

Stream isotherm shifts from climate change and implications for distributions of ectothermic organisms

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Abstract

Stream ecosystems are especially vulnerable to climate warming because most aquatic organisms are ectothermic and live in dendritic networks that are easily fragmented. Many bioclimatic models predict significant range contractions in stream biotas, but subsequent biological assessments have rarely been done to determine the accuracy of these predictions. Assessments are difficult because model predictions are either untestable or so imprecise that definitive answers may not be obtained within timespans relevant for effective conservation. Here, we develop the equations for calculating isotherm shift rates (ISRs) in streams that can be used to represent historic or future warming scenarios and be calibrated to individual streams using local measurements of stream temperature and slope. A set of reference equations and formulas are provided for application to most streams. Example calculations for streams with lapse rates of 0.8 °C/100 m and long-term warming rates of 0.1–0.2 °C decade⁻¹ indicate that isotherms shift upstream at 0.13–1.3 km decade⁻¹ in steep streams (2–10% slope) and 1.3–25 km decade⁻¹ in flat streams (0.1–1% slope). Used more generally with global scenarios, the equations predict isotherms shifted 1.5–43 km in many streams during the 20th Century as air temperatures increased by 0.6 °C and would shift another 5–143 km in the first half of the 21st Century if midrange projections of a 2 °C air temperature increase occur. Variability analysis suggests that short-term variation associated with interannual stream temperature changes will mask long-term isotherm shifts for several decades in most locations, so extended biological monitoring efforts are required to document anticipated distribution shifts. Resampling of historical sites could yield estimates of biological responses in the short term and should be prioritized to validate bioclimatic models and develop a better understanding about the effects of temperature increases on stream biotas.

Keywords: climate change, climate velocity, distribution shift, fish, global warming, isotherm, monitoring, range contraction, stream temperature

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Introduction

Freshwater environments cover <1% of the Earth's surface, yet contain 6% of all described species (Dudgeon *et al.*, 2006). Despite well-recognized social and ecological values, these environments are being rapidly degraded and experiencing declines in biodiversity and functionality that often exceed losses in terrestrial systems (Malmqvist *et al.*, 2008; Vorosmarty *et al.*, 2010; Burkhead, 2012). Global warming is predicted to accelerate losses of biodiversity this century as environmental trends associated with a warming climate interact with other forms of anthropogenic habitat degradation (Thomas *et al.*, 2004; Xenopoulos *et al.*, 2005; Lawler *et al.*, 2009a; Lawler *et al.*, 2009b). As the climate warms, species are forced to shift their distributions in space (poleward or toward higher elevations) and time (phenologic adaptations) to track thermally suitable

habitats. Some populations will encounter barriers (e.g., land/water interface, watershed divides, instream discontinuities from dams, or warm temperatures), run out of habitat (i.e., mountaintop islands, ephemeral headwater streams), or be overtaken and simply perish (Jump *et al.*, 2009; Loarie *et al.*, 2009). Stream biotas are expected to be particularly vulnerable to thermal alterations associated with climate change given ectothermic physiologies (Pörtner & Farrell, 2008), strong thermal regulation of growth and survival (Magnuson *et al.*, 1979; Elliott & Hurley, 2001; McMahon *et al.*, 2007), limited evolutionary potential in thermal tolerances (Crozier *et al.*, 2008; McCullough *et al.*, 2009), and constraint to river and stream networks that are often heavily fragmented by natural and anthropogenic factors (Zwick, 1992; Graf, 1999).

Species and population extinctions have been linked to climate change (e.g., Pounds *et al.*, 2006; Beever *et al.*, 2010), but for now, distribution shifts are more commonly documented. Case histories are sufficiently common that reviews encompassing dozens of

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terrestrial plant and animal taxa and hundreds of individual species have been published (Root *et al.* 2003; Parmesan & Yohe, 2003; Hickling *et al.*, 2006; Sunday *et al.*, 2012). For stream biotas, empirical evidence exists for shifts in the timing of migrations and spawning (Heino *et al.*, 2009; Wedekind & Kung, 2010; Crozier *et al.*, 2011), as well as poleward and upstream range expansions (Babaluk *et al.*, 2000; Hickling *et al.*, 2005; Milner *et al.*, 2011). However, little evidence exists of broadscale range contractions, which is troubling given the extensive and often dramatic changes predicted with numerous bioclimatic models in recent decades (Meisner, 1990; Eaton & Schaller, 1996; Keleher & Rahel, 1996; Rahel *et al.*, 1996; Mohseni *et al.*, 2003; Chu *et al.*, 2005; Xenopoulos *et al.*, 2005; Flebbe *et al.*, 2006; Battin *et al.*, 2007; Rieman *et al.*, 2007; Sharma & Jackson, 2008; Buisson & Grenouillet, 2009; Kennedy *et al.*, 2009; Williams *et al.*, 2009; Lyons *et al.*, 2010; Almodóvar *et al.*, 2012; Wenger *et al.*, 2011; Ruesch *et al.*, 2012; Tisseuil *et al.*, 2012). A lack of supporting biological evidence could contribute to an 'inertia of inaction' regarding difficult conservation choices or the misallocation of resources if decisions are based on inaccurate model projections (Dormann, 2006; Lawler *et al.*, 2009a; Lawler *et al.*, 2009b).

Several factors are responsible for the limited evidence regarding range contractions in stream organisms. First and most simply, few monitoring efforts of sufficient duration have been undertaken to assess the issue in meaningful ways. Shifts associated with climate change are likely to be relatively slow, easily masked by short-term (i.e., interannual or decadal) variation in climate or fish distributions (e.g., Durance & Ormerod, 2009; Copeland & Meyer, 2011), will interact with other global change stressors (Xenopoulos *et al.*, 2005; Vorosmarty *et al.*, 2010; Wenger *et al.*, 2011), and could require decades to describe accurately (Thomas *et al.*, 2006; Jackson *et al.*, 2009; Sunday *et al.*, 2012). Second, changes will typically occur near the historical boundaries of distributions, in habitats that are of marginal quality, and which are rarely monitored in ways that accurately describe the location of these boundaries (e.g., Rieman *et al.*, 2006; Tingley & Beissinger, 2009). Third, most bioclimatic model forecasts are based on predictions that are either untestable or imprecise (Wiens & Bachelet, 2009). In the former case, some models predict the locations of temperature isotherms and use these as surrogates for biological distributions (e.g., Meisner, 1990; Keleher & Rahel, 1996; Williams *et al.*, 2009). These models do not incorporate geographically referenced biological surveys that can later be resampled to assess possible changes. When biological data are used in bioclimatic models, a general lack of empirical stream temperature measurements usually

requires the use of surrogates like elevation or air temperature that are only correlates of the thermal conditions experienced by stream biotas. This may contribute to considerable error at fine scales, especially in complex mountainous terrain, where factors affecting stream heat budgets often change considerably across short distances (Johnson, 1971; Isaak & Hubert, 2001). As an example of the precision associated with these models, we recently estimated the lower elevation limit of juvenile bull trout across 74 stream populations in the Northwest United States to be 1567 m with a 95% confidence interval of 172 m (Rieman *et al.*, 2007). Assuming a long-term air temperature warming rate of $0.2\text{ }^{\circ}\text{C decade}^{-1}$ and perfect fidelity of bull trout to the isotherm associated with the historic distribution, it would take approximately 50 years before a comparable distribution estimate differed statistically from the current distribution (Calculations S1).

Clearly, better approaches are needed to document the response of stream biotas to climate change if conservation efforts are to be directed most effectively this century. Fundamental to understanding these responses are accurate predictions of the rate at which isotherms are shifting to higher elevations or latitudes near thermally mediated species boundaries. Such predictions set the a priori expectations against which biological patterns should be assessed to test a key assumption in most bioclimatic models – that species distributions are delimited by, and will track through time, a critical temperature isotherm. Previously, Loarie *et al.* (2009) developed an approach for mapping the 'velocity' at which isotherms shift across the Earth's land surfaces in response to climate warming that consists of the ratio between temporal and spatial temperature gradients (i.e., $^{\circ}\text{C yr}^{-1}/^{\circ}\text{C km}^{-1} = \text{km yr}^{-1}$). Here, we generalize Loarie *et al.* (2009) to provide a framework for predicting isotherm shift rates (ISRs) in the Earth's streams and rivers by modifying the calculations to accommodate the distinct properties of these systems, including: (i) more variable spatial temperature gradients, (ii) smaller long-term warming rates, (iii) channel patterns that vary from straight to highly sinuous, and (iv) restrictions on the topographic steepness of streams that most aquatic organisms can access. A set of reference curves and equations are developed that facilitate specific application to many types of streams. Lastly, we also describe the length of time for statistically significant isotherm shifts to occur given that short-term temperature variability will mask warming trends from biotas for extended periods. Implementing the ISR framework on a stream or river requires only easily obtained measurements of temperature and slope and yields several valuable applications that are subsequently discussed.

Materials and methods

ISR calculations

The calculations made by Loarie *et al.* (2009) for terrestrial systems used global climate model representations of contemporary spatial gradients in near surface air temperatures and projections of future warming. By dividing the warming rate ($^{\circ}\text{C yr}^{-1}$) by the spatial temperature gradient ($^{\circ}\text{C km}^{-1}$), the quotient is the rate at which an isotherm moves (km yr^{-1}) at a specific location for a given climate scenario. Global datasets of these input parameters are not available for the Earth's streams and rivers, but can be easily obtained or estimated for individual streams. Four basic measurements are required, the: (i) spatial temperature gradient (i.e., lapse rate) within a stream; (ii) long-term warming rate; (iii) stream slope; and (iv) stream sinuosity, which is relevant in flat streams that have meandering channel patterns.

Deriving an estimate of a stream's lapse rate requires measuring temperatures concurrently at multiple sites along the profile of a stream such that a sufficient elevation (or latitude) range is covered and the spatial temperature gradient is apparent. These measurements are easily obtained using modern temperature sensors (Isaak *et al.*, 2010a; Isaak & Horan, 2011) and Fig. 1a shows example temperature gradients from mountain streams in central Idaho, USA. Measurements often need to be spaced over several miles in steep streams and longer distances in flatter streams to observe meaningful temperature differences. The duration of measurements at individual sites should encompass at least

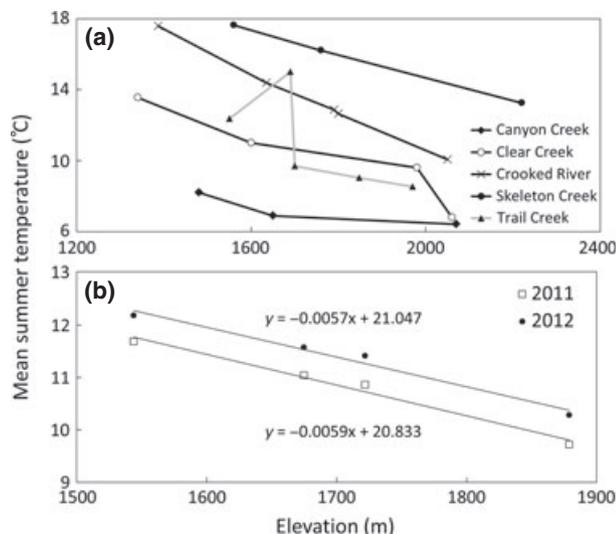


Fig. 1 Examples of temperature gradients in mountain streams from central Idaho, USA. Heterogeneity among streams is apparent because heat budget parameters change along the length of streams in association with riparian shade conditions, groundwater contributions, and other factors (a). Lapse rates within streams are relatively constant across years and changes in temperature because sites experience common changes in climatic conditions (b).

1 month during that part of the year which is thermally limiting, but longer term measurements (up to 12 months) may also be useful for calculating annual averages if the limiting period is unknown. Measurement periods longer than 1 year are not necessary because lapse rates remain relatively constant across years as temperatures change (Fig. 1b). Lacking direct measurements for estimating the lapse rate in a stream, data from nearby streams or the global average air temperature lapse rate of $0.6\ ^{\circ}\text{C}/100\ \text{m}$ elevation (Dodson & Marks, 1997; Rolland, 2003) might be used as first approximations.

The second measurement required is the long-term warming rate of a stream. These estimates may sometimes be obtained from monitoring records, but those long enough to describe anthropogenic climate change (i.e., 30–50 years) are rare because streams have been poorly monitored compared with terrestrial systems. Where long-term records are available, they are often associated with flow alterations (e.g., dams, water diversions) or urban environments that confound warming trends associated with climate change (e.g., Kaushal *et al.*, 2010). To estimate warming rates at less impacted sites, it may be necessary to use published values (e.g., Webb & Nobilis, 2007; Isaak *et al.*, 2012a) or to reconstruct trends by linking short-term stream temperature records to long-term air temperature and flow data available near many stream locations (e.g., Moatar & Gailhard, 2006; Isaak *et al.*, 2010b; van Vliet *et al.*, 2010). A last option would be the use of long-term air temperature trends as surrogates for stream temperature trends after applying a scaling factor of $0.4\text{--}0.8\ ^{\circ}\text{C}/^{\circ}\text{C}$ to account for the slower warming rates typical of streams (Morrill *et al.*, 2005; Hari *et al.*, 2006; Isaak *et al.*, 2012a).

The last two measurements needed for a stream ISR calculation, stream slope and sinuosity, may be measured in the field (Isaak *et al.*, 1999), obtained from digital elevation models in a geographic information system (Neeson *et al.*, 2008), or values used from existing hydrocoverage sources like the US Geological Survey 1 : 100 000-scale National Hydrologic Coverage (Cooter *et al.*, 2010). The latter two options are sufficiently precise and enable calculations to be made rapidly across an extended length of stream or river network as may often be desired.

The first step in a stream ISR calculation determines the vertical displacement (a) of an isotherm associated with a long-term warming rate (Fig. 2) by dividing the stream lapse rate into the warming rate as:

$$a = \frac{^{\circ}\text{C}/\text{decade}}{^{\circ}\text{C}/100\text{m}} \times 100 \quad (1)$$

Equation (1) yields values in vertical meters per decade (Table S1 summarizes values across ranges of lapse rates and warming rates) and the calculation is equivalent to Loarie *et al.* (2009) except that stream temperatures are used rather than air temperatures and the temperature gradient occurs relative to elevation rather than latitude or horizontal distance (e.g., Jump *et al.*, 2009). We focus on elevational gradients because these are readily discernible in steeper streams and these streams are often less altered by other anthropogenic factors that may confound climate assessments. However, ISR predictions can be made in very flat streams (i.e., $<0.1\%$ slope)

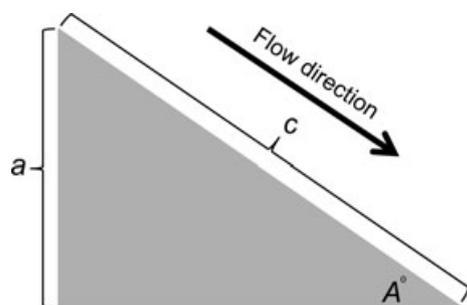


Fig. 2 Schematic representing a stream isotherm shift as parts of a right triangle. The short side of the triangle (*a*) represents the vertical elevation displacement of an isotherm from a temperature increase. The hypotenuse (*c*) represents the stream distance, an isotherm travels in association with a temperature increase and is calculated using the trigonometric relationship for a right triangle based on measurements of stream slope (*A*), lapse rate, and long-term warming rate. See text for more details.

using spatial temperature gradients expressed in horizontal distance or latitude as the denominator in Eqn (1).

The second step in the ISR calculation translates *a* to the distance in meters per decade along a stream using the trigonometric relationship for a right triangle, wherein the short side of the triangle is *a*, the hypotenuse represents the stream distance *c*, and stream slope (*A*) is expressed in degrees as (Fig. 2):

$$c = \frac{a}{\sin A^\circ} \tag{2}$$

Stream ecologists usually express stream slope as % (rise over run times 100) rather than degrees. This conversion is made as:

$$A^\circ = \tan^{-1} \left(\frac{\text{slope}\%}{100} \right) \tag{3}$$

ISR variability analysis

Short-term variation in stream temperatures at interannual and decadal timescales is large relative to the small temperature increases associated with climate change over short periods. This variability will partially mask isotherm shifts and cause population responses to lag temperature trends in ways that depend on species generation times and climate sensitivities (Araujo & Pearson, 2005; Jackson *et al.*, 2009). Therefore, understanding how short-term variability scales relative to long-term climate trends is necessary for designing biological monitoring efforts that conclusively test ISR predictions and climate warming effects on species distributions. Reasoning that a distribution shift would not occur before an isotherm had moved a statistically significant distance, we developed a series of curves that described the time required for such a movement as a function of the ISR and the amount of interannual variability in temperature. The first step in these calculations estimated how far an isotherm must move before it was in a statistically different location. This was done by calculating 95% confidence intervals in °C based on the standard deviation (SD) of interannual temperature variation observed in monitoring records (e.g., Kaushal *et al.*, 2010; Isaak *et al.*, 2012a). Confidence interval widths were translated to distances along streams varying in slope and lapse rates using Eqns (1) and (2). These distances were then divided by ISR values to describe the time required for significant isotherm shifts to occur.

Results

ISR characteristics

Simple power curves describing the relationship between ISR values calculated from Eqns (1)–(3) and stream slope are summarized in Table 1 (an example ISR calculation is provided in the supplementary materials, Calculations S2). Figure 3 plots two sets of these

Table 1 Reference equations for predicting stream ISRs (km decade⁻¹) from slope (*x*) for different combinations of lapse rates and long-term warming rates. Slope values are entered as %'s. In streams with meandering channel patterns, ISRs should be multiplied by the sinuosity ratio (thalweg length/straight line length) for greater accuracy

Stream lapse rate (°C/100 m)	Stream warming rate (°C decade ⁻¹)				
	0.1	0.2	0.3	0.4	0.5
0.1	$y = 10.0x^{-1}$	$y = 20.0x^{-1}$	$y = 30.0x^{-1}$	$y = 40.0x^{-1}$	$y = 50.0x^{-1}$
0.2	$y = 5.00x^{-1}$	$y = 10.0x^{-1}$	$y = 15.0x^{-1}$	$y = 20.0x^{-1}$	$y = 25.0x^{-1}$
0.3	$y = 3.30x^{-1}$	$y = 6.61x^{-1}$	$y = 10.0x^{-1}$	$y = 13.2x^{-1}$	$y = 16.5x^{-1}$
0.4	$y = 2.50x^{-1}$	$y = 5.00x^{-1}$	$y = 7.50x^{-1}$	$y = 10.0x^{-1}$	$y = 12.5x^{-1}$
0.5	$y = 2.00x^{-1}$	$y = 4.00x^{-1}$	$y = 6.00x^{-1}$	$y = 8.00x^{-1}$	$y = 10.0x^{-1}$
0.6	$y = 1.67x^{-1}$	$y = 3.34x^{-1}$	$y = 5.00x^{-1}$	$y = 6.67x^{-1}$	$y = 8.34x^{-1}$
0.7	$y = 1.43x^{-1}$	$y = 2.86x^{-1}$	$y = 4.29x^{-1}$	$y = 5.73x^{-1}$	$y = 7.16x^{-1}$
0.8	$y = 1.25x^{-1}$	$y = 2.50x^{-1}$	$y = 3.75x^{-1}$	$y = 5.00x^{-1}$	$y = 6.25x^{-1}$
0.9	$y = 1.11x^{-1}$	$y = 2.22x^{-1}$	$y = 3.33x^{-1}$	$y = 4.44x^{-1}$	$y = 5.55x^{-1}$
1.0	$y = 1.00x^{-1}$	$y = 2.00x^{-1}$	$y = 3.00x^{-1}$	$y = 4.00x^{-1}$	$y = 5.00x^{-1}$

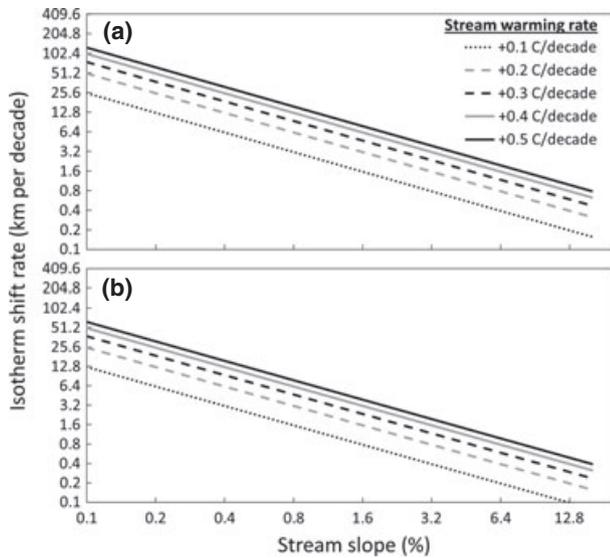


Fig. 3 Stream ISRs relative to slope for different long-term warming rates in streams with lapse rates of (a) 0.4 °C/100 m and (b) 0.8 °C/100 m. In streams with meandering channel patterns, ISR values should be multiplied by the sinuosity ratio (thalweg length/straight line length) for greater accuracy.

power curves on log scales for streams with lapse rates of 0.4 °C/100 m and 0.8 °C/100 m across a range of long-term warming rates. Several things about the ISR values depicted in these curves are noteworthy. First, stream slope has a dominant effect on ISRs, which vary by almost two orders of magnitude across a slope range from 0.1 to 13% that encompasses most streams accessible to fish and amphibians. Second, the long-term warming rate has an important effect on ISRs, but it scales linearly so that a doubling of the warming rate translates to a doubling of the ISR. Third, lapse rate is inversely related to ISR as evidenced by the systematic shift lower in the set of curves for streams with lapse rates of 0.8 °C/100 m (Fig. 3b).

The curves indicate that isotherm shifts would occur at 0.13–1.3 km decade⁻¹ in steep streams (2–10% slope) and 1.3–25 km decade⁻¹ in flat streams (0.1–1% slope) for lapse rates of 0.8 °C/100 m and long-term warming rates of 0.1–0.2 °C decade⁻¹. Isotherm shifts would occur at twice these rates in streams with lapse rates of 0.4 °C/100 m subject to similar warming. These predictions are conservative in streams where channel patterns meander and ISRs need to be multiplied by the sinuosity ratio (stream distance/straight line distance between stream endpoints) to account for the additional stream distance.

ISR applications

One use of the ISR calculations is to estimate the total distance isotherms shift in association with historic or future warming scenarios. These estimates can be made

at many scales, including individual streams, river networks, or even more broadly. It is, for example, straightforward to translate the often cited global average air temperature increase of 0.6 °C during the 20th Century (i.e., 0.06 °C decade⁻¹; IPCC, 2007) to a stream isotherm shift with some basic assumptions. If we apply the scaling factor of 0.6 °C/°C of air temperature increase to account for the slower warming rates of streams, and assume a consistent lapse rate among streams of 0.8 °C/100 m, the general prediction can be made that isotherms shifted 1.5–43 km during the previous century in streams ranging in slope from 0.1 to 3%. Under the same assumptions, but using a projected air temperature increase of 2 °C (i.e., a midrange IPCC (2007) warming scenario), isotherms can be predicted to shift another 5–143 km during the first five decades of the 21st Century.

Another use of the ISR calculations is mapping the velocity of isotherms (*sensu* Loarie *et al.*, 2009) within streams across river networks to portray spatial differences in shift rates. To illustrate, we map velocities across a 2500 km river network in a mountainous area of central Idaho, USA using the stream slope values associated with the US Geological Survey 1 : 100 000-scale National Hydrologic Coverage. The simplifying assumption was made that all streams in the basin had lapse rates of 0.4 °C/100 m and long-term warming rates of 0.2 °C decade⁻¹; values which approximate published estimates for streams in the region. The average ISR for streams in this network under these conditions was predicted to be 4.2 km decade⁻¹, but values varied by more than an order of magnitude (<1 to >16 km decade⁻¹; Fig. 4). Mainstem rivers and other streams with low slopes were predicted to have higher ISRs than steeper headwater streams, which will be a common pattern due to the concavity of most longitudinal stream profiles.

ISR variability analysis

The time required for a significant isotherm shift to occur was negatively related to ISR and positively related to interannual temperature variability (Fig. 5, Calculations S3). Moreover, streams with smaller lapse rates or lower slopes required longer periods for significant isotherm shifts. These differences were largely negated, however, if realistic ISR values associated with long-term warming rates of 0.1–0.3 °C decade⁻¹ (shaded area of Fig. 5) were used to constrain the range of values considered. A minimum time for a statistically significant isotherm shift to occur then is one decade under the best conditions of low interannual variability (SD = 0.5) and steep slope (Fig. 5b and d). However, greater thermal variability is typical of most streams, so two to four decades is a more general result.

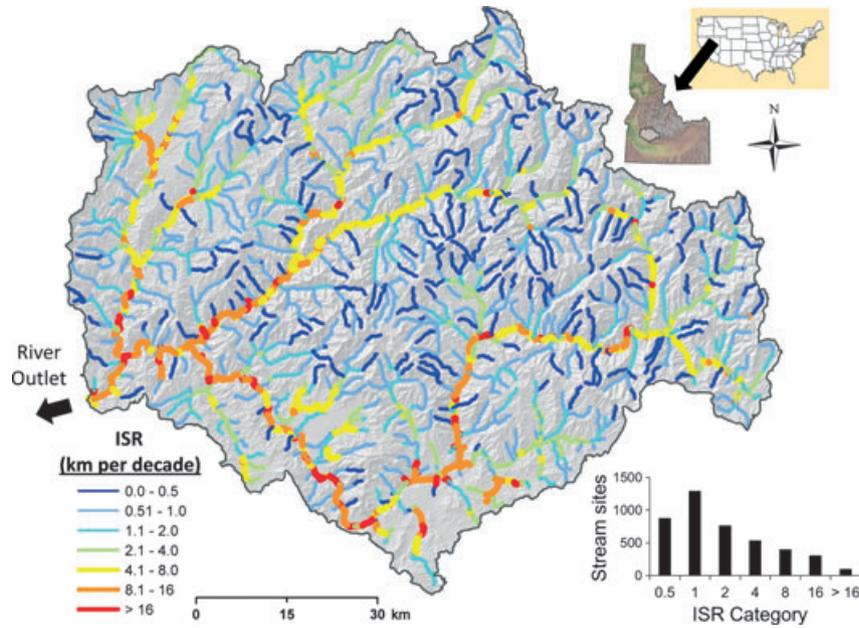


Fig. 4 Climate velocity map for the Boise River network in central Idaho. Isotherm shift rates were calculated assuming a long-term warming rate of $0.2\text{ }^{\circ}\text{C decade}^{-1}$ and stream lapse rate of $0.4\text{ }^{\circ}\text{C}/100\text{ m}$. The histogram summarizes the number of stream segments within each ISR category.

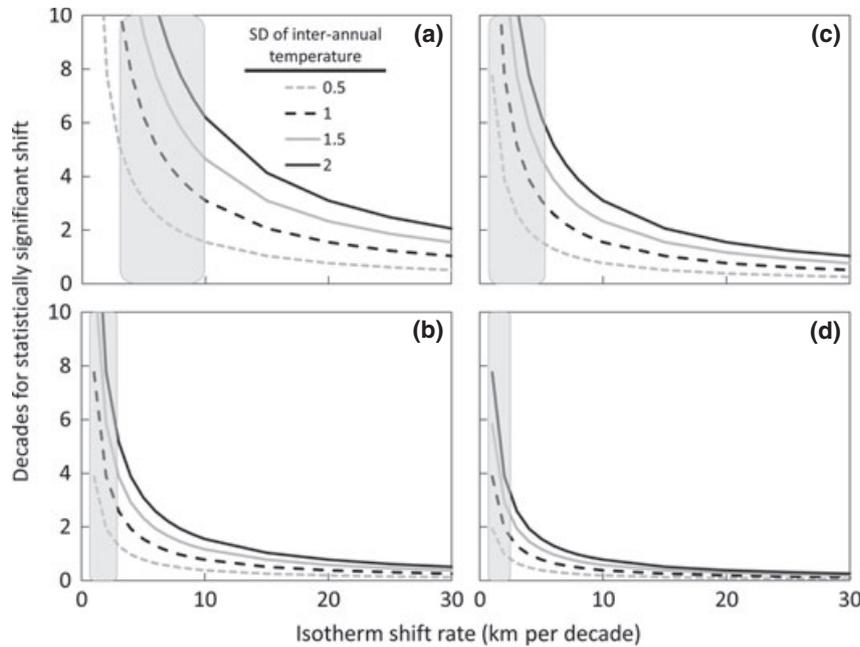


Fig. 5 Time required for a statistically significant isotherm shift to occur based on ISR values and interannual temperature variation. Curves depict relationships for streams with lapse rates and slopes of of: (a) $0.4\text{ }^{\circ}\text{C}/100\text{ m}$ and 1%; (b) $0.4\text{ }^{\circ}\text{C}/100\text{ m}$ and 4%; (c) $0.8\text{ }^{\circ}\text{C}/100\text{ m}$ and 1%; and (d) $0.8\text{ }^{\circ}\text{C}/100\text{ m}$ and 4%. Shaded portions of the curves highlight ranges for realistic ISRs based on long-term warming rates of $0.1\text{ }^{\circ}\text{C}-0.3\text{ }^{\circ}\text{C decade}^{-1}$.

Discussion

A variety of useful predictions can be made with the ISR framework to better anticipate, describe, and study how warming from climate change may affect stream

thermal conditions and biotas this century. Most sobering of these predictions are that the isotherm shifts which occurred during the entirety of the 20th Century will easily be exceeded in the first half of the 21st Century under current midrange projections for global

warming. Changes of this magnitude imply ISRs that are sixfold faster than the average 20th-Century ISR and populations near current distributional boundaries must adjust accordingly. Of course, a range of future warming scenarios exists for streams that is as wide as the range for air temperatures (IPCC, 2007), but recent warming trends and greenhouse gas emissions increasingly suggest that the Earth's climate is on a high-end warming trajectory (Pittock, 2006; Raupach *et al.*, 2007). Moreover, warming from climate change will be exacerbated in many streams by warming from urbanization and water development as human populations continue to expand (Xenopoulos *et al.*, 2005; Kaushal *et al.*, 2010; Vorosmarty *et al.*, 2010), so major thermal disruptions of stream communities appear likely this century.

The greatest thermal threats to biodiversity may be in the flattest streams, which generally include the largest and most biodiverse rivers within a region and globally. Also highly vulnerable are biotas in heavily fragmented streams with east-west orientations and those species with limited mobility and restricted ranges (*sensu* Angermeier, 1995). The dominant effect of slope on ISRs means that biotas in steeper streams will be less susceptible to thermal habitat shifts associated with temperature increases, although other aspects of climate change related to hydrology and disturbance regimes may still affect these populations (Stewart, 2009; Rieman & Isaak, 2010). One exception regarding thermal effects in steep streams occurs where small populations are already constrained by warm temperatures and lack elevational refugia due to upstream limits imposed by small stream size or steep slopes that preclude dispersal. These headwater populations are often already of conservation concern (Rieman *et al.*, 2007; Fausch *et al.*, 2009; Almodóvar *et al.* 2012) and those with less than 5 km of habitat could be particularly vulnerable to extirpation by midcentury.

Our work makes the general assumption that distributions of ectothermic stream organisms will track critical isotherms, but is based largely on observed spatial patterns rather than biological shifts. Metabolic theory (Brown *et al.*, 2004; Pörtner & Farrell, 2008) provides a strong mechanistic basis for why such shifts are anticipated, but predictions ultimately need to be tested with empirical data. Biological and stream temperature monitoring will be required to better understand how gradual warming trends are integrated by populations and translated to range or distribution shifts (Araujo & Pearson, 2005; Jackson *et al.*, 2009). Time lags between environmental trends and biological responses are likely (Morris *et al.*, 2008; Sunday *et al.*, 2012) and isotherm shifts may ultimately differ from the rates at which distributions change because multiple factors mediate population boundaries (Guo *et al.*, 2005; Weng-

er *et al.*, 2011). Nonetheless, Loarie *et al.*'s (2009) estimate that isotherms in Earth's terrestrial systems will shift 4.2 km decade⁻¹ under the A1B warming scenario (IPCC, 2007) is close to Parmesan & Yohe (2003) estimate that distributions of many terrestrial species are shifting poleward at 6.1 km decade⁻¹. More recent studies also find concordance between long-term ISRs and biological responses (e.g., Wilson *et al.*, 2005; Moritz *et al.*, 2008; Sunday *et al.*, 2012), but the details for streams have yet to be resolved.

A strength of the ISR framework is that it can be used to make precise local predictions that are paired with biological surveys to test these predictions. Ideally, such efforts would consist of dense temperature and biological survey sites spread along stream profiles with obvious temperature gradients that encompassed thermally mediated population boundaries (e.g., Rieman *et al.*, 2006). A series of these 'sentinel streams' might be replicated across a river network (e.g., Isaak *et al.*, 2009; Clews *et al.*, 2010) to increase the statistical power for trend detection, ensure patterns detected in one stream were not idiosyncratic to that location, and refine understanding of interacting and potentially confounding factors (e.g., Durance & Ormerod, 2009). Once consistent sets of baseline data were established, quantifying shifts in biological distributions, thermal associations, or measures of population performance would only require periodic site resurveys and comparisons (Tingley & Beissinger, 2009). If standardized sampling protocols were developed, various conservation interests and concerned stakeholders might even be engaged in formalized, distributed monitoring networks that tracked the status and trends of species throughout their ranges (e.g., Craine *et al.*, 2007).

Results of the variability analysis suggest that the best streams to detect climate-related trends have large ISRs and small interannual thermal variability. Even under ideal conditions, however, it would take at least a decade and usually much longer for isotherms to shift statistically significant distances at current rates of warming (e.g., Webb & Nobilis, 2007; Kaushal *et al.*, 2010; Isaak *et al.*, 2012a). Moreover, biological shifts would be expected to lag any discernible temperature trends, so new monitoring efforts are unlikely to yield estimates of spatial shifts in time for near-term conservation planning. Monitoring efforts that built on preexisting data, however, by resurveying historical sites along stream profiles with thermally mediated population boundaries, could be especially useful (e.g., Adams *et al.*, 2002; Hitt & Roberts, 2012). Many early stream profile studies meet these criteria (e.g., Vincent & Miller, 1969; Gard & Flittner, 1974; Platts, 1979) and provide fertile grounds for reexamination now that sev-

eral decades have elapsed during which species distributions may have shifted. Another option is to resample large numbers of historic sites (i.e., 100's) across many streams within a region and to then examine changes in a species' site occupancy relative to local climatic conditions (e.g., Beever *et al.*, 2010). If climate change is causing range contractions in some species, site extirpation should exceed colonizations and be skewed toward warm sites within a species' thermal niche. Large databases composed of 1000's of fish, macroinvertebrate, and amphibian surveys exist and could be used in these assessments (e.g., Buisson & Grenouillet, 2009; Wenger *et al.*, 2011). Monitoring that involves historical resurveys has to address issues of imprecise spatial locations, differences in sampling techniques, and changes caused by nonclimate factors (e.g., invasive species, habitat degradation; Magurran *et al.*, 2010), but also has the potential to yield estimates of biological shifts within a few years.

As empirical estimates of temperature effects on stream biotas become more common, this information can be used to validate and improve the predictions from bioclimatic models. Better accuracy would in turn improve the quality of climate vulnerability assessments and should lend itself to highlighting specific populations at risk and areas within stream networks that might warrant prioritization. This level of resolution is ultimately needed to design effective conservation networks for sensitive species within landscapes and river basins (Vos *et al.*, 2008; Williams *et al.*, 2011; Isaak *et al.*, 2012b). Moreover, when bioclimatic models are underpinned by observed biological changes, rather than being simple extrapolations of static historical patterns, it could strengthen resolve for implementing conservation actions. For species and populations confined to linear networks, removal of barriers or assisted migrations are two obvious options (Peterson *et al.*, 2008; Kostyack *et al.*, 2011), but many other actions are possible (Rieman & Isaak, 2010; Wilby *et al.*, 2010). Key to effective conservation this century will be choosing among these actions and implementing them in the best places because conservation needs will greatly exceed available resources (Wiens & Bachelet, 2009; Isaak *et al.*, 2012b).

In our view, the question is not whether, but how fast, stream biotas are shifting and sometimes being extirpated, by temperature increases associated with global climate change. Other anthropogenic and natural factors will contribute to, or ameliorate, these trends, but for ectotherms constrained to linear networks, temperature is destiny in a warming world. Several studies have recently documented multidecadal decreases in trout abundance in warm streams or lakes near species' southern range margins (Hari *et al.*, 2006; Winfield *et al.*, 2010; Almodóvar *et al.*, 2012).

Other studies have implicated factors associated with climate change in the extirpation of stream macroinvertebrate populations (Durance & Ormerod, 2010) and amphibians (Pounds *et al.*, 2006). These case histories are likely only the initial phase of a much broader global phenomenon that will be documented for the Earth's aquatic ecosystems as climate change continues and monitoring records improve. However, even with the best long-term monitoring efforts, or where seemingly obvious climate-related mass mortality 'events' occur (e.g., Cooke *et al.*, 2004; Doremus & Tarlock, 2008), direct attribution of biological outcomes to temperature increases will be difficult (Durance & Ormerod, 2010; Parmesan *et al.*, 2011). Temperature may be the ultimate cause, but will often interact with other factors like disease, invasive species, or altered trophic ecology to exact its toll (Rahel & Olden, 2008; Woodward *et al.*, 2010). It will be important to develop clearly testable hypotheses, effective monitoring protocols, and rigorous analyses that clarify the role of temperature in alteration of stream communities (e.g., Harper & Peckarsky, 2006; Coleman & Fausch, 2007) and provide insight regarding how effects are translated across biophysical and spatiotemporal scales. The ISR framework presented here is a useful tool for making better predictions at scales relevant to conservation efforts and can help focus research and monitoring to resolve these questions.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Calculations S1. Estimation of the time required for a regional bull trout distribution to shift a statistically significant elevation due to climate warming.

Calculations S2. Example ISR calculation for a stream with 2% slope, a lapse rate of 0.8 °C/100 m, long-term warming rate of 0.1 °C decade⁻¹, and no sinusity adjustment.

Calculations S3. Example variability calculation to determine the number of decades for a statistically significant isotherm shift to occur.

Table S1. Vertical elevation displacement rate (m decade⁻¹) for isotherms associated with different lapse rates and long-term warming rates.

Calculations S1. Estimation of the time required for the regional bull trout distribution as described in Rieman et al. (2007) to shift a statistically significant elevation due to climate warming. A statistically significant shift is defined as that elevational distance wherein the 95% confidence interval (172 m in this case) associated with the historic estimate of the bull trout elevation boundary would no longer overlap the future elevation boundary. It was assumed that the future boundary would be estimated with a similar amount of precision as the historic boundary. The time required for this shift was calculated using a regional air temperature lapse rate of 0.6 °C / 100 m (estimated in Rieman et al. 2007) and assuming a long-term air temperature warming rate of 0.2 °C / decade.

Step 1. Calculate the vertical elevation displacement rate (a) of a temperature isotherm using Equation 1:

$$a = \frac{0.2 \text{ }^\circ\text{C/decade}}{0.6 \text{ }^\circ\text{C}/100\text{m}} \times 100 = 33 \text{ m / decade as summarized in Table S1.}$$

Step 2. Divide the 95% confidence interval for the bull trout elevation boundary by the isotherm displacement rate to determine the time required for a statistically significant shift.

$$\text{Time for significant shift} = \frac{172 \text{ m}}{33 \text{ m/decade}} = 5.2 \text{ decades.}$$

Calculations S2. Example ISR calculation for a stream with 2% slope, a lapse rate of 0.8 °C / 100 m, long-term warming rate of 0.1 °C / decade, and no sinuosity adjustment.

Step 1. Calculate the vertical displacement (a) of a temperature isotherm using Equation 1:

$$a = \frac{0.1 \text{ }^\circ\text{C/decade}}{0.8 \text{ }^\circ\text{C}/100\text{m}} \times 100 = 12.5 \text{ m / decade as summarized in Table S1.}$$

If necessary, convert stream slope % to degrees using Equation 3:

$$A = \tan^{-1}\left(\frac{2\%}{100}\right) = 1.15^\circ$$

Step 2. Translate vertical displacement in Step 1 to distance along stream (c) using Equation 2:

$$c = \frac{12.5 \text{ m/decade}}{\sin 1.15^\circ} = 623 \text{ m / decade. Divide by 1,000 to convert to km / decade as summarized in Fig. 3 curves.}$$

Calculations S3. Example variability calculation to determine the number of decades for a statistically significant isotherm shift to occur. Values are for a stream with an ISR of 5 km/decade, standard deviation (SD) of 1.0 °C based on inter-annual temperature variation, 1% stream slope, and a lapse rate of 0.8 °C / 100 m.

Step 1. Convert stream temperature SD to a 95% confidence interval (here, we assume $n = 10$ years of monitoring effort):

$$95\% \text{ confidence interval} = x \pm 1.96 \left(\frac{\sigma}{\sqrt{n}}\right) = x \pm 1.96 \left(\frac{1.0 \text{ }^\circ\text{C}}{\sqrt{10}}\right) = x \pm 0.62 \text{ }^\circ\text{C}. \text{ Double } 0.62 \text{ }^\circ\text{C} \text{ to obtain the confidence interval width of } 1.24 \text{ }^\circ\text{C}.$$

Step 2. Convert 95% confidence interval to elevation displacement within a stream (a in Fig. 2) based on the lapse rate:

$$a = 1.24 \text{ }^\circ\text{C} \div \frac{0.8 \text{ }^\circ\text{C}}{100 \text{ m}} = 155 \text{ m}$$

Step 3. Translate elevation displacement to distance along a stream (c in Fig. 2) of 1% slope using Equation 2:

$$c = \frac{155 \text{ m}}{\sin 0.573^\circ} = 15,500 \text{ m}. \text{ Divide by } 1,000 \text{ to convert to } 15.5 \text{ kilometers}.$$

Step 4. Convert distance along stream to the number of decades for a statistically significant shift by dividing with the ISR.

$$\text{Time for significant shift} = 15.5 \text{ km} \div \frac{5 \text{ km}}{\text{decade}} = 3.1 \text{ decades as summarized in Fig. 5 curves}.$$

Table S1. Vertical elevation displacement rate (m / decade) for isotherms associated with different lapse rates and long-term warming rates. Values correspond to a in Equation 1 and Fig. 2.

Lapse rate (°C/100 m)	Warming rate (°C/decade)				
	0.1	0.2	0.3	0.4	0.5
0.1	100	200	300	400	500
0.2	50	100	150	200	250
0.3	33	67	100	133	167
0.4	25	50	75	100	125
0.5	20	40	60	80	100
0.6	17	33	50	67	83
0.7	14	29	43	57	71
0.8	13	25	38	50	63
0.9	11	22	33	44	56
1.0	10	20	30	40	50