Check for updates

Received: 9 February 2021 | Revised: 4 April 2021 | Accepted: 4 April 2021

DOI: 10.1002/eco.2295

REVIEW ARTICLE

WILEY

An ecohydrological typology for thermal refuges in streams and rivers

Christopher J. Sullivan[1] | Jason C. Vokoun[1] | Ashley M. Helton[1] | Martin A. Briggs[2] | Barret L. Kurylyk[3]

[1]Department of Natural Resources and the Environment, Wildlife and Fisheries Conservation Center, University of Connecticut, 1376 Storrs Road, Storrs, Connecticut, 06268, USA

[2]Earth System Processes Division, Hydrogeophysics Branch, U.S. Geological Survey, 11 Sherman Place, Storrs, Connecticut, 06268, USA

[3]Department of Civil and Resource Engineering, Dalhousie University, 1360 Barrington Street, Halifax, Nova Scotia, B3H 4R2, Canada

Correspondence
Christopher J. Sullivan, Department of Natural Resources and the Environment, Wildlife and Fisheries Conservation Center, University of Connecticut, 1376 Storrs Road. Storrs, CT 06268, USA.
Email: cjbsullivan2@gmail.com

Funding information
National Science Foundation, Division of Earth Sciences, Grant/Award Number: 1824820; Storrs Agricultural Experiment Station, Hatch Act, Grant/Award Number: CONS01039; US Geological Survey Toxic Substances Hydrology Program; NSERC Discovery Grant, Grant/Award Number: RGPIN-2018-05420

Abstract

Thermal refuges are thermally distinct riverscape features used by aquatic organisms during unfavourable thermal events, facilitating resilience in marginal environments. However, the thermal refuge concept is nebulous, and the often interchangeable use of the term 'thermal refugia' creates additional ambiguity. We argue that lexical differences resulting from divergent scholarly trainings hinder holistic understanding of thermal refuges; thus, existing studies would benefit from a structured framework for thermal refuge conceptualization. Herein, we articulate an ecohydrological typology for defining and characterizing thermal refuges in streams and rivers by identifying key hydrological and thermal characteristics and variations in ecological function described in the literature. We use concepts that are easily definable, measurable and transferable across disciplines, riverscapes and species to discriminate among thermal refuge types. Future work can use our typology as a basis for more informed interdisciplinary discussion and interpretation of thermal refuges' role in riverscapes through more hypothesis-driven research and conservation-focused management.

KEYWORDS
climate change, cold-water or warm-water patch, lotic ecosystems, thermal refuge, thermal refugia, typology

1 | INTRODUCTION

The term 'thermal refuge' represents a melting pot of hydrological, biological and ecological ideas in lotic ecosystems (i.e., streams and rivers). Fundamentally, 'refuge' refers to an area that offers an organism some protection from a temporary stressor in their natural habitat (Calow, 1999; Walker, 1988). Contemporary ecological definitions of a refuge are expanded and often context dependent. In streams and rivers, a 'thermal refuge' refers to an area used by an organism for spatiotemporal protection from temperature extremes prevalent throughout the system. There are persuasive reasons to believe that stream and river ecosystems are among the most sensitive systems to climate change (Jonsson & Jonsson, 2009; Pilgrim et al., 1998; Webb et al., 2008), where observational records already point towards higher but more heterogeneous temperature mosaics throughout riverscapes (Isaak et al., 2012; Kanno et al., 2014). Poikilotherms, organisms that rely on behaviour to regulate their body temperatures, compose most aquatic community biomass in streams and rivers. Thus, thermal refuges (e.g., areas of groundwater discharge, deep pools or groundwater-dominated tributary confluences; Bilby, 1984; Kurylyk, MacQuarrie, Linnansaari, et al., 2015) will play a pivotal role in protecting cool-water or cold-water adapted poikilotherms against

This is an open access article under the terms of the Creative Commons Attribution-NonCommercial License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited and is not used for commercial purposes.
© 2021 The Authors. *Ecohydrology* published by John Wiley & Sons Ltd.

higher temperatures (Ebersole et al., 2003a; Hertz et al., 1993), particularly in marginal habitats near a species' geographic range boundary (e.g., Lynch et al., 2014). Much research is directed towards understanding cool-water and cold-water refuges during high temperatures (Keefer et al., 2018; Power et al., 1999; Selwood et al., 2019), but refuges can also be warm-water areas (Buckingham et al., 1999; Peterson & Rabeni, 1996), depending upon season, geographic location and species. The gradual rise in the use of 'thermal refuge' in peer-reviewed literature and an increasingly diverse community of journals publishing articles using this term indicate an expanding interest in studying their structure, function and sensitivity to a changing climate (Figure 1).

Advancing understanding of thermal refuge phenomena requires a basic understanding of their fundamental defining characteristics, which must cross traditional disciplinary boundaries. Scientists of different training and background are concurrently developing new insights into the drivers, attributes and uses of thermal refuges. Although their recognition and identification are rapidly expanding, ambiguity persists. Hydrologists customarily consider a thermal refuge to be a thermal anomaly (i.e., area where water temperature deviates from ambient stream temperature), defined and created by the (incomplete) mixing of thermally and hydrologically distinct flows or thermal stratification, often with the tacit presumption of poikilotherm use. In contrast, biologists and ecologists define a thermal refuge as a cold-water or warm-water patch that is preferentially inhabited by an organism (i.e., biologically relevant thermal anomaly) when temperatures elsewhere are unfavourable, frequently giving less consideration to physical drivers that create the temperature deviation. Furthermore, researchers across disciplines often study thermal refuges in the context of climate change and, confusingly, refer to 'thermal refuges' as 'thermal refugia', a term that refers to regions important for the cross-generational survival of a population or metapopulation (Calow, 1999; Walker, 1988). As such, there is a disconnect forming across disciplinary knowledge bases that is limiting

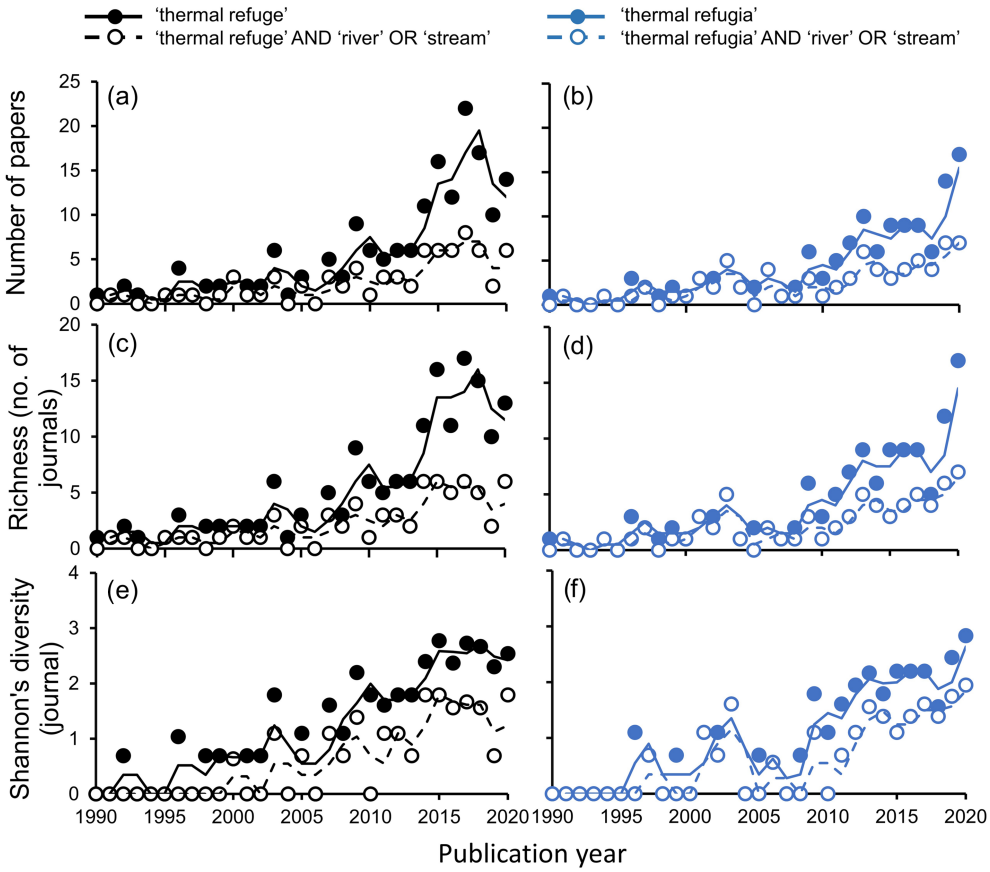

FIGURE 1 Trends in the use of 'thermal refuge' in peer-reviewed literature through time (source: Scopus). The number of articles that use the keyword 'thermal refuge' has increased over time, and a more diverse community of journals are publishing articles that use these terms (panels a, c, and e); only recently do we see an increase in their use in stream and river studies. We queried peer-reviewed articles labelled with the subject area 'agricultural and biological sciences' or 'environmental science' using Scopus (Elsevier B.V.) between 1985 and 2020 (data to 11 March 2021). We sought articles with the terms 'thermal refuge' or 'thermal refuge AND river OR stream' in the abstract, assuming that abstracts will include key terms used for indexing databases; we also searched for articles with the terms 'thermal refugia' or 'thermal refugia AND river OR stream' because 'refuge' and 'refugia' are often used synonymously (see text for details); we include these results in panels b, d, and f. In total, we queried individual 145 peer-reviewed articles, but note that some papers were queried in both literature searches. We used moving average trend lines to identify trends

the advancement of a holistic understanding of thermal refuges in streams and rivers. Defining, characterizing and understanding thermal refuges will become increasingly important for their conservation and preservation (intertwined with the organisms that use them) as climate change progresses. Interdisciplinary collaborations are a prerequisite for successful advancements; thus, a semantically and conceptually clearer lexicon for thermal refuges is needed.

In this article, we present a cross-disciplinary typology for identifying and characterizing thermal refuges. Our typology addresses the persistent ambiguity in the published literature, provides a basis for coordinated advancement in scientific knowledge across disciplines and informs river conservation and management. We have divided this task into three main components. First, we present an ecohydrological typology for cold-water or warm-water patches and thermal refuges in streams and rivers. We briefly review the localized physical processes that create cold-water or warm-water patches and their potential roles in providing refuge for poikilotherms, drawing on relevant interactions between hydrological and ecological processes to justify the typology components. We clarify that both cold-water and warm-water patches and thermal refuges are subsets of thermal anomalies where the temperature departure is of biological or ecological significance; however, a 'thermal refuge' only refers to areas known to be preferentially used by poikilotherms for thermal stress avoidance. Second, we evaluate the terms used to refer to thermal refuges in streams and rivers and how our typology can address inconsistencies in their use to improve interdisciplinary communication. In so doing, we hope to discourage the indiscriminate use of the singular term 'thermal refugium' (plural: refugia) as a substitute for 'thermal refuge'. Third, we present a conceptual model describing the likelihood of thermal refuge use by poikilotherms, providing researchers a tool for developing testable hypotheses that can drive future research and hopefully transfer knowledge to applied stream management. Because much of the peer-reviewed literature focuses on thermal refuges during heat stress (summer), our typology and conceptual model focus on cool-water and cold-water areas, but we suggest that both can extend to characterize warm-water thermal refuges.

2 | AN ECOHYDROLOGICAL TYPOLOGY

Our typology conceptually combines 'foundational' knowledge (i.e., cold-water or warm-water source and potential poikilotherm use) with information of relative size and temperature dynamics of the cold-water or warm-water area to describe, differentiate and define cold-water or warm-water patches and thermal refuges. Because of the physical heterogeneity of cold-water or warm-water patches and thermal refuges (Dugdale et al., 2013) and the variation in their descriptions in the literature (Table 1), we are inclusive in our determination of what features to use to discriminate various types or classes of patches and refuges. We suggest characterizing cold-water or warm-water patches or thermal refuges based on four criteria (Figure 2): (a) *physical controls*, (b) the *thermal regime* relative to main channel temperatures, (c) the *temperature threshold definition* used and (d) *poikilotherm use*. Each criterion applies to concepts that are easily definable and measurable. More importantly, the criteria are transferable across disciplines and rely on both hydrological (physical descriptors and thermal attributes) and ecological (specific poikilotherm requirements and use) methods. While the typology perhaps implies sequencing (e.g., physical controls must be defined before evaluating poikilotherm use), in most cases, the characterization will be asynchronous: some characterization criteria can be determined using instantaneous information (e.g., visual of fish in refuge), whereas other criteria must be determined using information collected over a period and analysed.

We recognize that both cold-water and warm-water patches and their use by poikilotherms occur along a continuum and vary spatiotemporally and that logistical or technical constraints can limit thorough investigations into these areas. It is, therefore, not always likely that a manager or researcher will have the opportunity to evaluate each of the four criteria proposed herein. However, our purpose here is to propose a typology that encourages a clearer and more thorough articulation of the distinctness of specific types of cold-water and warm-water patches and thermal refuges and encourages consideration of hydrological, biological and ecological aspects of patterns and processes. We elaborate on the four criteria in the following sections.

2.1 | Physical controls on cold-water or warm-water patches

Cold-water or warm-water patches arise due to temperature differences between converging hydrologic flows or layering of warm and cold waters, which are generally a result of distinct hydrologic and atmospheric processes. For example, tributaries discharging into larger streams or rivers may be markedly colder or warmer (depending on season and geographic location) due to different energy balances arising from their distinct channel geometries (width to depth ratios), source elevation, riparian shading, channel residence time and groundwater influence (Caissie, 2006). Also, the relatively stable annual thermal regimes of deeper groundwater can cause discharge from seeps and springs to be colder than the ambient surface water in the summer and warmer in the winter (e.g., Bilby, 1984; Peterson & Rabeni, 1996; Stanford & Ward, 1993), though shallow groundwater may more closely track seasonal temperature variation (Briggs, Johnson, et al., 2018; Hare et al., 2021). Smaller cold-water or warm-water patches can be formed by groundwater upwellings or interstitial flow, side channels or lateral springs or seeps that occur along streambanks or at the intersection of floodplains and hillslope groundwater systems (see Dugdale et al., 2013, or Ebersole et al., 2003a, for descriptions). The confluence zone of groundwater-dominated tributaries with other streams or rivers (Baird & Krueger, 2003; Ebersole et al., 2001; Mejia et al., 2020; Torgersen et al., 2012) and thermally stratified deep pools (Matthews & Berg, 1997; Tate et al., 2007) can also create larger cold-water or warm-water patches. In general, thermal patches

TABLE 1 General terms used to describe cold-water or warm-water patches and thermal refuges in streams and rivers

Term	Definition	Interchangeably used terms	Select references	Examples of definitions
Cold-water patch	A discrete area of water temperatures cooler (2–10°C) than ambient streamflow immediately upstream	Cool water area, cold pool, stratified pool	Bilby (1984); Ebersole et al. (2003a, 2003b); Nielsen et al. (1994); Ozaki (1988)	'Each reach was surveyed for the presence of discrete areas of colder water, hereafter "cold water patches," that were defined by the occurrence of water at least 3°C colder than the adjacent ambient stream-flow (after Ozaki, 1988) and at least 0.5 m^2 surface area' (Ebersole et al., 2003a: p. 357).
Thermal refuge	A cold-water patch that is used by poikilotherm avoiding higher temperatures	Cold-water refuge, ambient refuge, fish refuge	Berman and Quinn (1991); Brewitt and Danner (2014); Brewitt et al. (2017); Dugdale et al. (2013); Frechette et al. (2018); George et al. (2016); Greer et al. (2019); Kaya et al. (1977); Mejia et al. (2020); Peterson and Rabeni (1996); Snyder et al. (2020); Torgersen et al. (2012)	'Thermal refuges, areas that provide physiological refuge from stressful temperatures, are receiving increasing attention from both ecologists and managers' (Brewitt & Danner, 2014: pp. 1–2).
Physiological refuge	A patch of water with temperatures below a biologically critical threshold (rather than a thermal difference from main channel)		Daigle et al. (2015); Greer et al. (2019); Mejia et al. (2020)	'We use a 21°C criteria as a threshold for cold water preferences of juvenile steelhead and identify all areas within the confluences with temperatures below 21°C as "physiological microrefugia"'(Greer et al., 2019: p. 2).[a]

Note: We extracted definition examples from papers where presence of cold-water or warm-water adapted poikilotherms was confirmed.
[a]Note imprecise use of the term 'refugia'.

vary in size, configuration and hydrologic mechanism and are distributed throughout a riverscape, driven by the variation in fluvial geomorphic features, geology and landscape topographies (Ebersole et al., 2015; Malard et al., 2002; Monk et al., 2013; Stanford & Ward, 1993; Wawrzyniak et al., 2016). For example, cold-water patches in the Restigouche River watershed (Canada) are more numerous in river reaches with a sinuous channel and nearer tributary valleys, whereas patch clusters occur in moderately confined stream channels (Dugdale et al., 2013). Also, geologic heterogeneity can facilitate preferential groundwater flow zones and cause groundwater inflows to be focused, creating larger thermal patches (e.g., Harrington et al., 2017) compared to the moderate local thermal influence of diffuse groundwater discharge.

In some cases, managers and researchers can augment existing cold-water or warm-water patches to enhance their spatial extent or temperature difference. A channel deflection constructed of boulders or other rigid material can inhibit the immediate mixing of relatively cold or warm inflow water with main channel water, creating a larger thermal patch distinct from main channel flow (Kurylyk, MacQuarrie, Linnansaari, et al., 2015; Torgersen et al., 2012). Further, artificial shading may buffer cold-water or warm-water patches by an additional 2–4°C (Ebersole et al., 2003a), depending upon river flow regimes, water clarity, streambed colour, channel morphology and upstream conditions.

The intrusion of thermally distinct water into stream and river channels is an integral riverscape component regardless of the exact mechanism. We can use the physical controls of cold-water or warm-water patches described above to characterize or delimit the space in which poikilotherms may or may not take refuge within at least seven hydrological classifications (Figure 2): tributary confluence, lateral spring or seep, springbrook, side channel, alcove, wall-base channel or hyporheic upwelling. These hydrologic classifications are well defined (see Dugdale et al., 2013) and are rather insensitive to variations in physiographic and climatic settings across streams and rivers. They are, however, more sensitive to variations in size of the cold-water or warm-water patch via the variation in water depth, groundwater inflow concentration and main channel discharge at the stream or river scales. We argue for the use of the size of the cold-water

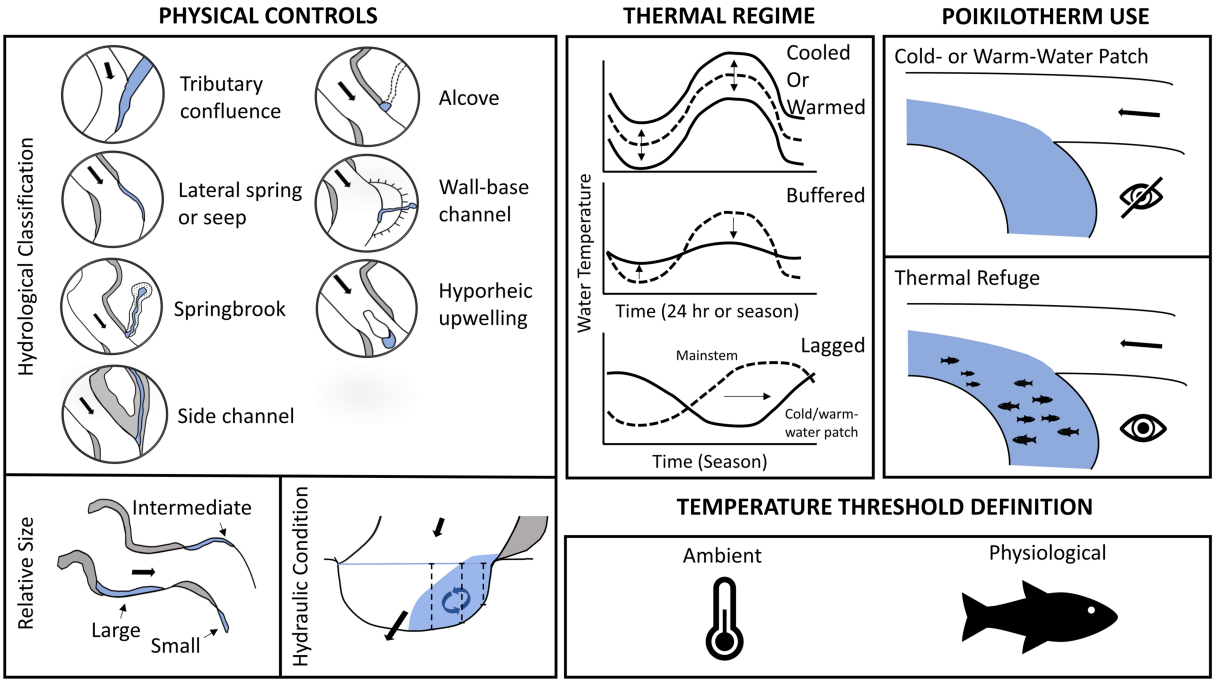

FIGURE 2 A typology for characterizing thermal anomalies as cold-water and warm-water patches and thermal refuges in streams and rivers. *Physical controls* represent hydrological classifications (Dugdale et al., 2013) and other physical descriptors used, including the relative size (based on specific poikilotherm ecology or biology) or the hydraulic conditions (e.g., depth-velocity relationships as expressed by Froude number), to characterize or delimit the area where thermally distinct water intrudes into stream and river channels. The cold-water or warm-water patch *thermal regime* (daily and/or seasonal timescales) describes the thermal regime relative to the main channel. Researchers could also define the *temperature threshold definition* used; the definition used is likely context-dependent and can help determine the range of conditions under which we study cold-water or warm-water patches or thermal refuges. Lastly, researchers should verify *poikilotherm use* of a cold-water or warm-water area, and the term 'thermal refuge' should only be used to refer to cold-water or warm-water patches that poikilotherms are known to use

or warm-water patch and local hydraulic conditions (e.g., Froude number; Yalin, 1992) to characterize cold-water or warm-water patches or thermal refuges. Preferred cold-water or warm-water patch size and hydraulic conditions are context dependent, and knowledge of specific poikilotherm ecology or biology should underpin the characterization. Using these physical descriptors, researchers can adequately describe cold-water or warm-water patches or thermal refuges while affording the flexibility to compare them between studies.

2.2 | Thermal regimes of cold-water or warm-water patches

Cold-water or warm-water patches are dynamic environments whose temperature regimes differ from that of the main (mixed) channel flow. In smaller streams, focused groundwater discharge can create a cold-water or warm-water section across the entire stream channel (e.g., Fernald et al., 2006), whereas focused groundwater discharge to larger streams and rivers typically creates a distinct thermal patch within the channel cross-section (e.g., Dugdale et al., 2013) or potentially only cools or warms the bed surface and not perceptibly the channel water (e.g., Rosenberry et al., 2016). Water temperatures in cold-water or warm-water patches that might serve as refuges are cooler in the summer and warmer in the winter relative to main channel temperatures. Summer water temperatures in patches or refuges are less variable and lower during the daily stream thermal maxima, where winter water temperatures would be less variable and higher during the daily stream thermal minima (e.g., Arrigoni et al., 2008). Similarly, their temperature regimes can be lagged and/or buffered relative to the main channel (Acuña & Tockner, 2009; Arrigoni et al., 2008; Caissie, 2006) because hyporheic and groundwater temperature signals are attenuated and phase shifted compared to surface water temperatures (Malard et al., 2001). Natural and anthropogenic fluctuations in stream or river discharges can also change the configuration, size and temperature distribution of cold-water or warm-water patches relative to the main channel; small patches (e.g., hyporheic upwellings) may only be present for short periods due to seasonal warming of shallow groundwater (Dugdale et al., 2013). Cold-water and warm-water patch thermal regimes are, therefore, dynamic habitats.

Cold-water or warm-water patches can be intermittently present at weekly, seasonal or annual temporal scales due to either changes in air temperatures or fluvial geomorphic features. For example, the seasonal, transient nature of groundwater-sourced patches are a function of meteorological conditions (Chen et al., 2002) and aquifer depth and hydraulic properties (Briggs, Lane, et al., 2018; Hare et al., 2021;

Kurylyk, MacQuarrie, Caissie, & McKenzie, 2015): common but less predictable causes include temporal variability in groundwater levels (Dugdale et al., 2013). As a result, temperature dynamics of warm-water and cold-water patches are complex, involving spatiotemporal components that can vary from site to site and with climatic conditions.

Temperature cycles of cold-water or warm-water patches are themselves functions of different physical controls (e.g., Ebersole et al., 2003a), and the assumption that patch water temperatures are consistently cooled or warmed relative to the main channel is overly simplistic. We suggest that researchers characterize patch thermal regimes as cooled or warmed, buffered and/or lagged (Figure 2). Relative to the mainstem channel flow, cooled or warmed denotes a decrease or increase in mean temperatures, respectively; buffered denotes a difference in the temporal range or variance in temperatures and lagged denotes a phase-shifted thermal regime (Arrigoni et al., 2008). By definition, a phase-shifted thermal regime experiences thermal maxima and minima that are not coincident with those of the main channel, potentially creating periodic cold-water and warm-water anomalies. Cooled/warmed and buffered thermal regimes operate at diurnal and seasonal time scales, whereas thermal regimes are generally lagged at seasonal time scales except, perhaps, for hyporheic discharge (Arrigoni et al., 2008). Characterizing thermal regimes in cold-water or warm-water patches relative to the main channel will require continuous monitoring of temperatures when differences are greatest (e.g., late summer in temperate streams) and will provide insight into potential distinctions useful for delineating and assessing various patches for their potential to provide thermal refuge. If managers or researchers identify both the hydrologic mechanism and the thermal regime classification, the potential resilience of a thermal refuge (and refugia) across seasons, years or even decades may be more predictable (Briggs, Lane, et al., 2018; Fullerton et al., 2018; Kurylyk et al., 2014).

2.3 | Poikilotherm use of cold-water or warm-water thermal refuges

Poikilotherms seek out and use cold-water or warm-water thermal refuges during periods of stressful or even lethal temperatures (i.e., they behaviourally thermoregulate; Figure 3; e.g., Hertz et al., 1993). Poikilotherms are constantly seeking the optimal environment in accordance with their thermal preference, and movements to areas of preferred temperatures occur during periods with low or high water temperatures outside of preferred ranges. Use of a thermal refuge can lower or raise a poikilotherm's body temperature and reduce metabolic costs associated with temperatures exceeding their upper (e.g., Westhoff et al., 2016) and lower (e.g., Peterson & Rabeni, 1996) thermal preference, thereby increasing survival,

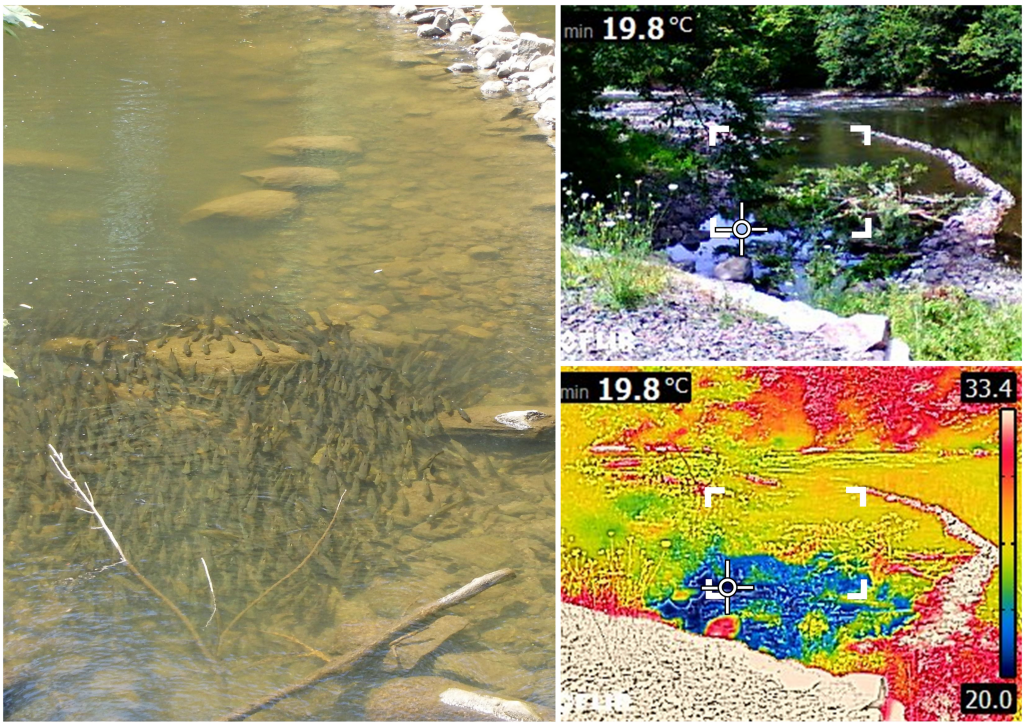

FIGURE 3 An aggregation of brown trout (*Salmo trutta*), rainbow trout (*Oncorhynchus mykiss*) and brook trout (*Salvelinus fontinalis*) at the confluence of a groundwater-dominated tributary (Furnace Brook) with the Housatonic River, Connecticut, USA (left; photo credit: M. Humphreys). Summer water temperatures regularly exceed physiological preferences of trout, and trout must use this thermal refuge for summer survival during most summers (i.e., behaviourally thermoregulate). Visual (top right) and thermal infrared (TIR; bottom right) images of the thermal refuge show the spatial extent of the cold-water thermal plume, but the plume is likely larger than depicted because TIR cameras only capture surface water temperature. The white crosshair represents the coldest measured temperature in the image

particularly for species that inhabit already marginal habitats. Given the abundance of evidence showing that extreme high summer temperatures are increasing in frequency and magnitude (Pachauri & Meyer, 2014), many studies focus on cold-water or cool-water adapted species use of cold-water refuges such as Atlantic salmon *Salmo salar* (Dugdale et al., 2013; Frechette et al., 2018; Jonsson & Jonsson, 2009), Chinook salmon *Oncorhynchus tshawytscha* (Berman & Quinn, 1991; Keefer et al., 2018; Tiffan et al., 2003; Torgersen et al., 1999), trout (brook trout *Salvelinus fontinalis*, brown trout *Salmo trutta* or rainbow trout *Oncorhynchus mykiss*; Hitt et al., 2017; Petty et al., 2012; Ritter et al., 2020; Wilbur et al., 2020), bull trout *Salvelinus confluentus* (Gutowsky et al., 2017; Howell et al., 2010), and smallmouth bass *Micropterus dolomieu* (Westhoff et al., 2016). Though fishes have been most often studied, other diverse poikilothermic taxa groups of course exist in rivers and streams, and far less is known of how they may use or depend upon thermal refuges (e.g., Friele et al., 2016).

Although cold and warm water can provide critical refuge habitat during periods of extreme temperatures, variation in both physical habitat and thermal regimes across thermal refuges can lead to some areas serving as refuge, whereas others do not (e.g., Wilbur et al., 2020). Poikilotherms must also balance cold-water or warm-water refuge use with other biological needs, implying that local habitat conditions, connectivity, sex, size, life stage (e.g., juvenile versus adult) and other factors likely influence use (e.g., Breau et al., 2007; Brewitt et al., 2017; Hitt et al., 2017; Petty et al., 2012; Snyder et al., 2020; Wilbur et al., 2020). For example, shallow cold-water patches with low dissolved oxygen levels due to anoxic groundwater discharge may never, or only rarely, function as a refuge (Ebersole et al., 2001). Further, the presence or occurrence of a cold-water or warm-water patch needs to overlap with the occurrence of thermal stress in the main channel for a specific poikilotherm, which may vary depending on life stage (e.g., Breau et al., 2007; Brewitt et al., 2017).

As a result, we cannot assume that every cold-water or warm-water patch serves as thermal refuge since temperature is only one of many attributes of a refuge. We suggest that researchers use the term 'cold-water patch' or 'warm-water patch' to refer to cold-water or warm-water areas not used by poikilotherms during extreme temperatures or for which use has yet to be evaluated. A 'thermal refuge' is, therefore, a subset of cold-water or warm-water patches that poikilotherms are known to use during extreme temperatures (Figure 2). In using the two terms, we clearly articulate what we know and do not know about poikilotherm use, often a key implication of thermal anomaly research, while providing the flexibility required to encapsulate the many ways in which poikilotherms use thermal refuges.

3 | TERMINOLOGY USED IN THE LITERATURE AND A PLEA FOR MORE PRECISE USAGE

The term 'thermal refuge' was initially used informally and seemed to first appear in peer-reviewed literature in the 1970s, though the concept itself is far older. Kaya et al. (1977) adopted the term from terrestrial ecology to refer to areas where rainbow trout and brown trout concentrated during unfavourable temperatures. The transition to a more precise usage began in the 1980s, when water temperature differentials (e.g., area of water is ≥2°C cooler or warmer than adjacent streamflow) defined a thermal refuge (Moss, 1985). However, multiple competing terms surfaced during this period, such as 'cool-water area' (Bilby, 1984), 'cold pool' (Ozaki, 1988), 'stratified pool' (Nielsen et al., 1994), 'fish refuges' (Peterson & Rabeni, 1996) and eventually a 'cold-water patch' (Ebersole et al., 2003a, 2003b). Similarly, the term 'warm-water thermal refuge' surfaced during the late 1980s to refer to warm-water areas used by poikilotherms during unfavourably cold temperatures (e.g., warm-water patch or refuge; Cunjak & Power, 1986; Reynolds & Wilcox, 1994), but studies are less frequent. Whether by transfer or independent invention, all competing terms refer to discrete areas ≥2–10°C cooler or warmer than the ambient environment. Use of the area by poikilotherms is, however, often not reported in prior studies, making it difficult to ascertain if an area functioned as a refuge or not.

During the 2010s, the characterizations and definitions of a thermal refuge expanded for more robust applications due in large part to technological advances. Though some researchers did define a 'thermal refuge' as previously described (e.g., Brewitt & Danner, 2014; Torgersen et al., 2012), others pointed out that previous definitions were overlooking the temporal variability of thermal refuges (e.g., Dugdale et al., 2013) due to the complex ways that groundwater and surface water interact but suggested no classifications. Further, researchers have recently re-defined the temperature differential of a thermal refuge for more specific meaning. Greer et al. (2019) suggested two different definitions of a thermal refuge: an 'ambient refuge' that is defined by temperature differentials from ambient conditions (similar to definitions previously described) and also a 'physiological refuge' defined as an area with temperatures below a biologically relevant threshold (e.g., area with water temperatures ≤21°C used by juvenile steelhead *O. mykiss*). The definition of a physiological refuge would, therefore, be species-specific, determined by the temperature where maximum oxygen consumption, cessation of feeding and behavioural changes transpire (e.g., Daigle et al., 2015). A summary of terms used to describe thermal refuges in streams and rivers can be found in Table 1.

All definitions (Table 1) are practical and measurable, but the term 'thermal refuge' is often used much more loosely than any of these definitions. Using the peer-reviewed articles identified in Figure 1, we systematically examined how articles characterized or defined a thermal refuge (see Supporting Information S1 for methodology). Our literature search revealed that 61% (88/145) of articles did not directly evaluate poikilotherm use of a supposed thermal refuge. In these cases, 'thermal refuge' was applied to discrete areas of water that met some temperature differential criteria, but this can build a disconnect between their physical properties and how they may function biologically or ecologically. This could lead to unrealistic expectations of poikilotherm adaptive capacity. In contrast, 37% (53/145) of articles did not measure water temperature but assumed an area was a

thermal refuge because individuals were observed aggregating in a specific area during an extreme temperature-based weather event. Thus, although some areas identified as thermal refuges are thermally well characterized and known to protect individuals, it is not clear what proportion satisfies both criteria.

The term 'thermal refugia' is often applied indiscriminately or interchangeably to refer to areas of thermal refuge. This practice can confound the role of riverscapes in long-term species persistence in an area (thermal refugium) with processes occurring at smaller scales relevant to the short-term survival of individuals (thermal refuge; Box 1). Using the 145 peer-reviewed articles identified in Figure 1, we examined the current use of thermal 'refugium' (plural refugia) and 'refuge' terms. Of the 145 articles, 32% (47/145) used both terms interchangeably throughout the paper. Surprisingly, 41% (60/145) of peer-reviewed articles did not directly define either thermal 'refugium' or 'refuge', whereas only 21% (30/145) clearly define either term, demonstrating that, when used, their meanings are often ambiguous. Though some articles suggest no formal difference between 'refugia' and 'refuge', there are clear differences in scale between the two terms (Box 1). There is, of course, no one clear spatial and temporal threshold that works across species for demarcation between the two terms as poikilothermic life histories are diverse; however, functionally there is a sharp demarcation between a thermal refugium and thermal refuge that needs clearer distinction in the literature (e.g., Davis et al., 2013; Torgersen et al., 2012).

There are three general, key features of thermal refuges: they are thermally distinct riverscape features that are spatially distributed, their presence can vary through time and poikilotherms use them to seek temporary shelter from unfavourable temperatures. Clearly, inconsistencies exist regarding how a thermal refuge or a cold-water or warm-water patch is defined and described, and numerous terms have been used. Our typology mitigates these inconsistencies by providing a consistent framework for defining and characterizing a cold-water or warm-water patch or thermal refuge. Characterizing a cold-water or warm-water patch or thermal refuge is often context-dependent and can be obscured by the variability of species' and life stage thermal tolerances and field methods used. Researchers should clarify whether they define a cold-water or warm-water patch or thermal refuge by an 'ambient' or a 'physiological' temperature threshold (or both; Figure 2), as described above, that is species and life-stage specific. The distinction between an ambient and a physiological temperature threshold helps determine the range of conditions under which cold-water or warm-water patches or thermal refuges are being studied. This context includes the specific area under consideration, the physical controls on temperature regimes, the species and life stage considered and their use of the area and the spatiotemporal scales at which it is studied.

Box 1 Distinguishing between 'refugium' and 'refuge'

Textbook definitions of 'refugia' and 'refuge' are as follows:

- *Refugia*: In biogeographical terms, a 'refugium' is a discrete area where a species population has survived for generations in isolation from unfavourable, surrounding climatic conditions (Calow, 1999; Torgersen et al., 2012; Walker, 1988). A 'refugium' is a metaphorical island, and for an area to be considered a refugium, a species must have occupied this area before the onset of unfavourable conditions elsewhere, and it must offer protection to a population (Keppel et al., 2012; Stewart et al., 2020).
- *Refuge*: A 'refuge' is an area that individuals retreat to when conditions are unfavourable elsewhere in their habitat, providing temporary shelter in an area otherwise not preferentially occupied (Calow, 1999; Walker, 1988).

We argue that biologically relevant scales differentiate a "thermal refugium" and "thermal refuge" (e.g., Davis et al., 2013; Keppel et al., 2012; Reside et al., 2019; Robson et al., 2013) and define both as follows:

- *Thermal refugium*: an area that buffers a species from unfavourable, sustained climatic thermal conditions relatively nearby. Using this definition, a thermal refugium is important for the survival of multiple generations of a population or metapopulation and persists on timescales relevant to their persistence and adaptation to prevailing thermal conditions (e.g., Isaak et al., 2016).
- *Thermal refuge*: an area that individuals of a population or metapopulation move to in response to unfavourable event-based thermal conditions and reside within for shorter periods (minutes to months). A thermal refuge, therefore, refers to smaller, localized areas that organisms can move short distances to for temporary behavioural thermoregulation (e.g., Brewitt et al., 2017; Ebersole et al., 2003b; Robson et al., 2013).

4 | A CONCEPTUAL MODEL FOR POIKILOTHERM USE OF THERMAL REFUGES

To help move cold-water or warm-water patch and thermal refuge research from a predominately descriptive endeavour (acknowledging more basic descriptive work is still needed) towards a more hypothesis-driven posture, we offer a conceptual model predicting some drivers of the utility of refuges to poikilotherms. Cold-water and warm-water patches in streams and rivers range in size, configuration and temporal persistence, and their distribution throughout a riverscape is heterogeneous (Dugdale et al., 2013; Ebersole et al., 2015; Wilbur et al., 2020) and not necessarily collocated with distributions or timing of thermally stressed poikilotherms. As a result, not all cold-water or warm-water patches function as thermal refuge and refuges themselves likely vary widely in functional utility (i.e., when and for

how long they provide thermal stress avoidance). How individual poikilotherms use thermal refuges may vary based on their life stage, size, physiology and mobility and depend on community composition (e.g., competition).

The evidence that poikilotherms identify and use thermal refuges in complex ways is mounting (e.g., Corey et al., 2020; Hitt et al., 2017; Keefer et al., 2018; Matthews & Berg, 1997) and underscores the need for future research to develop more specific hypotheses that will bear out the generality of poikilotherm behaviour or, on the contrary, the specificity of landscape or species context. Our conceptual model (Figure 4) provides an interdisciplinary visualization of how the configuration and thermal regime of a cold-water patch might affect its functional utility as a thermal refuge. We focus on cold-water areas but suggest similar generalities apply to warm-water areas. Given data reported to date, we can uncontroversially predict that the general pattern of increasing ambient main channel temperature would increase the likelihood of thermal refuge need and use by poikilotherms. But we also hypothesize that inherent differences in hydrological conditions (Figure 2) across riverscapes could modulate the observed patterns of use. According to our model, a poikilotherm will be more likely to use thermal refuges that are larger and provide more suitable temporary habitat (e.g., deep, slow mixing water) but would only use smaller or less suitable refuges as temperatures increase. It is also the case that some cold-water patches may not be used at all. As an example of this phenomenon, brook trout are a cold-water adapted fish that survives in marginal riverscapes by temporarily inhabiting thermal refuges (Kanno et al., 2014; Meisner, 1990). During high temperature events, brook trout actively search for nearby thermal refuge; however, individuals select for micro cold-water habitats that are closer in character to their regular habitats (Petty et al., 2012) with deeper and slower velocity (Baird & Krueger, 2003; Wilbur et al., 2020) and do not simply move into the coldest patch available. The likelihood of thermal refuge use is, therefore, influenced by several factors.

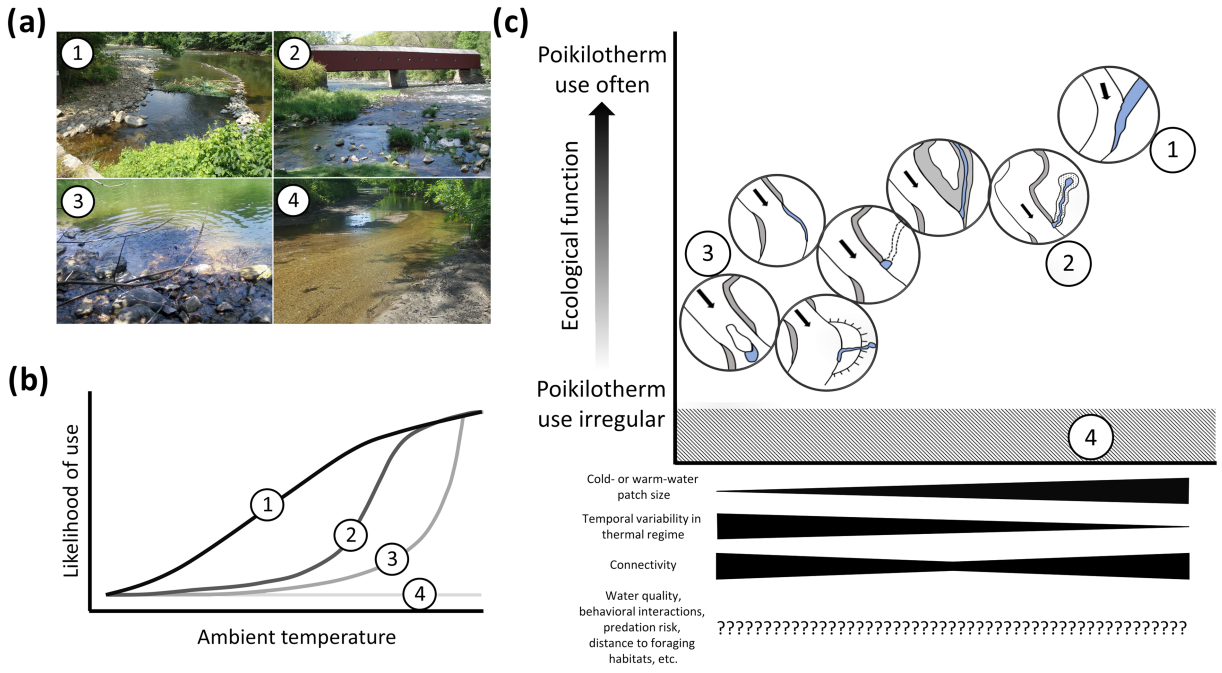

FIGURE 4 Conceptualization of the likelihood of different hydrologically classified cold-water patches to provide thermal refuge based on their relative size, connectivity, and thermal regime relative to ambient stream or river temperature, and examples displaying a range of physical controls and poikilotherm use. (a) Examples of thermal refuges and a cold-water patch from the Housatonic River, Connecticut, USA, where trout species must behaviourally thermoregulate for summer survival (photo credit: M. Humphreys): 1 = a large, deep, slow-mixing cold-water tributary confluence where vegetated cover and a channel deflecting rock wall creates a large thermal refuge for hundreds of cold-water fish; 2 = a intermediately sized, shallow cold-water tributary confluence with no vegetated cover that provides refuge for 50–100 cold-water fish; 3 = a small cold-water springbrook confluence with little cover that provides refuge for 1–50 cold-water fish; 4 = a shallow cold-water tributary with no cover or preferred substrate that does not provide refuge for cold-water fish (i.e., a cold-water patch). (b) Likelihood of a cold-water adapted poikilotherm using a cold-water patch for thermal refuge over a range of ambient stream temperatures. Numbered circles refer to examples in panel a. (c) Different hydrologically classified cold-water patches (Figure 2) vary in their ability to function as a thermal refuge for cold-water adapted poikilotherms and vary in relative size, connectivity and thermal regime relative to the main channel. It is not completely understood yet how various water quality parameters, behavioural interactions, predation risk and connectivity to foraging habitats influence the ability of differently hydrologically classified cold-water patches to function as thermal refuge. Hydrologically classified cold-water patches are derived from Dugdale et al. (2013). The dashed area indicates a cold-water patch that is never used during extreme temperatures. Our conceptualization can also be applied to warm-water patches and refuges. Numbered circles refer to examples in panel a

Our model provides a simple framework we hope future research will enrich over time. Additional factors that may influence the functionautility of thermal refuges are inter-individual behavioural interactions, feeding requirements, predation risks, the relationship of the refuge to foraging habitats and water quality parameters (e.g., Armstrong et al., 2013; Brewitt et al., 2017; Ebersole et al., 2003b; Hitt et al., 2017; Matthews & Berg, 1997; Figure 4), and perhaps individual fish physiology (Morash et al., 2021). There are also interesting riverscape-level hypotheses to be tested centred around whether individual animals move back and forth among multiple refuges near one another and to what advantage. It may also be the case that thermal refuges could become ecological traps (e.g., Robertson & Hutto, 2006), thereby decreasing survival, if selected for over adjacent, more suitable patches. For example, angling (Keefer et al., 2009) or avian predation (Ritter et al., 2020) pressure in thermal refuges can mitigate the thermoregulatory benefits of refuges, or trade-offs between migration and refuge use may prohibit fish from reaching spawning areas (e.g., Snyder et al., 2020). Sufficient data are lacking at present to formulate conceptualizations of these additional factors, but informed by our basic conceptual framework, we believe rapid progress in understanding can be achieved.

In summary, our conceptual model raises two important predictive points: (i) the likelihood of a poikilotherm using a thermal refuge will vary as a function of at present incompletely understood physical characteristics, and (ii) it is highly possible to have a cold-water or warm-water patch that does not function as a thermal refuge. Linking these complexities back to the typology proposed here, different physical characteristics of cold-water or warm-water patches and thermal refuges are often inadequately characterized when using current terminology (Table 1), and our literature search revealed that few studies (3%; 4/145) described any primary physical characteristics (i.e., those beyond temperature) of a thermal refuge at all (Supporting Information S1). We aim to accommodate these complexities, which must be better understood if riverine management and conservation are to truly embrace proactive thermal management (e.g., Kurylyk, MacQuarrie, Linnansaari, et al., 2015) as will be necessary during the coming decades as average stream temperatures continue to rise, and, perhaps more urgently, the frequency of extreme temperature events increases.

5 | APPLICATIONS TO CURRENT AND EMERGING CHALLENGES

There are benefits to the classification of cold-water or warm-water patches and thermal refuges within conservation and environmental management. Classifications are necessary for reporting, mapping, monitoring and comparative analyses of habitat data, which are instrumental for enacting, monitoring and adapting various regulatory actions. Providing a typology that creates an accessible framework for managers and researchers to communicate and consistently characterize cold-water or warm-water patches and thermal refuges is, therefore, prerequisite to their conservation and management globally.

A rather substantial challenge is the need for mass identification and inventory of cold-water or warm-water patches and thermal refuges across watersheds. Managers and researchers tasked with monitoring, maintaining or conserving poikilotherm populations need to know where suitable cold-water or warm-water patches and thermal refuges exist contiguously throughout entire watersheds, which may span rugged or highly populated terrain. Failure to do so could limit the conservation potential of thermal refuges; for example, groundwater pumping can intercept groundwater that would otherwise discharge to nearby surface waters, resulting in a loss of potential thermal refuge habitats (Kurylyk, MacQuarrie, Linnansaari, et al., 2015). Because different landscape features influence the location of cold-water or warm-water patches (e.g., Ebersole et al., 2015), managers and researchers can develop analytical tools to make predictions regarding patch or refuge locations but must be ground-truthed to know if poikilotherms actually use these areas during times of thermal stress. Using our ecohydrological typology, we assert that watershed and river associations/groups can now engage in community science efforts cooperatively with managers and researchers to inventory and classify cold-water or warm-water patches and thermal refuges.

The distributions of many cold-water adapted poikilotherms are shifting poleward or restricted to higher elevations within temperate latitudes (e.g., Jonsson & Jonsson, 2009); however, most lotic populations lack appropriate aquatic corridors to shift their ranges far enough to escape increasingly marginal habitat, which highlights the need for long-term conservation of groundwater sources. Monitoring the thermal resilience or sensitivity to changing climatic conditions of stream discharging groundwater is a relatively understudied component to predicting long-term changes of patch and refuge habitats (e.g., Daigle et al., 2015). Cold-water or warm-water patch temperature regimes are largely dictated by different energy balances exerted by fluvial geomorphic features, geology and landscape topographies (e.g., Mejia et al., 2020; Wawrzyniak et al., 2016), which can in turn influence their response to increasing air temperatures. Loss or degradation of known (and yet undiscovered) thermal refuges will threaten the success and survival of poikilotherms increasingly subjected to increasing thermal stress. Such losses will be difficult to visualize as temperature monitoring at the resolution needed to reveal thermal refuge change through time is challenging at present. But loss of refuge function is indeed a form of habitat degradation and will increase in importance in coming decades. Because the ecohydrological typology takes into account physical controls on surface-groundwater interactions, users can make process-based predictions of how some patches and refuges may persist into the future. Thermal refuges with buffered thermal regimes are not as sensitive to variations in meteorological conditions. Presumably, these types of thermal refuges, such as those sourced by deep groundwater, may also persist longer in a warmer climate (e.g., Hare et al., 2021). More research is needed to ascertain if short-term thermal resilience (e.g., buffered seasonal

signals) translates to long-term (e.g., decadal) thermal resilience. This typology can provide a basic structure for these monitoring-based investigations.

We provide an example regulatory application of our typology and classify a well-known cold-water tributary (Furnace Brook) confluence with the Housatonic River, Connecticut, USA. We classify Furnace Brook as a *large*, *tributary confluence thermal refuge* that is critical for the summer survival of Brown Trout (see Box 2 for details). The Connecticut Department of Energy and Environmental Protection (CT DEEP) Fisheries Division prohibits recreational fishing within 30.48 m (100 ft) of the Furnace Brook thermal refuge seasonally (closed 15 June to 15 September) protecting refuge-seeking fish (CT DEEP, 2021). Such a management approach is site-specific but represents a progressive regulatory approach to thermal refuge conservation and management. Expanding management applications to larger spatial scales will require novel and creative approaches.

Box 2 Application of the ecohydrological typology: A case study

Housatonic River, Connecticut, USA

Description: The Housatonic River is Connecticut's second-longest river (240 km) and supports some of the state's premier cool-water and cold-water fisheries (brown trout, rainbow trout, brook trout and smallmouth bass). Main channel water temperatures exceed 17°C for a large portion of the year (e.g., June to mid-September); temperatures ≥25°C are common from early July to late August. A 15-km river reach provides numerous cold-water patches critical for the summer survival of cool-water and cold-water fisheries; however, discrete, dense aggregations of fish only form in select areas during high summer temperatures. We focus on one such area, the confluence of Furnace Brook with the Housatonic River (Figure 5).

Physical controls: Furnace Brook is a third-order, groundwater-dominated tributary of the Housatonic River and originates at the confluence of Birdseye and Valley brooks and is confined between Dean Hill (1100 ft. elevation) and Coltsfoot Mountain (1400 ft. elevation). During the summer, the *tributary confluence* of Furnace Brook (latitude: 41°49′16″N, longitude: 73°22′16″W) is a *large* cold-water patch (~13.0-m maximum width, 1.5-m maximum depth, 100-m length; Figure 3) relative to other patches throughout the entire river reach.

Temperature threshold definition: Brown trout are a focal species of fishery and river management in the Housatonic River and are labelled as a species of greatest conservation need in Connecticut. As such, we will use a *physiological* temperature threshold for defining a cold-water patch or thermal refuge, focusing specifically on brown trout. Brown trout behaviourally thermoregulate once water temperatures exceed 23°C (e.g., Popoff & Nuemann, 2005), and we use this as a temperature threshold.

Temperature cycles: Temperature loggers (Pro v2 Data Logger, ONSET Computer Corporation, Bourne, Massachusetts) were placed upstream of the mixing confluence waters within the main channels of both the Housatonic River and Furnace Brook to monitor water temperatures from 26 May to 6 October 2020. Summer daily water temperature time series suggest that the Furnace Brook thermal regime is persistently *cooled* relative to the Housatonic River during the warm summer months (Figure 5).

Poikilotherm use: Hundreds of brown trout use the confluence of Furnace Brook with the Housatonic River for days to months during extreme summer temperatures (Hyatt et al., 1999; Figure 3), likely due to consistent temperatures below 23°C. Visual and barge electrofishing surveys (Figure 5) during these periods identify and capture brown trout in the Furnace Brook confluence, in comparison to other river sections that lack aggregations of this species, and, therefore, it is considered a *thermal refuge*.

Classification: We characterize the confluence of Furnace Brook as a *large*, *tributary confluence thermal refuge*, defined by *physiological* relevant temperatures for brown trout, whose temperatures are *cooled* relative to the mainstem flows.

6 | CONCLUDING THOUGHTS

The ecological functions of thermal refuges are important for a wide breadth of poikilothermic species globally. We leaned on the work of many hydrologists, biologists and ecologists to synthesize a typology that builds a bridge among inter-related disciplines to support needed research into, and the ongoing management of streams and rivers, that can be applied over different geophysical settings. Our ecohydrological typology clarifies the key characteristics used to describe and define instream thermal refuges, facilitates their identification and characterization and paves a more transparent path ahead by ending the lexical ambiguity stemming from different scholarly understandings. We believe that our article provides a platform for a more predictive research agenda and a more proactive approach to poikilotherm management and conservation in streams and rivers. Looking forward, we encourage use and adaptation of our ecohydrological typology as more precise classification can lead to better communication, research and applications at the ecohydrological nexus that thermal refuges embody. More extensive data collections

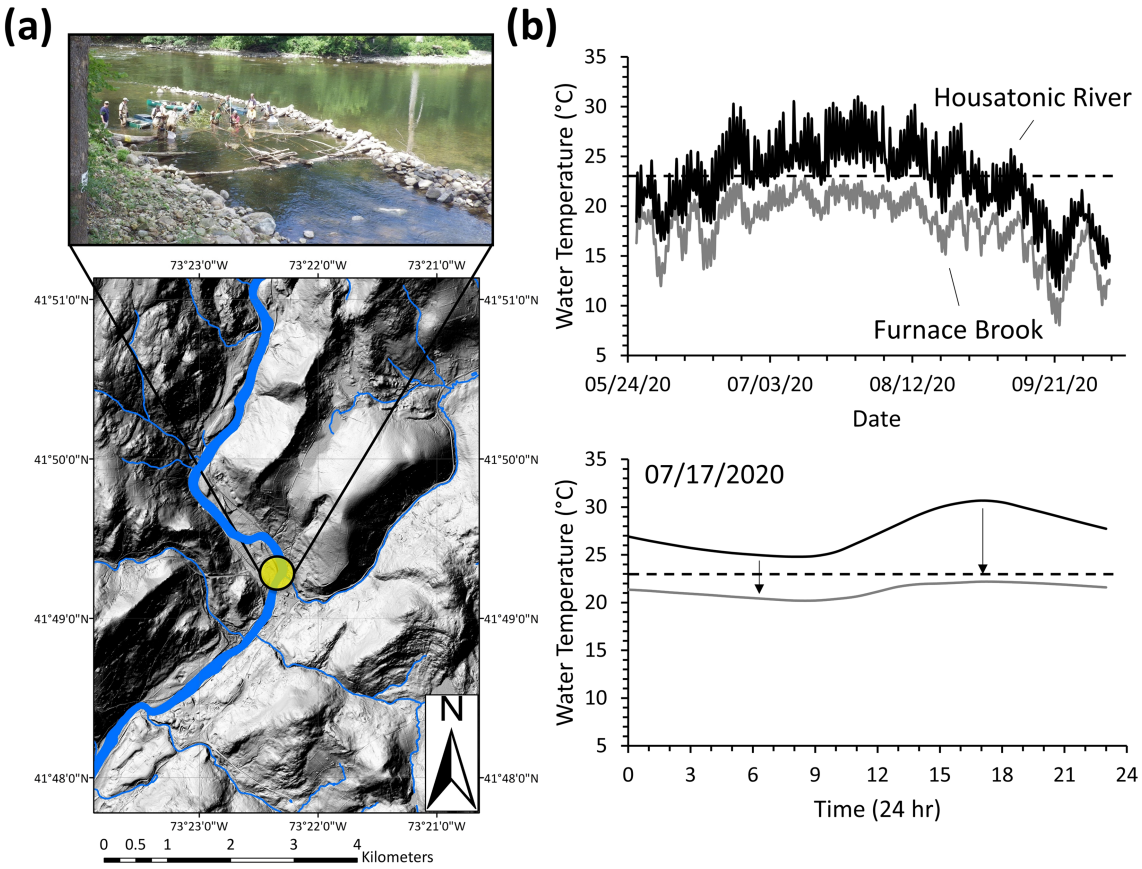

FIGURE 5 Map depicting the location of the confluence of Furnace Brook with the Housatonic River (panel a; bottom). The confluence is a large thermal refuge used by various cool-water and cold-water fish throughout the summer. Biologists barge electrofish (panel a; top; photo credit: M. Humphreys) the area to capture and monitor brown trout populations. Summer thermal regimes in Furnace Brook are cooled relative to the Housatonic River; summer and early fall water temperatures are consistently lower in Furnace Brook, where temperature differentials are greatest during mid-summer (panel b; top). Furnace Brook daily water temperatures are also cooled relative to the Housatonic River (panel b; bottom). The horizontal dashed line represents the upper thermal limit for brown trout (panel b)

and analyses will further refine the typology for more precise and robust usage and incorporate more complex ecological patterns into our characterizations.

ACKNOWLEDGEMENTS

Parts of this study were funded by the Storrs Agricultural Experiment Station, Hatch Act (Award No. CONS01039) to JCV and the National Science Foundation, Division of Earth Sciences (NSF-EAR; Award No. 1824820) to AMH and MAB. Open access fees were partially covered by the US Geological Survey Toxic Substances Hydrology Program and an NSERC Discovery Grant (Award No. RGPIN-2018-05420) to BLK. We thank Francine Mejia, Aimee Fullerton and the anonymous reviewers for their constructive reviews that substantially improved the manuscript. Any use of trade, firm or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

CONFLICT OF INTEREST

There is no conflict of interest declared in this article.

DATA AVAILABILITY STATEMENT

Data that support the findings of this study are available in the supporting information or from the corresponding author upon reasonable request.

ORCID

Christopher J. Sullivan https://orcid.org/0000-0001-7214-3789
Jason C. Vokoun https://orcid.org/0000-0001-5008-5928
Ashley M. Helton https://orcid.org/0000-0001-6928-2104
Martin A. Briggs https://orcid.org/0000-0003-3206-4132
Barret L. Kurylyk https://orcid.org/0000-0002-8244-3838

REFERENCES

Acuña, V., & Tockner, K. (2009). Surface-subsurface water exchange rates along alluvial river reaches control the thermal patterns in an Alpine river network. *Freshwater Biology*, *54*(2), 306–320. https://doi.org/10.1111/j.1365-2427.2008.02109.x

Armstrong, J. B., Schindler, D. E., Ruff, C. P., Brooks, G. T., Bentley, K. E., & Torgersen, C. E. (2013). Diel horizontal migration in streams: Juvenile fish exploit spatial heterogeneity in thermal and trophic resources. *Ecology*, *94*(9), 2066–2075. https://doi.org/10.1890/12-1200.1

Arrigoni, A. S., Poole, G. C., Mertes, L. A. K., O'Daniel, S. J., Woessner, W. W., & Thomas, S. A. (2008). Buffered, lagged, or cooled? Disentangling hyporheic influences on temperature cycles in stream channels. *Water Resources Research*, *44*(9), 1–13. https://doi.org/10.1029/2007WR006480

Baird, O. E., & Krueger, C. C. (2003). Behavioral thermoregulation of brook and rainbow trout: Comparison of summer habitat use in an Adirondack river, New York. *Transactions of the American Fisheries Society*, *132*(6), 1194–1206. https://doi.org/10.1577/t02-127

Berman, C. H., & Quinn, T. P. (1991). Behavioural thermoregulation and homing by spring chinook salmon, *Oncorhynchus tshawytscha* (Walbaum), in the Yakima River. *Journal of Fish Biology*, *39*(3), 301–312. https://doi.org/10.1111/j.1095-8649.1991.tb04364.x

Bilby, R. E. (1984). Characteristics and frequency of cool-water areas in a western Washington stream. *Journal of Freshwater Ecology*, *2*(6), 593–602. https://doi.org/10.1080/02705060.1984.9664642

Breau, C., Cunjak, R. A., & Bremset, G. (2007). Age-specific aggregation of wild juvenile Atlantic salmon *Salmo salar* at cool water sources during high temperature events. *Journal of Fish Biology*, *71*, 1179–1191. https://doi.org/10.1111/j.1095-8649.2007.01591.x

Brewitt, K. S., & Danner, E. M. (2014). Spatio-temporal temperature variation influences juvenile steelhead (*Oncorhynchus mykiss*) use of thermal refuges. *Ecosphere*, *5*(7), 1–26. https://doi.org/10.1890/ES14-00036.1

Brewitt, K. S., Danner, E. M., & Moore, J. W. (2017). Hot eats and cool creeks: Juvenile pacific salmonids use mainstem prey while in thermal refuges. *Canadian Journal of Fisheries and Aquatic Sciences*, *74*(10), 1588–1602. https://doi.org/10.1139/cjfas-2016-0395

Briggs, M. A., Johnson, Z. C., Snyder, C. D., Hitt, N. P., Kurylyk, B. L., Lautz, L., Irvine, D. J., Hurley, S. T., & Lane, J. W. (2018). Inferring watershed hydraulics and cold-water habitat persistence using multi-year air and stream temperature signals. *Science of the Total Environment*, *636*, 1117–1127. https://doi.org/10.1016/j.scitotenv.2018.04.344

Briggs, M. A., Lane, J. W., Snyder, C. D., White, E. A., Johnson, Z. C., Nelms, D. L., & Hitt, N. P. (2018). Shallow bedrock limits groundwater seepage-based headwater climate refugia. *Limnologica*, *68*, 142–156. https://doi.org/10.1016/j.limno.2017.02.005

Buckingham, C. A., Lefebvre, L. W., Schaefer, J. M., & Kochman, H. I. (1999). Manatee response to boating activity in a thermal refuge. *Wildlife Society Bulletin*, *27*(2), 514–522.

Caissie, D. (2006). The thermal regime of rivers: A review. *Freshwater Biology*, *51*(8), 1389–1406. https://doi.org/10.1111/j.1365-2427.2006.01597.x

Calow, P. (1999). In P. Calow (Ed.), *Blackwell's concise encyclopedia of ecology*. Blackwell Science.

Chen, Z., Grasby, S. E., & Osadetz, K. G. (2002). Predicting average annual groundwater levels from climatic variables: An empirical model. *Journal of Hydrology*, *260*, 102–117. https://doi.org/10.1016/S0022-1694

Connecticut Department of Energy and Environmental Protection [CT DEEP]. (2021). *Fishing guide (formerly anglers guide)*. Connecticut: Connecticut Department of Energy and Environmental Protection, Fisheries Division. https://portal.ct.gov/DEEP/Fishing/General-Information/Fishing-Guide

Corey, E., Linnansaari, T., Dugdale, S. J., Bergeron, N., Gendron, J. F., Lapointe, M., & Cunjak, R. A. (2020). Comparing the behavioural thermoregulation response to heat stress by Atlantic salmon parr (*Salmo salar*) in two rivers. *Ecology of Freshwater Fish*, *29*(1), 50–62. https://doi.org/10.1111/eff.12487

Cunjak, R. A., & Power, G. (1986). Winter habitat utilization by stream resident brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*). *Canadian Journal of Fisheries and Aquatic Sciences*, *43*(10), 1970–1981. https://doi.org/10.1139/f86-242

Daigle, A., Jeong, D. I., & Lapointe, M. F. (2015). Climate change and resilience of tributary thermal refugia for salmonids in eastern Canadian rivers. *Hydrological Sciences Journal*, *60*(6), 1044–1063. https://doi.org/10.1080/02626667.2014.898121

Davis, J., Pavlova, A., Thompson, R., & Sunnucks, P. (2013). Evolutionary refugia and ecological refuges: Key concepts for conserving Australian arid zone freshwater biodiversity under climate change. *Global Change Biology*, *19*, 1970–1984. https://doi.org/10.1111/gcb.12203

Dugdale, S. J., Bergeron, N. E., & St-Hilaire, A. (2013). Temporal variability of thermal refuges and water temperature patterns in an Atlantic salmon river. *Remote Sensing of Environment*, *136*, 358–373. https://doi.org/10.1016/j.rse.2013.05.018

Ebersole, J. L., Liss, W. J., & Frissell, C. A. (2001). Relationship between stream temperature, thermal refugia and rainbow trout Oncorhynchus mykiss abundance in arid-land streams in the northwestern United States. *Ecology of Freshwater Fish*, *10*(1), 1–10. https://doi.org/10.1034/j.1600-0633.2001.100101.x

Ebersole, J. L., Liss, W. J., & Frissell, C. A. (2003a). Cold water patches in warm streams: Physicochemical characteristics and the influence of shading. *Journal of the American Water Resources Association*, *39*(2), 355–368. https://doi.org/10.1111/j.1752-1688.2003.tb04390.x

Ebersole, J. L., Liss, W. J., & Frissell, C. A. (2003b). Thermal heterogeneity, stream channel morphology, and salmonid abundance in northeastern Oregon streams. *Canadian Journal of Fisheries and Aquatic Sciences*, *60*(10), 1266–1280. https://doi.org/10.1139/f03-107

Ebersole, J. L., Wigington, P. J., Leibowitz, S. G., Comeleo, R. L., & Van Sickle, J. (2015). Predicting the occurrence of cold-water patches at intermittent and ephemeral tributary confluences with warm rivers. *Freshwater Science*, *34*(1), 111–124. https://doi.org/10.1086/678127

Fernald, A. G., Landers, D. H., & Wigington, P. J. (2006). Water quality changes in hyporheic flow paths between a large gravel bed river and off-channel alcoves in Oregon, USA. *River Research and Applications*, *22*, 1111–1124. https://doi.org/10.1002/rra.961

Frechette, D. M., Dugdale, S. J., Dodson, J. J., & Bergeron, N. E. (2018). Understanding summertime thermal refuge use by adult Atlantic salmon using remote sensing, river temperature monitoring, and acoustic telemetry. *Canadian Journal of Fisheries and Aquatic Sciences*, *75*(11), 1999–2010. https://doi.org/10.1139/cjfas-2017-0422

Friele, P. A., Paige, K., & Moore, R. D. (2016). Stream temperature regimes and the distribution of Rocky Mountain tailed frog at its northern range limit, Southeastern British Columbia. *Northwest Science*, *90*(2), 159–175. https://doi.org/10.3955/046.090.0208

Fullerton, A. H., Torgersen, C. E., Lawler, J. J., Steel, E. A., Ebersole, J. L., & Lee, S. Y. (2018). Longitudinal thermal heterogeneity in rivers and refugia for cold-water species: Effects of scale and climate change. *Aquatic Sciences*, *80*, 3. https://doi.org/10.1007/s00027-017-0557-9

George, S. D., Baldigo, B. P., Smith, M. J., McKeown, D. M., & Faulring, J. W. (2016). Variations in water temperature and implications for trout populations in the Upper Schoharie Creek and West Kill, New York, USA. *Journal of Freshwater Ecology*, *31*(1), 93–108. https://doi.org/10.1080/02705060.2015.1033769

Greer, G., Carlson, S., & Thompson, S. (2019). Evaluating definitions of salmonid thermal refugia using in situ measurements in the Eel River, Northern California. *Ecohydrology*, *12*, e2101. https://doi.org/10.1002/eco.2101

Gutowsky, L. F. G., Harrison, P. M., Martins, E. G., Leake, A., Patterson, D. A., Zhu, D. Z., Power, M., & Cooke, S. J. (2017). Daily temperature experience and selection by adfluvial bull trout (*Salvelinus confluentus*). *Environmental Biology of Fishes*, *100*(10), 1167–1180. https://doi.org/10.1007/s10641-017-0634-x

Hare, D. K., Helton, A. M., Johnson, Z. C., Lane, J. W., & Briggs, M. A. (2021). Continental-scale analysis of shallow and deep groundwater contribution to streams. *Nature Communications*, *12*, 1450 (2021). https://doi.org/10.1038/s41467-021-21651-0

Harrington, J. S., Hayashi, M., & Kurylyk, B. L. (2017). Influence of a rock glacier spring on the stream energy budget and cold-water refuge in

an alpine stream. *Hydrological Processes*, *31*(26), 4719–4733. https://doi.org/10.1002/hyp.11391

Hertz, P. E., Huey, R., & Stevenson, R. D. (1993). Evaluating temperature regulation by field-active ectotherms: The fallacy of the inappropriate question. *The American Naturalist*, *142*(5), 796–818. https://doi.org/10.1086/285573

Hitt, N. P., Snook, E. L., & Massie, D. L. (2017). Brook trout use of thermal refugia and foraging habitat influenced by brown trout. *Canadian Journal of Fisheries and Aquatic Sciences*, *74*(3), 406–418. https://doi.org/10.1139/cjfas-2016-0255

Howell, P. J., Dunham, J. B., & Sankovich, P. M. (2010). Relationships between water temperatures and upstream migration, cold water refuge use, and spawning of adult bull trout from the Lostine River, Oregon, USA. *Ecology of Freshwater Fish*, *19*(1), 96–106. https://doi.org/10.1111/j.1600-0633.2009.00393.x

Hyatt, W. A., Humphreys, M., & Hagstrom, N. T. (1999). *A trout management plan for Connecticut's rivers and streams*. https://portal.ct.gov/-/media/DEEP/fishing/fisheries_management/Trout-Research-and-Management/trout-management-plan-1999-hyatt-et-al.pdf

Isaak, D. J., Wollrab, S., Horan, D., & Chandler, G. (2012). Climate change effects on stream and river temperatures across the northwest U.S. from 1980-2009 and implications for salmonid fishes. *Climatic Change*, *113*(2), 499–524. https://doi.org/10.1007/s10584-011-0326-z

Isaak, D. J., Young, M. K., Luce, C. H., Hostetler, S. W., Wenger, S. J., Peterson, E. E., Ver Hoef, J. M., Groce, M. C., Horan, D. L., & Nagel, D. E. (2016). Slow climate velocities of mountain streams portend their role as refugia for cold-water biodiversity. *Proceedings of the National Academy of Sciences*, *113*(16), 4374–4379. https://doi.org/10.1073/pnas.1522429113

Jonsson, B., & Jonsson, N. (2009). A review of the likely effects of climate change on anadromous Atlantic salmon *Salmo salar* and brown trout *Salmo trutta*, with particular reference to water temperature and flow. *Journal of Fish Biology*, *75*(10), 2381–2447. https://doi.org/10.1111/j.1095-8649.2009.02380.x

Kanno, Y., Vokoun, J. C., & Letcher, B. H. (2014). Paired stream-air temperature measurements reveal fine-scale thermal heterogeneity within headwater brook trout stream networks. *River Research and Applications*, *30*, 745–755. https://doi.org/10.1002/rra.2677

Kaya, C. M., Kaeding, L. R., & Burkhalter, D. E. (1977). Use of a cold-water refuge by rainbow and brown trout in a geothermally heated stream. *Progressive Fish-Culturist*, *39*(1), 37–38. https://doi.org/10.1577/1548-8659

Keefer, M. L., Clabough, T. S., Jepson, M. A., Johnson, E. L., Peery, C. A., & Caudill, C. C. (2018). Thermal exposure of adult Chinook salmon and steelhead: Diverse behavioral strategies in a large and warming river system. *PLoS One*, *13*(9), 1–29. https://doi.org/10.1371/journal.pone.0204274

Keefer, M. L., Peery, C. A., & High, B. (2009). Behavioral thermoregulation and associated mortality trade-offs in migrating adult steelhead (Oncorhynchus mykiss): variability among sympatric populations. *Canadian Journal of Fisheries and Aquatic Sciences*, *66*, 1734–1747. https://doi.org/10.1139/F09-131

Keppel, G., Van Niel, K. P., Wardell-Johnson, G. W., Yates, C. J., Byrne, M., Mucina, L., Schut, A. G. T., Hopper, S. D., & Franklin, S. E. (2012). Refugia: identifying and understanding safe havens for biodiversity under climate change. *Global Ecology and Biogeography*, *21*(4), 393–404. https://doi.org/10.1111/j.1466-8238.2011.00686.x

Kurylyk, B. L., MacQuarrie, K. T. B., Caissie, D., & McKenzie, J. M. (2015). Shallow groundwater thermal sensitivity to climate change and land cover disturbances: Derivation of analytical expressions and implications for stream temperature modeling. *Hydrology and Earth System Sciences*, *19*(5), 2469–2489. https://doi.org/10.5194/hess-19-2469-2015

Kurylyk, B. L., MacQuarrie, K. T. B., Linnansaari, T., Cunjak, R. A., & Curry, R. A. (2015). Preserving, augmenting, and creating cold-water thermal refugia in rivers: Concepts derived from research on the Miramichi River, New Brunswick (Canada). *Ecohydrology*, *8*(6), 1095–1108. https://doi.org/10.1002/eco.1566

Kurylyk, B. L., MacQuarrie, K. T. B., & Voss, C. I. (2014). Climate change impacts on the temperature and magnitude of groundwater discharge from shallow, unconfined aquifers. *Water Resources Research*, *50*(4), 3253–3274. https://doi.org/10.1002/2013WRO14588

Lynch, H. J., Rhainds, M., Calabrese, J. M., Cantrell, S., Cosner, C., & Fagan, W. F. (2014). How climate extremes-not means-define a species' geographic range boundary via a demographic tipping point. *Ecological Monographs*, *84*(1), 131–149. https://doi.org/10.1890/12-2235.1

Malard, F., Mangin, A., Uehlinger, U., & Ward, J. V. (2001). Thermal heterogeneity in the hyporheic zone of a glacial floodplain. *Canadian Journal of Fisheries and Aquatic Sciences*, *58*(7), 1319–1335. https://doi.org/10.1139/cjfas-58-7-1319

Malard, F., Tockner, K., Dole-Olivier, M. J., & Ward, J. V. (2002). A landscape perspective of surface-subsurface hydrological exchanges in river corridors. *Freshwater Biology*, *47*(4), 621–640. https://doi.org/10.1046/j.1365-2427.2002.00906.x

Matthews, K. R., & Berg, N. H. (1997). Rainbow trout responses to water temperature and dissolved oxygen stress in two southern California stream pools. *Journal of Fish Biology*, *50*(1), 50–67. https://doi.org/10.1006/jfbi.1996.0274

Meisner, J. D. (1990). Effect of climatic warming on the southern margins of the native range of brook trout, *Salvelinus fontinalis*. *Canadian Journal of Fisheries and Aquatic Sciences*, *47*, 1065–1070. https://doi.org/10.1139/f90-122

Mejia, F. H., Torgersen, C. E., Berntsen, E. K., Maroney, J. R., Connor, J. M., Fullerton, A. H., Ebersole, J. L., & Lorang, M. S. (2020). Longitudinal, lateral, vertical, and temporal thermal heterogeneity in a large impounded river: Implications for cold-water refuges. *Remote Sensing*, *12*(9), 1386. https://doi.org/10.3390/rs12091386

Monk, W. A., Wilbur, N. M., Allen Curry, R., Gagnon, R., & Faux, R. N. (2013). Linking landscape variables to cold water refugia in rivers. *Journal of Environmental Management*, *118*, 170–176. https://doi.org/10.1016/j.jenvman.2012.12.024

Morash, A. J., Speers-Roesch, B., Andrew, S., & Currie, S. (2021). The physiological ups and downs of thermal variability in temperate freshwater ecosystems. *Journal of Fish Biology*, 1–12. https://doi.org/10.1111/jfb.14655

Moss, J. L. (1985). Summer selection of thermal refuges by striped bass in Alabama reservoirs and tailwaters. *Transactions of the American Fisheries Society*, *114*, 77–83. https://doi.org/10.1577/1548-8659

Nielsen, J. L., Lisle, T. E., & Ozaki, V. (1994). Thermally stratified pools and their use by steelhead in northern California streams. *Transactions of the American Fisheries Society*, *123*(4), 613–626. https://doi.org/10.1080/1548-8659(1994)123<0613:TSPATU>2.3.CO;2

Ozaki, V. (1988). Geomorphic and hydrologic conditions for cold pool formation on Redwood Creek, California. Redwood National Park, Technical Report 24. Arcata, California.

Pachauri, R. K., & Meyer, L. A. (2014). Climate change 2014: Contributions of Working Groups I, II, and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. https://www.ipcc.ch/report/ar5/syr/

Peterson, J. T., & Rabeni, C. F. (1996). Natural thermal refugia for temperate warm-water stream fishes. *North American Journal of Fisheries Management*, *16*(4), 738–746. https://doi.org/10.1577/1548-8675

Petty, J. T., Hansbarger, J. L., Huntsman, B. M., & Mazik, P. M. (2012). Brook trout movement in response to temperature, flow, and thermal refugia within a complex Appalachian riverscape. *Transactions of the*

American Fisheries Society, *141*(4), 1060–1073. https://doi.org/10.1080/00028487.2012.681102

Pilgrim, J. M., Fang, X., & Stefan, H. G. (1998). Stream temperature correlations with air temperatures in Minnesota: Implications for climate change. *Journal of the American Water Resources Association*, *34*(5), 1109–1121. https://doi.org/10.1111/j.1752-1688.1998.tb04158.x

Popoff, N. D., & Neumann, R. M. (2005). Range and movement of resident holdover and hatchery brown trout tagged with radio transmitters in the Farmington River, Connecticut. *North American Journal of Fisheries Management*, *25*(2), 413–422. https://doi.org/10.1577/M03-151.1

Power, G., Brown, R. S., & Imhof, J. G. (1999). Groundwater and fish—Insights from northern North America. *Hydrological Processes*, *13*(3), 401–422. https://doi.org/10.1002/(SICI)1099-1085(19990228)13:3<401::AID-HYP746>3.0.CO;2-A

Reside, A. E., Briscoe, N. J., Dickman, C. R., Greenville, A. C., Hradsky, B. A., Kark, S., Kearney, M. R., Kutt, A. S., Nimmo, D. G., Pavey, C. R., Read, J. L., Ritchie, E. G., Roshier, D., Skroblin, A., Stone, Z., West, M., & Fisher, D. O. (2019). Persistence through tough times: Fixed and shifting refuges in threatened species conservation. *Biodiversity and Conservation*, *28*, 1303–1330. https://doi.org/10.1007/s10531-019-01734-7

Reynolds, J. E., & Wilcox, J. R. (1994). Observations of Florida manatees (*Trichechus manatus latirostris*) around selected power plants in winter. *Marine Mammal Science*, *10*(2), 163–177. https://doi.org/10.1111/j.1748-7692.1994.tb00258.x

Ritter, T. D., Zale, A. V., Grisak, G., & Lance, M. J. (2020). Groundwater upwelling regulates thermal hydrodynamics and salmonid movements during high-temperature events at a montane tributary confluence. *Transactions of the American Fisheries Society*, *149*(5), 600–619. https://doi.org/10.1002/tafs.10259

Robertson, B. A., & Hutto, R. L. (2006). A framework for understanding ecological traps and an evaluation of existing evidence. *Ecology*, *87*(5), 1075–1085. https://doi.org/10.1890/0012-9658(2006)87[1075:AFFUET]2.0.CO;2

Robson, B. J., Chester, E. T., Mitchell, B. D., & Matthews, T. G. (2013). Disturbance and the role of refuges in mediterranean climate streams. *Hydrobiologia*, *719*, 77–91. https://doi.org/10.1007/s10750-012-1371-y

Rosenberry, D. O., Briggs, M. A., Delin, G., & Hare, D. K. (2016). Combined use of thermal methods and seepage meters to efficiently locate, quantify, and monitor focused groundwater discharge to a sand-bed stream. *Water Resources Research*, *52*(6), 4486–4503. https://doi.org/10.1002/2016WR018808

Selwood, K. E., Cunningham, S. C., & Mac Nally, R. (2019). Beyond refuges: Identifying temporally dynamic havens to support ecological resistance and resilience to climatic disturbances. *Biological Conservation*, *233*, 131–138. https://doi.org/10.1016/j.biocon.2019.02.034

Snyder, M. N., Schumaker, N. H., Dunham, J. B., Keefer, M. L., Leinenbach, P., Brookes, A., Palmer, J., Wu, J., Keenan, D., & Ebersole, J. L. (2020). Assessing contributions of cold-water refuges to reproductive migration corridor conditions for adult salmon and steelhead trout in the Columbia River, USA. *Journal of Ecohydraulics*, 1–13. https://doi.org/10.1080/24705357.2020.1855086

Stanford, J. A., & Ward, J. V. (1993). An ecosystem perspective of alluvial rivers: Connectivity and the hyporheic corridor. *Journal of the North American Benthological Society*, *12*(1), 48–60. https://doi.org/10.2307/1467685

Stewart, J. R., Lister, A. M., Barnes, I., & Dalén, L. (2020). Refugia revisited: individualistic responses of species in space and time. *Proceedings of the Royal Society B*, *277*, 661–671. https://doi.org/10.1098/rspb.2009.1272

Tate, K. W., Lancaster, D. L., & Lile, D. F. (2007). Assessment of thermal stratification within stream pools as a mechanism to provide refugia for native trout in hot, arid rangelands. *Environmental Monitoring and Assessment*, *124*, 289–300. https://doi.org/10.1007/s10661-006-9226-5

Tiffan, K. F., Haskell, C. A., & Rondorf, D. W. (2003). Thermal exposure of juvenile fall chinook salmon migrating through a lower Snake River reservoir. *Northwest Science*, *77*(2), 100–109.

Torgersen, C. E., Ebersole, J. L., & Keenan, D. M. (2012). Primer for identifying cold-water refuges to protect and restore thermal diversity in riverine landscapes. https://nepis.epa.gov/Exe/ZyPDF.cgi/P100E45N.PDF?Dockey=P100E45N.PDF

Torgersen, C. E., Price, D. M., Li, H. W., & McIntosh, B. A. (1999). Multiscale thermal refugia and stream habitat associations of Chinook salmon in northeasten Oregon. *Ecological Applications*, *9*(1), 301–319. https://doi.org/10.1890/1051-0761(1990)009[0301:MTRASH]2.0.CO;2

Walker, P. M. B. (1988). *Cambridge dictionary of science and technology*. Cambridge University Press.

Wawrzyniak, V., Piégay, H., Allemand, P., Vaudor, L., Goma, R., & Grandjean, P. (2016). Effects of geomorphology and groundwater level on the spatio-temporal variability of riverine cold water patches assessed using thermal infrared (TIR) remote sensing. *Remote Sensing of Environment*, *175*, 337–348. https://doi.org/10.1016/j.rse.2015.12.050

Webb, B. W., Hannah, D. M., Moore, R. D., Brown, L. E., & Nobilis, F. (2008). Recent advances in stream and river temperature research. *Hydrological Processes*, *22*, 902–918. https://doi.org/10.1002/hyp.6994

Westhoff, J. T., Paukert, C., Ettinger-Dietzel, S., Dodd, H., & Siepker, M. (2016). Behavioural thermoregulation and bioenergetics of riverine smallmouth bass associated with ambient cold-period thermal refuge. *Ecology of Freshwater Fish*, *25*(1), 72–85. https://doi.org/10.1111/eff.12192

Wilbur, N. M., O'Sullivan, A. M., MacQuarrie, K. T. B., Linnansaari, T., & Curry, R. A. (2020). Characterizing physical habitat preferences and thermal refuge occupancy of brook trout (*Salvelinus fontinalis*) and Atlantic salmon (*Salmo salar*) at high river temperatures. *River Research and Applications*, *36*(5), 769–783. https://doi.org/10.1002/rra.3570

Yalin, M. S. (1992). *River mechanics*. Pergamon.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

How to cite this article: Sullivan CJ, Vokoun JC, Helton AM, Briggs MA, Kurylyk BL. An ecohydrological typology for thermal refuges in streams and rivers. *Ecohydrology*. 2021;14:e2295. https://doi.org/10.1002/eco.2295