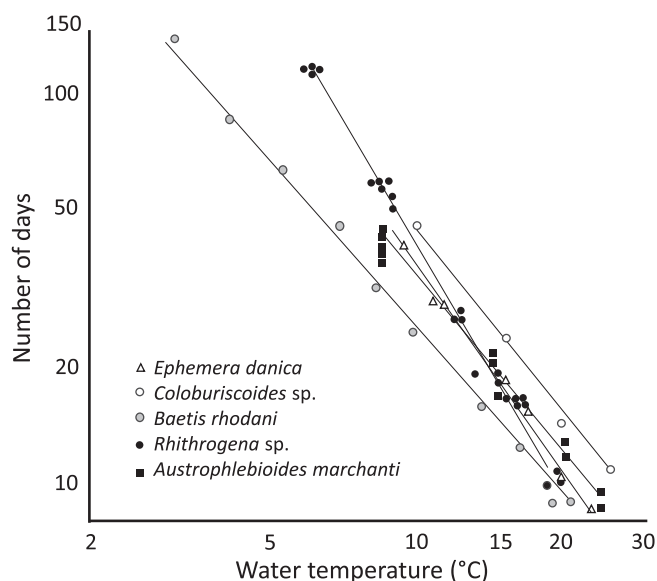


FIGURE 4 Egg development time to hatching at different uniform temperatures under laboratory conditions. Data compiled from the following sources: Bennett (2007, *Ephemera danica*), Brittain and Campbell (1991, *Coloburiscoides* sp.), Elliott and Humpesch (1980, *Baetis rhodani*), Humpesch and Elliott (1980, *Rhithrogena* sp.), and Parnrong and Campbell (2003, *Austrophlebioides marchanti*). Note the log scales.

2.5 | Range shifts and migration along warming rivers

Mobile animals can move to areas with lower T_w (e.g., upstream areas) as rivers warm (Cordellier et al., 2012; Domisch et al., 2012; Gallardo & Aldridge, 2013; Haase et al., 2019). This can occur at the scale of the individual, such as fish temporarily using local thermal refuges (Ebersole et al., 2020; Schaefer et al., 2003) or the population, such as a movement towards mountain stream refugia (e.g., Isaak et al., 2015) or the poleward drift in aquatic macroinvertebrates observed between 1970 and 1990 in Europe in response to warming (Hickling et al., 2006). For example, in the River Rhône, 1.5°C of warming over 20 years led to a shift in fish communities, with the replacement of cold-water species (such as Dace) by Chub and Barbel, which are representative of more thermally generalist (Daufresne et al., 2004). Such movements can benefit the species that are mobile but alter competition between species at the destination sites. For example, there is concern about Atlantic Salmon (*Salmo salar*) migrating into waters populated by Arctic Charr (*Salvelinus alpinus*) with negative implications for the latter species (Bilous & Dunmall, 2020; Svenning et al., 2016). At the scale of individuals, juvenile Atlantic salmon (*Salmo salar*) have been shown to move toward cooler areas as T_w approaches/exceeds 23°C (Breau et al., 2007; Corey et al., 2020; Dugdale et al., 2016), with adults also seeking out refuge areas at generally lower temperatures (17–19°C; Frechette et al., 2018).

Shifts in geographic range are dependent on the dispersal ability of individuals and species (Haase et al., 2019; Hickling et al., 2006; Parmesan & Yohe, 2003; Rundle et al., 2007). In general, organisms with narrower ranges have lower thermal thresholds than those with wider ranges, as observed by Calosi et al. (2010) for diving beetles in the genus *Agabus*. Although some organisms will be able to move poleward as temperatures rise others will not, such as cold-adapted organisms that already live at higher latitudes with less scope to expand their range further poleward (Hering et al., 2009; Jarić et al., 2018). Similarly, as T_w increases, organisms can migrate upstream to higher elevations, although Li et al. (2016) suggest that in the Himalayas, elevational shifts in invertebrate communities will not be able to keep up with the pace of climate change. This is supported by coupled hydrological/temperature and habitat suitability index models driven by Global Circulation Models (GCMs), which project that future changes in river T_w will shift the habitats of aquatic insects towards upstream reaches, and that some species will lose their habitat entirely by the end of the 21st century (Nukazawa et al., 2018). Communities living near the source of rivers in upstream, mountainous regions are likely to be amongst the most vulnerable to future warming as they will typically be cold-adapted and have less options for upstream migration (Buisson et al., 2008; Heino et al., 2009; Macadam et al., 2022). These organisms will not only be unable to move but will also potentially face additional competition from those migrating to higher elevations/latitudes (Bilous & Dunmall, 2020; Shepard et al., 2020). Therefore, those organisms that already have a restricted spatial distribution, such as isolated or relict taxa (e.g., Dipteromimidae mayfly; Barber-James et al., 2008; Takenaka et al., 2019) or those associated with specific habitats (e.g., Arctic Charr; Svenning et al., 2016), are most likely to be lost in the future.

Temperature impacts dispersal ability. Jourdan et al. (2019) found that wing length in the crane fly (*Tipula maxima*) increased by 5.6% for every 1°C of warming, but equivalent 17.8% and 26.9% increases in body weight for females and males, respectively, resulted in a negative impact on dispersal ability, with potentially significant effects on animal resilience to future change (Jourdan et al., 2019). Negative impacts on dispersal have also been reported in fish because swimming speed can be constrained by aerobic scope, limited by the lower oxygen concentrations in warmer water (Brett, 1964; Salinger & Anderson, 2006; Svendsen et al., 2004). In general, swimming speed increases with temperature to an optimum and then rapidly declines (Claireaux et al., 2006; Wardle, 1980). Activity levels in juvenile salmon have also been reported to decline above optimum temperatures (Roussel et al., 2006). Sharp thermal contrasts can act as thermal barriers. For example, Frechette et al. (2018) observed high temperatures (and low flows) are barriers to Atlantic salmon accessing thermal refugia. While this can occur naturally in some rivers, the importance of thermal refuge and the presence of thermal barriers, are both likely to increase with climate change.

2.6 | Trophic restructuring

Temperature changes and other factors will affect trophic interactions (Whitney et al., 2014) that form the scaffolding of freshwater food webs with propagating impacts to ecosystem processes and services vital for human wellbeing. Theory predicts that the rate of heterotrophic metabolism will increase more rapidly with warming than autotrophic metabolism due to cellular differences in activation energy between respiration and photosynthesis (Allen et al., 2005; O'Connor et al., 2009). Consequently, freshwater herbivores could exert stronger top-down control on primary

producers with increasing temperatures (Shurin et al., 2012). Additionally, warming water may elevate feeding rates of predatory fish (Kratina et al., 2012), resulting in a strengthening of trophic cascades (Hoekman, 2010; Su et al., 2021); however, such responses will likely be modified by other pressures, including eutrophication, predator manipulations, and invasive species (Kratina et al., 2012; O'Connor et al., 2009; Rolls et al., 2017). Although previous studies have demonstrated the effects of warming on trophic cascades by quantifying “bulk” changes in populations (e.g., abundance and biomass), recent work has begun to explore more subtle effects on individuals (e.g., metabolism, foraging, behavior) and the quality of food resources (see Ilić et al., 2021). Most studies examining the influence of warming on the strength and patterning of freshwater trophic cascades have traditionally relied on small-scale experiments to uncover causal mechanisms in controlled settings. Despite the utility of these approaches, less is known if such findings will occur at larger scales (see Hampton et al., 2008 and Lin et al., 2017 for examples in lakes), and additional research that complements experimental work with either long-term or larger-scale comparative observations may greatly improve our understanding of how warming will influence trophic cascades in natural riverine settings.

Warming is also expected to shift communities towards smaller individuals via direct physiological constraints (Atkinson, 1994; Rubalcaba et al., 2020) and reshuffle communities to include a higher proportion of smaller thermal-tolerant species (Bergmann, 1847; Yvon-Durocher et al., 2011). These changes in size structure will likely impact individual growth rates, carbon sequestration, nutrient cycling, and the flux of energy through aquatic food webs and into riparian ecosystems (Jennings & Blanchard, 2004; Woodward et al., 2005; Yvon-Durocher et al., 2011). For instance, detailed observational work across a natural geothermal gradient in Iceland shows that higher stream temperatures coincide with decreased invertebrate sizes but increased growth rates (Junker et al., 2023). Such changes further resulted in lower standing biomass stocks, neutral effects on secondary production, and a rerouting of energy from slower to faster pathways in food webs after accounting for changes in basal resources (Junker et al., 2023). Additionally, prey resources that are repackaged into smaller sizes may be of lower quality for predators that exhibit strong prey size selection (e.g., drift-feeding salmonids), leading to reduced growth of top predators despite abundant prey in the environment (Dodrill et al., 2016). The loss of large-bodied predators, in particular, can disrupt top-down control and destabilize food webs, especially if the predator is mobile and couples spatially distinct patches of prey resources through feeding (McCann, 2012; Rooney et al., 2008). However, it is important to note that the effects of warming described above are not universal, and unexpected responses, including increased invertebrate body size (Nelson et al., 2017a) and positive responses of predatory fish (O’Gorman et al., 2016), have also been observed. Thus, future research is needed to clarify the mechanisms underpinning these more nuanced responses and explore the extent to which they occur in nature.

Along with size structure changes, warming-induced shifts in species ranges, and phenology (described above) may mismatch consumers and their resources (Bartley et al., 2019; Durant et al., 2007; Perkins et al., 2010; Tunney et al., 2014). For example, ongoing changes in fish assemblages driven by growing numbers of warm water tolerant species are currently rewiring food webs in the Mississippi River, USA (Staudinger et al., 2021), and some aquatic insects are shifting their emergence to when essential nutrients are available, supporting bird reproduction in the eastern USA (Shipley et al., 2022). Although detailed outcomes of trophic restructuring are difficult to predict, these novel food webs will likely have stronger feeding interactions (Rall et al., 2012), reduced complexity and connectivity (O’Gorman et al., 2019; Petchey et al., 2010), lower efficiency in transferring energy (Barneche et al., 2021) and may be more unstable and less resilient over time (McCann, 2012; O’Gorman et al., 2012). However, the pace of such changes remains uncertain, and little is known about whether they will occur linearly with warming, or if systems may reach “tipping points” (see Scheffer et al., 2001, for an example in lakes) at which point rapid change is possible. Clearly, warming is likely to influence a myriad of aspects of trophic dynamics in riverine ecosystems. However, further research is needed to understand how rising T_w will influence trophic dynamics across space and time scales, and how the effects of warming compare to, and may be modified by, other global change drivers including species invasion, land use change, predator removal, and eutrophication.

3 | INDIRECT THERMAL IMPACTS ON RIVERINE ANIMALS

Warming will occur in parallel to, and interact with, other hydrological changes. For example, lower summer flows (White et al., 2023), altered terrestrial environments (Marteau, Piégay, et al., 2022), and changing water usage (review Kędra & Wiejaczka, 2018). In addition to the direct impacts of future warming on river ecosystems, many indirect effects will also occur (Jackson et al., 2016). Rising T_w is likely to aggravate existing pressures on freshwaters, such as

eutrophication, chemical pollution, and disease. The indirect impact of warming in aggravating water quality issues can be identified from large datasets where rising temperatures have led to the loss of pollution-sensitive invertebrate taxa (Daufresne et al., 2007; Jourdan et al., 2019).

3.1 | Eutrophication

Of particular concern is eutrophication, which is caused by elevated nutrient concentrations associated with agricultural activities and waste-water treatment plant discharges. Elevated nutrients already cause significant harm to rivers globally (e.g., Javie et al., 2013). This is because high nutrient loads promote algal growth that can block sunlight, reduce photosynthesis by macrophytes and other primary producers, and significantly reduce dissolved oxygen levels, which are already lower in warmer water than colder water, with wider implications for plants and animals. In a future where rivers are warmer with lower summer flows, eutrophication could further increase in magnitude and spatial extent, with low flows concentrating nutrients in warmer water that promotes algal growth (Coffey et al., 2018; Glibert, 2020; Sin & Lee, 2020). Jeppesen et al. (2010) identify key interactions between warming and eutrophication, including changes in the growth and respiration of organisms potentially leading to lower net primary productivity, enhanced oxygen consumption, and increased risk of oxygen depletion and increased nutrient release from sediments. They conclude that rising T_w could exacerbate eutrophication in lakes (Jeppesen et al., 2010), although future freshwater management may reduce similar pressures in river networks by reducing nutrient inputs.

Analysis of regional datasets indicates an interactive effect of T_w and water chemistry on macroinvertebrate communities. Bowler et al. (2017) found long-term shifts in aquatic macroinvertebrate communities due to climate change were less predictable than for terrestrial environments and hypothesized that this was due to the confounding impacts of water quality. The interaction between rising T_w and generally improving water quality is discussed within a framework of “climatic debt” by Vaughn and Gotelli (2019). They identify that, averaged across the UK, an increase in T_w of approximately 0.6°C between 1990 and 2010 was offset by improved water quality, thereby mitigating potential direct ecological impacts associated with warming (Vaughn & Gotelli, 2019). The underlying mechanisms of this climate debt remain poorly understood, not least because of a lack of information on the longer-term consequences of sub-lethal impacts of warming and multiple stressors in rivers. Jourdan et al. (2018) assert that past research has also paid less attention to the potential impacts of altered climate extremes, instead focusing on longer-term chronic changes in average conditions.

3.2 | Temperature interactions with chemical pollutants

T_w can alter the toxicity of pollutants. The impact of some pollutants is enhanced when exposure is combined with elevated T_w , termed climate-induced toxicant sensitivity (Noyes & Lema, 2015). Elevated temperature is known to alter the toxicity of nutrients such as ammonia (Eriksen, 1985), pesticides (Berger et al., 2017; Verheyen et al., 2022), and other chemicals, such as polyaromatic hydrocarbons (PAHs; Noyes & Lema, 2015). There is also evidence that elevated T_w can alter the bioavailability, toxicity, and bioaccumulation of toxic metals (Fritioff et al., 2005). The mirrored impact of how pollutants may affect the ability of an organism to cope with rising temperatures (i.e., toxicant-induced climate sensitivity) is less known. Nonetheless, Op de Beeck et al. (2017) found that larvae of the damselfly *Ischnura elegans* had reduced upper thermal tolerance when exposed to pulses of the organophosphate pesticide Chlorpyrifos, than those that were not.

This interaction between chemical pollution and T_w is related to the ability of both pollutants and temperature to impair aerobic capabilities and increase energy demand, which contributes to setting thermal maxima (Sokolova & Lannig, 2008). There are still relatively few studies focusing on these potentially important interactions, and those that do have identified species-specific and sex-specific impacts, which can be unexpected. For example, Delnat et al. (2019) found that the heat tolerance of larvae and adult male mosquitoes (*Culex pipiens*) was reduced when exposed to the pesticide Chlorpyrifos (i.e., toxicant-induced climate sensitivity), but female adults were unaffected.

Although studies have generally found that higher T_w amplifies the detrimental impacts of pollutants, there are exceptions. For example, some pesticides degrade quickly in warmer water (Hooper et al., 2013). Overall, this demonstrates that toxicity of chemicals and rising T_w could interact, but this synergistic effect is likely to be variable and, therefore, population-level impacts hard to predict (see review of Polazzo et al., 2021). Also, because T_w can influence

growth rates, phenology, and trophic structures (see above), there may be changes to the transfer of pollutants through food webs, although such interactions are not understood in rivers (but see Alava et al., 2017 for an example in marine environments).

3.3 | Disease

Increased T_w may promote the spread of disease in wildlife (IPCC, 2022). Johnson et al. (2009) note that if T_w rises it is possible that bacterial and viral infections, as well as pathogens that have relatively high temperature thresholds, are more likely to establish and spread. For example, Marco-López et al. (2010) developed a risk framework for disease spread in freshwater fish due to climate change and predicted endemic diseases of salmonids including enteric red mouth, furunculosis, and white spot, which will become more prevalent. They also note that the threat of some diseases may decline as some diseases (e.g., hemorrhagic septicemia) generally establish when T_w is lower than 14°C. Tops et al. (2006) found proliferative kidney disease in fish caused mortality at T_w above 15–16°C whereas Johnsen and Jensen (1994) show how thermal stress contributed to outbreaks of furunculosis in salmon in Norwegian rivers during the 1980s. Animals living in an environment characterized by high T_w , lower flows, and eutrophication are likely to have reduced immune response and be more susceptible to disease. Animals could also be exposed to novel diseases and parasites from incoming organisms driven poleward and/or to higher latitudes. For example, Strøm et al. (2020) found that exposing Arctic Char to salmon lice (*Lepeophtheirus salmonis*), brought from northward shifting Atlantic Salmon, led to detrimental alterations in feeding and migratory behavior. The potential implications of climate change for the spread of wildlife disease are not well understood, but represent an area of great significance.

4 | RESILIENCE TO FUTURE WARMING

4.1 | Resilience of river environments to thermal change

While there is a high degree of confidence that the average T_w of rivers will rise (see review by Wanders et al., 2019), regional variations in warming, changed temperature extremes, altered T_w ranges, and compound impacts associated with other hydrological alterations (including abstraction), are not well understood. Given that the future is uncertain, at least in part because of the complexity of ecological interactions, strategies are needed to ensure rivers are resilient to whatever the future holds. Optimal resilience is provided by a river free from anthropogenic disturbance that is fully connected to groundwater and its floodplain, with an erodible corridor and longitudinal connectivity, with the ability to respond in unconstrained ways to changes in climatic drivers (Johnson et al., 2019). Clearly, such rivers are globally rare, at least for any major, continuous distance. However, the more capacity that rivers have to respond to the changing climate, the more resilient the socio-ecological communities within them are likely to be, buying time to adapt by removing other pressures and constraints on river ecosystems (Palmer et al., 2009; Tonkin et al., 2019; Wilby, 2020).

Shading of solar radiation from rivers can impact T_w . Hence, the widespread historic removal of riparian vegetation has been linked to rising T_w (Fuller et al., 2022; Johnson et al., 2014; Moore et al., 2005). One meta-analysis found that, on average, rivers with bankside trees have lower mean and maximum T_w when compared with those without trees (Bowler et al., 2012). Therefore, some of the most vulnerable river reaches to climate change are those lacking riparian and/or topographical shading. While other habitats in the river warm, organisms can survive by exploiting thermal refuges (i.e., such as hyporheic upwelling, deep pools, groundwater inflows) or thermal refugia (larger parts of the river system where temperatures are more amenable, such as upland tributaries; e.g., Arrigoni et al. 2008; Frechette et al., 2018; Mejia et al., 2023). Fish are known to use thermal refuges and refugia to regulate their body temperature, moving into cooler areas of water when T_w are high (Breau et al., 2007; Dugdale et al., 2016). For example, Breau et al. (2007) found juvenile Atlantic salmon (*Salmo salar*) utilized a cool-water plume, with 2+ year age groups using the coolest areas of the plume and 1+ year age groups using warmer parts of the plume that were still cooler than the main river. Furthermore, Frechette et al. (2018) recorded adult Atlantic salmon using cool and warm water refuges to thermoregulate even when T_w was well below “normal” thermal tolerance thresholds, indicating the importance of cool water habitats for maintaining body temperature within an optimal range. Protecting thermal refuges and refugia could, therefore, be critical to the resilience of communities under climate change, especially when they are associated with groundwater inputs into rivers that are buffered from changes in air temperature. Recent research (e.g., Kurylyk

et al., 2015; Marteau, Michel, & Piégay, 2022; Mejia et al., 2023; Sullivan et al., 2021) focusing on developing appropriate management strategies, typologies, and conservation frameworks for critical thermal habitats in rivers provide a promising avenue for investigation in this regard.

Groundwater temperatures are dependent on aquifer source, groundwater depth, and geology, but are typically much less variable than surface water temperature and, where not geothermally heated, approximate the annual average air temperature (Younger, 2006). As such, groundwater inputs can exert a significant control on thermal regimes and buffer against high and low temperatures driven by solar radiation. If groundwater discharge into a channel decreases, or the T_w of groundwater increases, this could place significant pressure on ecological communities utilizing thermal refuges to survive warming. However, warming of groundwater due to climate change is observed from measured and modeled work in cold and temperate regions (e.g., Daigle et al., 2015; Kurylyk et al., 2014; Menberg et al., 2014) and monthly measurements of T_w from springs in Sweden and Finland show evidence of a warming trend, on average of 0.03°C per year (Jyväsjärvi et al., 2015).

When attempting to improve river resilience to climate-driven temperature increases, restoration science may need to place increased emphasis on restoring rivers with river-wetland corridors, where lateral connection to floodplains occurs at low, as well as high flows, preserving and enhancing (thermal) habitat heterogeneity (Cluer & Thorne, 2014; Johnson et al., 2019). While channel form depends on the climate, geology, surrounding biome, and anthropogenic use, designing channels that promote regular sub-annual connection to floodplains, that provide thermal refuge by driving groundwater connectivity, and buffering higher summer temperatures, could significantly improve resilience to future change (Johnson et al., 2019; Ouellet et al., 2020; Figure 5). Providing riparian shading to such channels to mitigate downstream warming will also improve thermal buffering and will likely extend the thermal benefits of a restored, reconnected channel further downstream. However, such refuges are only useful if accessible to animals, so promoting river connectivity to enable migration to more thermally suitable conditions should also be a key consideration in future climate adaptation strategies (Ebersole et al., 2020).

4.2 | Resilience and resistance of ecological communities to thermal change

The resilience of an ecosystem is usually defined as the ability of the system to return to an equilibrium state and/or maintain structure and function after disturbance (Ingrisch & Bahn, 2018). Resilience reflects the self-healing capacity of ecosystems, which is an example of self-organization (Folke et al., 2004). The concept of resilience used herein is taken in the broadest sense and therefore considers both the resistance and the recovery of an ecosystem (Ingrisch & Bahn, 2018), which are related to the functional traits of the organisms that comprise the ecosystem. For example, if key functions are provided by multiple taxa with diverse dispersal traits and habitat requirements (redundancy), such ecosystem functions will be more resilient to change than an equivalent system where that function is provided by few, similar taxa (Biggs et al., 2020). Although ecosystem functions are generally thought to be resilient to chronic changes, if these functions are lost ecosystem collapse is possible. For example, many invertebrate animals shred organic matter, providing an important function to other organisms that feed on fine particulate material. Yet, Statzner and Bêche (2010), Jourdan et al. (2018), and Pyne and Poff (2017) found detrital shredders and algal grazers to be particularly vulnerable to rising T_w compared to other feeding groups, thereby increasing the vulnerability of the ecosystem as a whole.

Anthropogenic activities (such as channel alteration, flow alteration, floodplain disconnection, and riparian land-use change) impact resilience to warming whenever they prevent or retard adaptation to changing conditions, and where they reduce functional redundancy through habitat simplification. Anthropogenic impacts tend to shift communities towards more stress-tolerant species (Arantes et al., 2019; Flourey et al., 2012). Hence, degraded habitats may be more susceptible to detrimental future T_w change because of a decrease in functional redundancy. Counterbalancing this is the fact that ecosystem functions will likely be provided by more stress-tolerant taxa making future prediction challenging and likely river and context-specific. The interaction between functional resilience and habitat degradation means that reducing nonclimatic anthropogenic stresses may buy time for exposed ecosystems, and potentially for organisms to adapt (Hansen et al., 2003; Wilby, 2020).

van Looy et al. (2018) detail three key aspects that define river resilience, namely, resources, recruitment, and refugia. If resources become depleted, ecological communities will respond through competition and/or facilitation (van Looy et al., 2018). Warming is likely to alter resource dynamics in freshwaters, including alterations in the transfer of organic matter from terrestrial to freshwater systems (e.g., Larsen et al., 2015). After a disturbance, the ecological

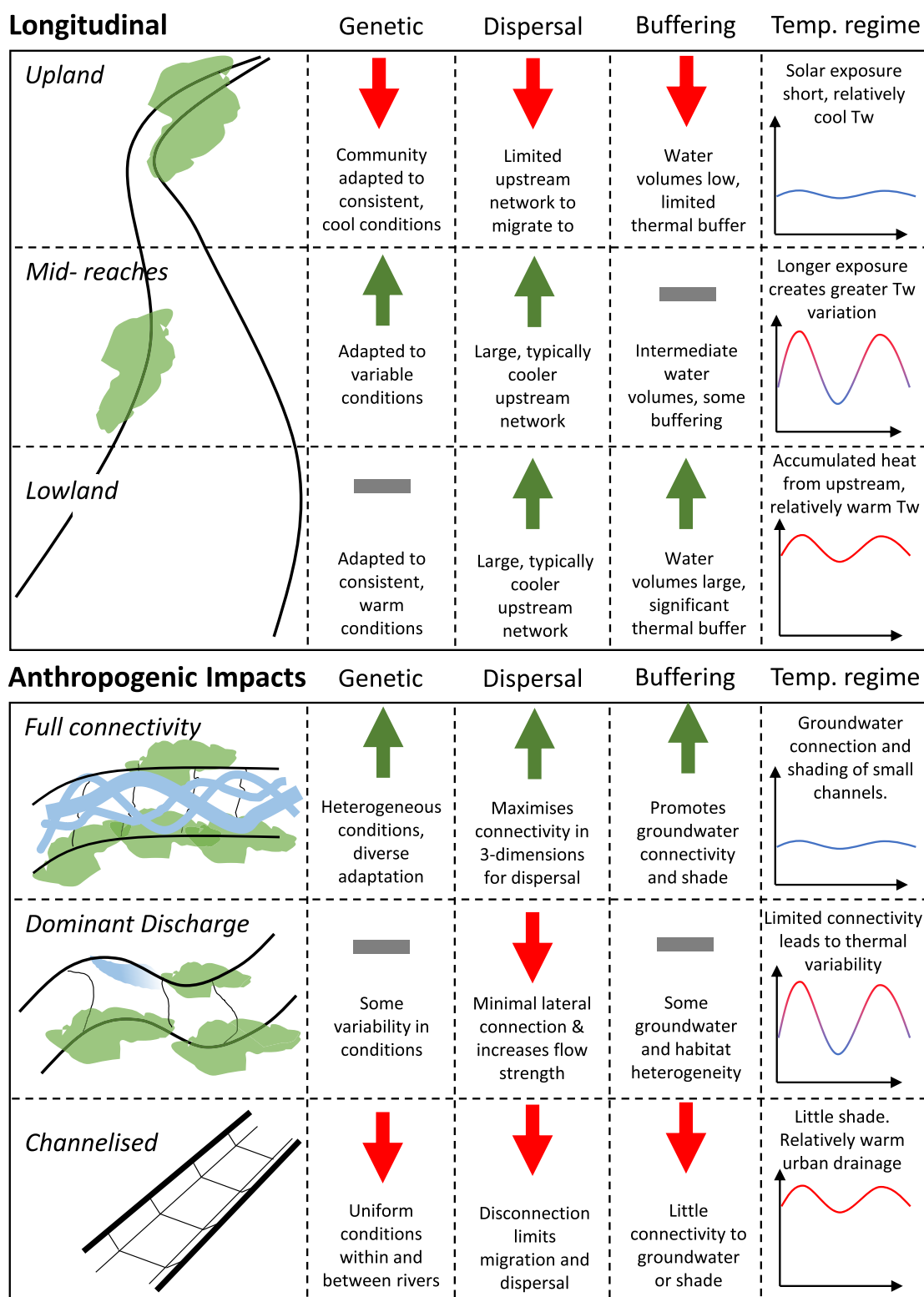


FIGURE 5 Schematic of river resilience based on (a) longitudinal position within catchments and (b) anthropogenic impacts on channel connectivity. Resilience to warming is represented by a green arrow and vulnerability to warming by a red arrow. “Genetic” is the potential resilience imparted by diversity in ecological communities; “Buffering” is the thermal cushioning against warming due to landscape conditions; “Dispersal” is the ability of animals to find refuge or migrate; and “Temp regime” is the typical temperature profile for each condition. Longitudinal positions are relative, running from source to mouth. Anthropogenic impacts are for a fully “Channelized” river, disconnected laterally and likely widened; a sinuous but single-thread channel design based on the concept of a “Dominant discharge,” that is connected laterally only episodically; and “Full connectivity” is when there is a complex channel that is fully connected laterally with a surrounding floodplain that is flooded at low-to-moderate flows driven by even modest increases in discharge.

community will reassemble, and the more readily a community reassembles, the more resilient it is likely to be. Reassembly of a community is dependent on the dispersal ability of individuals and the connectivity of the disturbed site to the regional species pool. Therefore, past management that has disconnected rivers longitudinally via dams, weirs, and other barriers (e.g., Belletti et al., 2020) may impact resilience to warming. Recruitment after disturbance can also occur at local scales, linked to the presence of refugia. This is because organisms can persist in refugia, sustaining populations and providing a community pool for recruitment, post-disturbance. The ability of organisms to find and use such refuges is species-specific but, in general, the more heterogeneous the habitat and the greater the level of longitudinal, lateral, and vertical connectivity, the more likely refugia will be present and utilized by the ecological community (Astorg et al., 2020; DelVecchia et al., 2022; Keppel et al., 2011; Morelli et al., 2020). However, the importance of refuges/refugia for ecological resilience must of course be considered in the context of the capacity of the refuges/refugia to resist larger-scale climate-driven Tw warming.

The resilience of individual taxa to warming is related to their life strategies. For example, the emergence strategies and timings of insects may influence their resilience to future change. Some species have multiple emergence periods throughout the year (multivoltine) which is likely to be a more resilient strategy than species that only have one, short, emergence period per year (univoltine; Halsh et al., 2021; Hershkovitz et al., 2017). Switches in voltinism are possible (Carey et al., 2021); for example, the mayfly *Ephemera danica* in the River Dove, UK, transitioned from a 2-year life cycle to a 1-year life cycle between 2006 and 2013 (annual average Tw 9.3–10.9°C) but retained a 2-year life cycle in

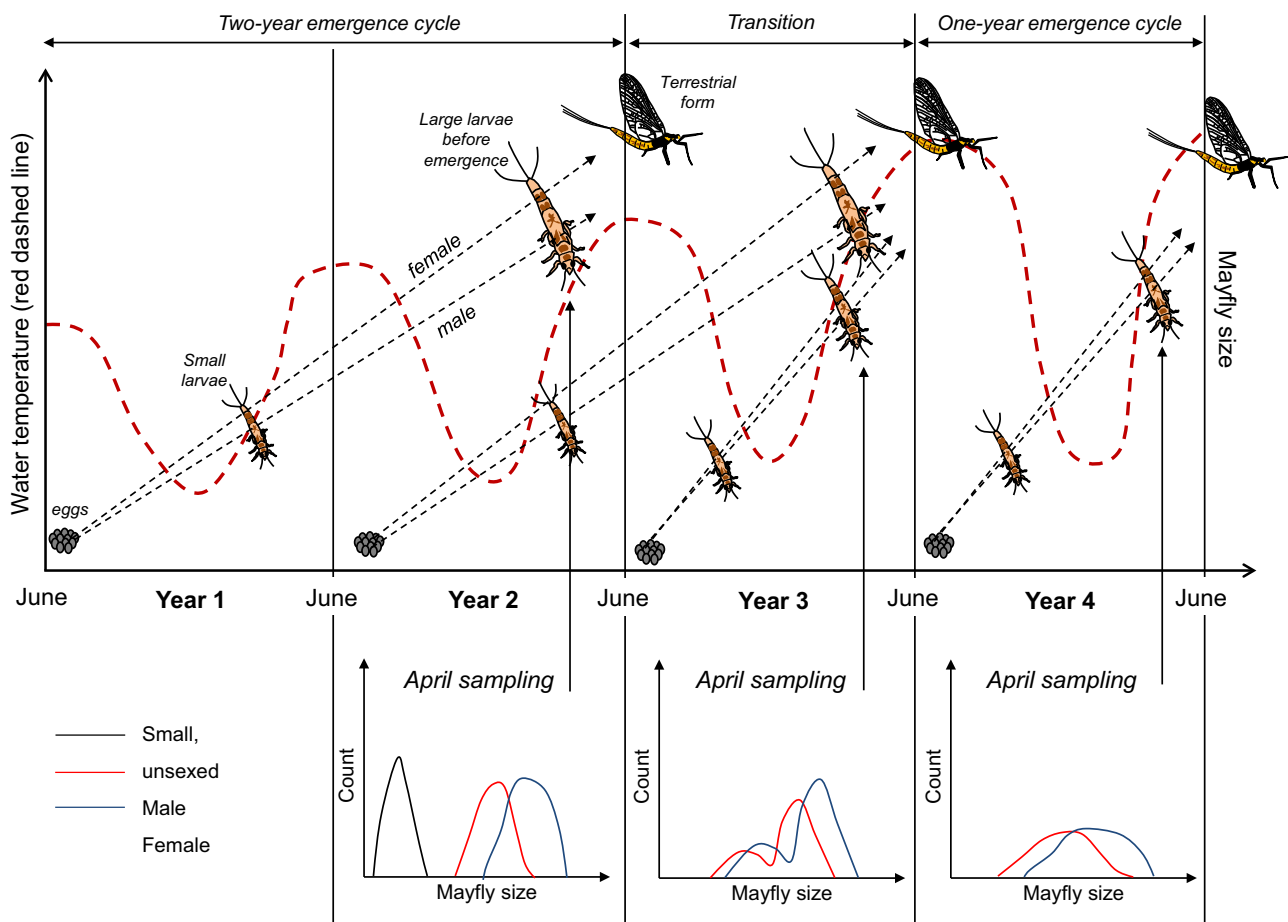


FIGURE 6 Representation of the phenology of *Ephemera danica*. From hatching, larvae develop depending on accumulated heat over two-year periods. As males have a lower minimum growth threshold, they grow larger than females over the same time-period. Emergence occurs in early-June. Sampling in April of year 2, catches both large males and females forming distinct size classes and a peak of small individuals which require an additional year of growth. In a 1-year cycle, as shown in year 4, mayflies do not grow as large and males and females do not form as distinct groups because of the more limited number of degree days for development. Reproduced with permission from Everall et al. (2014).

groundwater-dominated areas where T_w remained cool and more stable (annual average T_w 8.4–9.1°C; Everall et al., 2014). In this case, a 1-year life cycle represents a vulnerable population structure because any threats during the few days of emergence will disproportionately impact the population with no reserve animals remaining in the river, requiring re-colonization from elsewhere in the river network (Figure 6).

5 | CONCLUSIONS

Biodiversity and ecosystem functions are affected to varying degrees by the direct and indirect impacts of thermal warming in rivers. Indeed, such impacts are already widely observable (IPCC, 2022) and the services freshwater ecosystems provide are under threat (Capon et al., 2021). Cool-water-adapted river species are likely to be more vulnerable to climate change than other species because (1) genetic adaptation to relatively stable cool temperatures over long periods (i.e., many thousands of years) is likely to make them much less able to adapt their phenotype to future temperature changes; (2) animals are likely to be at the limit of their thermal range without the opportunity to migrate upstream or poleward to more thermally amenable habitats in the future, and; (3) warming is predicted to be greatest at higher latitudes. These regions and habitats are also among the most data sparse (see Birrell et al., 2020), resulting in less information to inform appropriate monitoring and management. Developing novel approaches, for example, that include the use of (drone-based) remote sensing, novel sensors, and eDNA techniques, will be important to better monitor these regions, especially near the sources of upland streams that are at particular risk from climate change.

The impacts of warming temperatures on rivers are already evident, although they may be offset in some cases by improvements in water quality (Vaughn & Gotelli, 2019). Future climate change is expected to further degrade rivers, exacerbating existing pressures from eutrophication, low summer flows, and chemical pollutants (Whitehead et al., 2009). Impacts on ecosystems will be highly river specific, with some more resilient to change than others. While it is likely that species will be lost to climate change—particularly those that already reside near their upper thermal limits—it is expected that key remaining ecological functions will be resilient. This is partly because many rivers are already heavily degraded and so the scope for further degradation of aquatic communities is limited (Palmer et al., 2009). By extension, this means those rivers that are relatively unimpacted by anthropogenic alterations and harbor diverse communities have the furthest to fall and should be the focus of conservation efforts. Confidence in these general assertions is high, but confidence in more species- and site-specific responses is low because of the predominant focus on upper thermal limits, with more limited understanding of changes at lower temperatures, as well as complex interactions between sub-lethal pressures, the modulating impacts of environmental context and a lack of suitable baseline data to be able to clearly identify the manifestation of climate change on communities.

Climate change is expected to bring more extreme weather events and high temperatures, which are likely to have greater impacts on ecological communities than rises in average temperature. For example, climate extremes have been found to be a major driver of local extinctions and range contractions due to climate change across environments (Barbarossi et al., 2021; Román-Palacios & Wiens, 2020). Warming could also lead to changes in the timing of snow-melt, ice break-up, and other hydrological events with thermal consequences, which could have significant, sudden impacts on aquatic populations, communities, and biodiversity (Berghuijs et al., 2014; Kendrick et al., 2018; Li et al., 2022). Changes in the timing or magnitude of such events could impact populations via effects on the success of egg deposition (Peckarsky et al., 2000) or adult emergence (Lytle, 2008).

Although we have a strong understanding of the direct effects of temperature on physiology under controlled laboratory conditions, many factors including food availability, may modify outcomes and lead to unexpected changes in river ecosystems (Solokas et al., 2023; Warren et al., 2022). Therefore, past research conducted under controlled, experimental conditions may not reflect actual responses to climate change because of the complex interactions between organisms, resource availability, and environments. Research in the following areas could help resolve uncertainties in the response of aquatic ecosystems to warming; (1) field-based studies of the sub-lethal implications of warming, particularly in areas already known to be warming; (2) the implications of climate change at the lower end of organisms' thermal tolerances, as opposed to the current emphasis on maximum temperatures; (3) nontemperate zone rivers, particularly tropical rivers and high latitude rivers where animals are likely adapted to live close to their thermal limits; (4) investigations that look beyond individual species and considers how warming will impact animal interactions; and (5) how anthropogenic alterations to river channels may influence the resilience of ecological communities to warming.

Though future changes to aquatic ecosystems are not predictable with certainty, managing rivers in a manner that builds resilience to a multitude of pressures may mitigate changes aquatic ecosystems are likely to face. Indeed, it is

anticipated that the ecological impacts of pollution and habitat loss could exceed those of climate change over the next century (Scholze et al., 2006). The most resilient rivers are likely to be those with good connectivity longitudinally, laterally, and vertically, with minimal changes to flow regimes and catchment hydrology. Accordingly, promoting restoration focused on reconnection and rewetting will be key to buying time for river ecosystems to adjust to rising Tw. Focusing conservation and restoration efforts on refugia and building resilience of the riverine system through improving connectivity and associated heterogeneity in conditions will be important in the adaptation of river systems to climate-driven water temperature change.

AUTHOR CONTRIBUTIONS

Matthew F. Johnson: Conceptualization (equal); project administration (equal); writing – original draft (equal); writing – review and editing (equal). **Lindsey K. Albertson:** Writing – original draft (equal); writing – review and editing (equal). **Adam C. Algar:** Writing – original draft (equal); writing – review and editing (equal). **Stephen J. Dugdale:** Writing – original draft (equal); writing – review and editing (equal). **Patrick Edwards:** Writing – original draft (equal); writing – review and editing (equal). **Judy England:** Writing – original draft (equal); writing – review and editing (equal). **Christopher Gibbins:** Writing – original draft (equal); writing – review and editing (equal). **So Kazama:** Writing – original draft (equal); writing – review and editing (equal). **Daisuke Komori:** Writing – original draft (equal); writing – review and editing (equal). **Andrew D. C. MacColl:** Writing – original draft (equal); writing – review and editing (equal). **Eric A. Scholl:** Writing – original draft (equal); writing – review and editing (equal). **Robert L. Wilby:** Writing – original draft (equal); writing – review and editing (equal). **Fabio de Oliveira Roque:** Writing – original draft (equal); writing – review and editing (equal). **Paul J. Wood:** Writing – original draft (equal); writing – review and editing (equal).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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