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Special Section:

Winter limnology in a changing world

Audrey Thellman and Kathi Jo Jankowski shared first authorship.

Key Points:

- River ice is changing but limited study of the ecology of ice-covered rivers impairs our ability to understand its ecological effects
- Ice processes differ with river size and thus affect ecological processes differently throughout river networks
- Further study is needed of ice processes in small rivers and ecological processes during winter across rivers of all sizes

Supporting Information:

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

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Abstract Many of the world's rivers are ice-covered during winter months but increasing evidence indicates that the extent of river ice will shift substantially as winters warm. However, our knowledge of rivers during winter lags far behind that of the growing season, limiting our understanding of how ice loss will affect rivers. Physical, chemical, and biological processes change from headwaters to large rivers; thus, we expect ice processes and resulting effects on the ecology of rivers could also vary with river size, as a result of the associated changes in geomorphology, temperature regimes, and connectivity. To conceptualize these relationships, we review typically disparate literature on ice processes and winter ecology and compare what is known in the smallest and largest rivers. In doing so, we show that our ability to link ice with ecology across river networks is made difficult by a primary focus on ice processes in larger rivers and a lack of study of ecosystem processes during winter. To address some of these gaps, we provide new scenarios of river ice loss and analyses of how the annual importance of winter gross primary productivity (GPP) varies with river size. We show projected ice loss varied with large-scale watershed characteristics such as north-south orientation and that the importance of winter to annual GPP was greatest in the smallest rivers. Finally, we highlight information needed to fill knowledge gaps on winter across river networks and improve our understanding of how rivers may change as climate and ice regimes shift.

Plain Language Summary Many rivers are ice-covered for a portion of the year, but ice is being lost as the climate warms. However, we know little about the role of ice in the ecology of rivers and the effects of changes in ice cover will not be uniform within river networks. To synthesize what is known and highlight areas for further research, we review literature on how ice and its effect on ecological processes vary between the largest and smallest rivers. We show that our ability to link changes in ice cover with river ecology is difficult because we lack information about ice in the smallest rivers and ecology in the largest ones. To fill some of these gaps, we provide new data on ice loss in large rivers and provide comparisons of winter productivity across rivers ranging in size. We found that ice loss patterns varied based on whether rivers flowed north-south or east-west and that the importance of winter to annual productivity was greatest in the smallest rivers. Finally, we highlight future research that is needed to increase our knowledge of winter across watersheds and how the ecology of rivers may change as the climate and ice cover shift.

1. Introduction

Many of the world's rivers are ice covered for a portion of the year. For instance, the largest database of river ice cover documents that more than half of all of Earth's large rivers are seasonally ice covered (Yang et al., 2020). Freshwater systems are losing ice rapidly, however (Sharma et al., 2019); global scale predictions of river ice cover show that by 2100, average ice duration will decrease by 16.7 days, decreasing linearly with increases in annual mean temperature (Yang et al., 2020). These global scale patterns are further confirmed by *in situ* river ice records (de Rham et al., 2020; Magnuson et al., 2000; Prowse et al., 2007) and are projected to result in increasingly intermittent or completely ice free conditions in rivers of all sizes across the globe (Beltaos 2002, 2004; Beltaos et al., 2003; Rokaya et al., 2018; Yang et al., 2020).



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Writing – review & editing: Audrey Thellman, Kathi Jo Jankowski, Brian Hayden, Xiao Yang, Wayana Dolan, Adrianne P. Smits, Antóin M. O'Sullivan Despite this rapid change in river ice, we have little understanding of its implications for river ecology. The winter season is underrepresented in ecological studies and monitoring programs because of a traditional assumption that processes during the winter are a small component of how ecological dynamics play out on annual scales (Prowse, 2001; Studd et al., 2021) as well as the sheer difficulty of sampling rivers during winter (Block et al., 2018). Thus, our understanding of the ecology of rivers has primarily been based on dynamics during the growing season (Junk et al., 1989; Thorp & Delong, 1994; Vannote et al., 1980), as ecological studies often do not incorporate winter or the role of spatial or temporal dynamics of ice cover in river structure and function (e.g., Blackadar et al., 2020). The physical effects of river ice have the potential to rearrange and disrupt watershed-scale patterns in productivity and population distributions (Bernhardt et al., 2018; Hampton et al., 2017; Koenig et al., 2019), having effects that may extend throughout the year. Defining and understanding these effects is challenging due to the varying nature of river ice formation and duration (Prowse & Ommaney, 1991; Woo, 2012) as ice formation and timing can vary a great deal within and across watersheds (Cooley & Pavelsky, 2016; Turcotte & Morse, 2013, 2017). This can alter basic physical features of the river template including flow dynamics, light availability, and geomorphic or habitat structure (Brown et al., 2010; Cunjak, 1986; Newbury, 1968). In addition, ice movement has the potential to rearrange materials and biota through physical scour or through 'rafting' habitats downstream (Katz et al., 2015; Twiss et al., 2012).

Work in lakes and marine ecosystems has increasingly shown strong connections between what happens during the winter and how processes and communities unfold throughout the rest of the year (Cavaliere & Baulch, 2020; Hampton et al., 2017), but our ecological knowledge of the winter season and specifically the role of ice cover in rivers lags behind these other aquatic systems (Prowse, 2001). Although there is a long history of studying winter habitat conditions for fish communities (Brown et al., 2011) and substantial work on the winter ecology of macroinvertebrates (Danks, 2007), we have limited understanding of the dynamics of river food webs and ecosystem processes during winter (Blackadar et al., 2020; Casson et al., 2012; Contosta et al., 2019; Humphries et al., 2017; Jankowski et al., 2021; Prowse, 2001; Shogren et al., 2020). Previous work suggests several possible future scenarios for rivers as winters warm and ice cover declines: (a) the timing and duration of primary productivity will shift or expand (Mejia et al., 2019), (b) the timing and magnitude of nutrients from snowmelt pulses will shift or decline (Casson et al., 2012, 2019), (c) the distribution of winter-specialist insects and fish will change as a result of shifting thermal regimes (Fenoglio et al., 2014; Prowse, 2001), and (d) systems that had consistent annual ice cover will transition to experiencing more mid-winter breakups (Casson et al., 2019) or intermittent ice cover (Sharma et al., 2019), which could have ecosystem-wide consequences (e.g., Myrstener et al., 2020). Although not vet widely documented, these types of effects on river ecosystems will become more widespread as colder regions further resemble their warmer counterparts. Thus, integrating winter dynamics into our understanding of river function is increasingly imperative as the nature and duration of the cold season across the globe are rapidly changing (Jacobs et al., 2016).

Although winter occurs (and is changing) across a broad set of geographies, it can manifest very differently across biomes from the Arctic to the temperate zone. In addition, there can be a wide degree of variation among watersheds within a given biome based on factors such as elevation or land use, making it difficult to define a general set of principles for the role of winter in rivers. River or watershed size is often used to conceptualize river function as it can exert broad-scale controls on fundamental physical features of rivers such as light availability (Finlay, 2011) and flow (Poff et al., 1997) and is linked to changes in metabolic regimes (Bernhardt et al., 2018), nutrient processing rates (Creed et al., 2015; Marinos et al., 2020; Wollheim et al., 2021), and energy flow through food webs (Thorp & Delong, 1994; Vannote et al., 1980). Importantly, size is also correlated with patterns in ice formation and duration (Turcotte & Morse, 2013), indicating that there may be general patterns in winter ecological processes that also scale with river size. Studies of river ice ecology are patchy across river networks, however. For instance, studies of ice cover dynamics are much more common in large rivers whereas ecological studies tend to occur in headwater streams, limiting our understanding of how these processes scale. Moreover, few studies have attempted either to integrate the physical and biological aspects of river ice (e.g., Turcotte & Morse, 2017) or evaluate winter ecological processes and patterns across river networks (e.g., Mejia et al., 2019).

Thus, our principal aim in this review is to integrate knowledge about current and future ice processes in rivers with what is known about ecological processes and communities, subjects that remain fairly distinct



in the literature. In doing so, we assess whether there are general patterns in ice and winter ecological dynamics that vary across river networks by comparing how they differ between headwaters and larger rivers. We chose to focus on the "end members" of the river size spectrum (roughly defining small rivers as first to third order streams and large rivers as sixth order or greater) because of the lack of information spanning entire river networks. We searched Web of Science and Google Scholar with search terms including winter, river ice formation/breakup/phenology/ecology, climate impacts on river ice, winter limnology/ecology, watershed size, season, winter habitat/overwintering/macroinvertebrate/fish, and ecosystem metabolism. Because of data availability, we focused on Northern Hemisphere rivers with seasonal ice or snowpack and used "winter" and "cold-season" interchangeably to describe the period during the year in which there is snow or ice cover on rivers or the riparian zone.

Next, to fill some of the data gaps we identified, we provide new analyses evaluating longitudinal projections for river ice loss in several large rivers and quantifying how the importance of winter productivity to annual productivity varies with river size. Finally, we highlight the types of information needed to better understand the role of winter in rivers.

2. Ice Processes

Ice formation, ice type, and breakup are major physical forces that can influence the ecology of rivers during the winter. Most studies that monitor river ice patterns focus on large rivers that can either be resolved from remote sensing (Beaton et al., 2019; Chaouch et al., 2014; Chu & Lindenschmidt, 2016; Cooley & Pavelsky, 2016; Huntington et al., 2003; Pavelsky & Smith, 2004; van der Sanden et al., 2021), from in situ data in accessible locations (Arp et al., 2020; Janowicz, 2010; Lacroix et al., 2005; Magnuson et al., 2000; Rokaya et al., 2018; Shiklomanov & Lammers, 2014; Smith, 2000), or estimated using physically based models (Lindenschmidt, 2017; Park et al., 2016; Shen et al., 1995). Ice cover can vary greatly across biomes, varying from frequent solid ice formation in Arctic streams and rivers to open water conditions in steep alpine streams, for example. In addition, ice varies across and within river networks because of interactions with river gradient (gravitational forces and flow velocity) and thermal energy (e.g., thermal inertia, connection to groundwater (Turcotte & Morse, 2013, 2017). For example, while temperature exerts a greater control on ice cover dynamics of large rivers, other factors like vegetation, snow, channel morphology, and geologic setting, groundwater interaction, flow velocity, and geographic location become more important in regulating ice cover on small streams (Lind et al., 2016). Thus, given the importance of these multiple factors that determine ice cover, it remains a challenge to derive a comprehensive set of controls and predictions for river ice dynamics. The following three sections enumerate differences in ice types and formation, breakup, and trends across river sizes, highlighting a particular need for increased research on patterns of ice change within small streams.

2.1. Ice Types and Formation

River ice formation processes are driven by interactions among climatic factors, like temperature and precipitation; hydrologic processes, such as flow and turbulence; and channel characteristics (Prowse et al., 2007; Turcotte & Morse, 2013). Although earlier literature describing river ice formation generally centered on ice processes in large low-gradient rivers (e.g., floating ice cover; Beltaos, 1995; Newbury, 1968), newer models and studies have begun to expand focus to rivers across the size continuum (Buffin-Bélanger et al., 2013; Turcotte & Morse, 2013) and consider implications of different ice types on hydrological conditions within rivers (Lind et al., 2016; Stickler et al., 2010; Turcotte & Morse, 2017). Models of watershed ice regimes predict different types of ice cover based on winter intensity and interactions between channel width and steepness (Turcotte & Morse, 2013). The Turcotte and Morse (2013) model indicates that in low-grade to moderate-grade reaches, floating ice cover dominates (e.g., Figure 1f). In contrast, high-gradient reaches support suspended ice cover (moderate-steep channels) and ice shells (very steep channels) (Figure 1e), which are often a combination of spray ice, or wave-induced icings. In smaller rivers, ice shells can form in lower gradient reaches than observed in larger rivers. Solid ice cover typically forms in rivers representing a specific intersection of width and climate. For example, in narrow channels solid ice cover can form only in Arctic climates, but in headwater streams, it can also occur in sub-Arctic climates. Spanning all river sizes, frazil ice, tiny ice crystals that form because of supercooling from turbulent zones, are known to accumulate





Figure 1. Images of common ice formations in rivers and streams. (a) Ice jam on the Upper Mississippi River near Bellevue, Iowa (photo: Travis Kueter, Iowa Department of Natural Resources); (b) Surface ice core filled with filamentous algae from a backwater of the Upper Mississippi River near La Crosse, Wisconsin (Photo credit: Rebecca Kreiling, U.S. Geological Survey); (c) Anchor ice on the margins of the Elbow River near Calgary, Alberta, Canada (Photo: Liz Perkin, Native Fish Society); (d) Frazil ice consolidating into surface ice in the mainstem and solid ice in a backwater of the Rum River near Anoka, Minnesota (Photo: Adam Pender); (e) Suspended ice cover over Plante Creek near Obed, Alberta (Photo: Liz Perkin, Native Fish Society); (f) Aerial image of lateral variation in ice formation across a river channel - solid ice formation along channel margins and frazil ice in the main channel of the Rum River near Anoka, Minnesota (Photo: Adam Pender).

and adhere to each other following ice-free turbulent zones in rivers, like riffles, or form in rivers that do not completely freeze over during the winters but experience freezing climates (Martin, 1981). Because frazil ice rapidly accumulates, it can form other ice features, such as anchor ice or ice jams by adhering to other stationary features like rocks, pilings, or ice (Martin, 1981). Thus, the interactions between channel width, steepness, and winter intensity result in a myriad of ice types in rivers, described in detail in the supporting information (Table S2).

Interactions between dynamic climatic or hydrologic factors and watershed or channel characteristics produce spatial and temporal variation in ice formation. While ice types can be predicted from models, empirical work to characterize ice formation in different sized rivers and channel types is limited to a few studies that describe heterogeneity and controls on ice cover and formation, primarily in boreal or Arctic areas of Scandinavia and Canada (Buffin-Bélanger et al., 2013; Lind et al., 2016; Stickler et al., 2010; Turcotte & Morse, 2017; Turcotte et al., 2014b). Although ice formation can vary substantially across biomes (e.g., boreal, alpine, temperate forest), four major themes emerged from the literature. First, ice types in small





Hydrogeomorphic template of ice-covered rivers alters the space available for ecological processes and impacts ecologically-relevant physical factors: light, flow, turbulence, and temperature

Ice cover types impact light and stream velocity, which are important factors for autotrophs, biogeochemical processing, and habitat condition

Ice cover types impact both the turbulence and the water temperature under ice, critical factors for rates of ecosystem processing and habitat selection of stream organisms, like macroinvertebrates and fish.

Figure 2. Conceptualization of how ice cover and type (Panel 1) affect ecologically important aspects of a river's physical template through altering flow, light, turbulence, and temperature. Panel 2-Light availability and flow velocity. Ice transparency changes with ice type, formation, and snow depth. For example, ice jams and thick river ice reduce light penetration, thin and clear layers of ice may not change the light environment, but snow can impede most light. At a constant streamflow, ice can reduce the total cross-sectional area of the river and increase flow velocity. Panel 3-Turbulence: Under ice, turbulent conditions form and affect habitat availability; especially under ice jams (Caissie et al., 1997; Martin, 1981). Panel 4-Temperature: Water in direct contact incident radiation tends to be warmer than water under ice, with the notable exception of interference from warmer groundwater (Barrineau et al., 2005; Beltaos & Burrell, 2006; Berg, 1994; Marsh & Prowse, 1987; Prowse & Beltaos, 2002). However, turbulent water supports "supercooling," forming frazil ice. This phenomenon decreases water temperature in turbulent zones (Martin, 1981). Finally, throughout the figure we identify presumed linkages between physical effects of ice and their ecological effects through the annotations. We note, however, that this simple conceptualization of how the "ice-scape" affects ecology is limited to one hypothetical river reach, and will vary across biomes, land use types, with watershed geomorphology (e.g., slope, width, geology, connectivity), and this template is simplified to assume no major groundwater influence.

rivers differ substantially from that of large rivers and the way ice forms is highly dependent on channel gradient, channel morphology, and weather characteristics such as the amount and type of precipitation (Buffin-Bélanger et al., 2013; Turcotte & Morse, 2013; Turcotte et al., 2012). In general, smaller rivers tend to have a wider range of ice types than large rivers (e.g., anchor ice-Figure 1c, suspended ice cover and ice shells-Figure 1e, solid ice coverage, floating ice), due to variation in channel morphology (e.g., presence of woody debris dams) and degree of warming from groundwater (Turcotte & Morse, 2017; Turcotte et al., 2014a).

Second, the timing of freeze-up among rivers in a given region varies with river size. Within a river network, excluding effects from groundwater input, small streams experience an earlier freeze-up than larger rivers which have substantially more thermal inertia (Danks, 2007; Turcotte & Morse, 2017). For example, in channels with little groundwater influence such as the Etchemin watershed in Canada, the second (Bélair-Sud Creek-3m width) and third (Le Bras Stream-20m width) order streams froze up over approximately two weeks. In the much larger fourth order river (Etchemin River-60m width), the freeze-up took six weeks (Turcotte & Morse, 2017). In larger rivers, different parts of the channel freeze at different times. Ice often forms first on channel margins, on objects within the channel such as bridges or boulders, or in off-channel areas, prior to formation along the thalweg, if it does in fact freeze at all (Danks, 2007; Figures 1d and 1f).

Third, this variation in ice formation processes (both ice type and timing of ice formation) within and among streams in a network can change the heterogeneity and stability of flow conditions (Figure 2; Lind et al., 2016; Stickler et al., 2010; Turcotte & Morse, 2017). In many cases, ice formation induces a positive



feedback loop whereby initial ice formation reduces streamflow which promotes more ice formation (Lind et al., 2016; Stickler et al., 2010; Turcotte & Morse, 2017). For example, in small streams, complete ice (either through ice dams or anchor ice) shifts streams from mainly fast flowing habitat to slow-flow pools, despite no overall change in streamflow (Stickler et al., 2010). Flow velocity and turbulence can also increase in association with ice formation (Figure 2). These shifts are likely to have particularly important implications for winter habitat and ecosystem processing rates, but their effects have not been widely studied.

Fourth, the spatial heterogeneity of river ice formation is linked to surface water-groundwater interactions, which is not necessarily predictable with river size and adds additional complexity to understanding how ice formation scales across river networks. The influence of groundwater on winter hydrological processes is tightly linked to the depth from which groundwater is sourced (Woo, 2012). Groundwater discharging from relatively deep sources (e.g., >7 m in northern temperate regions—see Kurylyk et al., 2013, or from thermal hot springs) remains at a constant temperature through time. As such, groundwater discharge into rivers can be buffered from contemporary air temperature flux, and thus can limit the development of river ice (see O'Sullivan et al., 2019). However, shallow groundwater is more influenced by contemporary air temperature and is absent from rivers in winter (see Clark et al., 2001). In addition, in some cases groundwater can also induce ice growth (e.g., naled, icing, or aufeis ice formations; Ensom et al., 2020).

Although river geomorphology and latitudinal climatic gradients lend some predictability to patterns in river ice formation across watersheds (Turcotte & Morse, 2013), climatic events at sub-seasonal time scales, such as rain on snow, and winter "whiplash" events (*sensu* Casson et al., 2019) can alter the timing of ice formation (Turcotte & Morse, 2017). Specific weather patterns can have divergent responses with respect to ice cover, depending on local context and antecedent conditions. For example, rain on snow followed by cold days can promote more ice formation, whereas consistent early snow can have an insulating effect, limiting ice cover growth (Turcotte & Morse, 2017). More detailed studies of the scope of variation in river ice within a season, across years, and in ecosystems or biomes where ice-formation processes are rarely described (e.g., alpine) are needed to characterize watershed 'ice regimes.'

2.2. Ice Breakup

Ice breakup processes are often influenced by the types of ice formed on the channel. In contrast to freezeup, however, the dominant controls on ice breakup, timing, and style are climatic rather than geomorphic. Ice breakup remains poorly studied in smaller rivers, with a biased research focus on large, high-order, rivers (Turcotte & Morse, 2013). In part, this discrepancy is likely due to (a) the high economic impact of ice breakup-associated ice jam floods on large rivers which cause an estimated \$300 million (2017 USD) of damage each year in North America (Rokaya et al., 2018), (b) the importance of these high-order rivers for transportation (Lonergan et al., 1993; Stephenson et al., 2011), and (c) the ease of large-scale ice detection on high-order rivers using remote sensing (Beaton et al., 2019; Chaouch et al., 2014; Chu & Lindenschmidt, 2016; Cooley & Pavelsky, 2016; Pavelsky & Smith, 2004).

In large river systems, breakup is often described as a balance between driving forces such as increased streamflow caused by snowmelt or rain on snow events, warming air temperature, and groundwater input, and resisting forces such as river ice thickness and strength (Beltaos & Prowse, 2009; Jones et al., 2015; Prowse et al., 2007; Turcotte & Morse, 2013). The balance between driving and resisting forces causes the breakup process to range between mechanical and thermal breakup, each with different biological, hydrological, and ecological effects.

Within large rivers, mechanical breakups also referred to as premature breakups, are often associated with rapid runoff and high rainfall events prior to ice melt. The severity of these events is directly related to the presence of high resisting forces such as thick poorly degraded ice in conjunction with the rapid onset of strong driving forces such as increased streamflow due to rain on snow events (Beltaos, 1997; Beltaos & Prowse, 2009). It is these mechanical-style breakups that are commonly associated with ice jam flooding (Figure 1d). This flooding is often damaging to human infrastructure (Rokaya et al., 2018) and can be responsible for transporting extremely elevated levels of sediment and nutrients, such as phosphorus and nitrogen, downstream and to adjacent floodplain ecosystems (Beltaos & Burrell, 2016; Burrell & Beltaos, 2019; Milburn & Prowse, 2000; Moore et al., 2013; Prowse, 1993; Scrimgeour et al., 1994; Toniolo et al., 2013). Ad-



ditionally, these events cause rapid increases in river water temperature, which can be harmful to riverine flora and fauna (Scrimgeour et al., 1994). In contrast, thermal, or overmature breakups, are associated with slow deterioration of river ice (resisting force) due to warming air temperatures (driving force) and are usually not associated with rain-on-snow events (Prowse et al., 2007). Thermal breakups are rarely associated with ice jam flooding and allow water temperature to rise more slowly (Scrimgeour et al., 1994). Less sediment and nutrient transport is associated with this breakup type (Beltaos & Burrell, 2016; Burrell & Beltaos, 2019; Prowse, 1993).

Within headwater streams, the framework of breakup as a balance between driving forces and resisting forces still applies; however, the specific forces may differ (Turcotte & Morse 2013, 2017). In steep systems, breakup timing is a balance between suspended ice cover and elevation (resisting forces) relative to water level (driving force), or ice dam size (resisting force) relative to channel width (driving force; Turcotte & Morse, 2013). Both breakup endmembers are also possible within these headwater systems but manifest differently than in their larger counterparts (Turcotte & Morse, 2017; Turcotte et al., 2014a). Bedfast/anchor ice and ice dams are common, and thermal breakup occurs when these ice types are sufficiently thick enough for increases in discharge to flow over the top of the ice and melt it slowly. Alternatively, mechanical breakups commonly begin when an increase in streamflow mobilizes suspended ice features that lead to ice jams and javes (Turcotte & Morse, 2013) and likely disrupt benthic communities or ecosystems encased in ice.

While we can generally summarize each of these breakup types, it is key to acknowledge that the interplay between river width, driving forces, resisting forces, and breakup style is highly location specific, even within low order streams in the same watershed. For example, a study that focused on the variability of ice processes in channels of varying width within the lower Montgomery River watershed in Canada (Turcotte et al., 2014a) highlights the importance of multi-scale controls on ice breakup. They showed that for the smallest studied channel (1–2 m width), mechanical breakup was impossible because most ice cover, if it had been there at all during the winter, had weakened or vanished due to groundwater input prior to the Spring freshet. Contrastingly, in the next largest channel (3–4 m), both surface ice and channel border ice were present at the time of breakup. During the breakup, surface ice was removed first, but border ice was able to stay in place and melt slowly while being submerged by increasing discharge for several hours because it was strongly attached to channel margins. In the next largest channel (15–20 m), breakup of surface ice and lower-level ice occurred at approximately the same time once boulders in the channel were submerged by increasing streamflow. This differed from the next smallest channel because many of these ice features were structurally independent, were not fused as strongly to channel margins, and were, therefore, easier to mobilize.

2.3. Ice Timing Trends

Ice timing and duration are shifting due to warming winter temperatures (Magnuson et al., 2000; Prowse et al., 2010; Yang et al., 2020) but how these trends are occurring in small versus large rivers is not well studied. Further, the response of ice cover patterns to warming temperatures may not be straight-forward: predicted climate warming is hypothesized to decrease water temperatures in steep headwater channels due to reduced insulation from ice cover, whereas larger channel water temperature may increase due to larger-scale climate factors such as winter intensity and duration (Turcotte & Morse, 2017). Given the difficulty of observing large scale ice cover in headwater streams, trends in ice timing have not yet been widely quantified in headwater catchments, therefore we are not able to enumerate trends and patterns in these small systems in this review. However, ice timing trends in medium and large rivers have been well-evaluated using both *in situ* (Huntington et al., 2003; Janowicz, 2010; Lacroix et al., 2005; Magnuson et al., 2000; Prowse et al., 2007; Rokaya et al., 2018; Shiklomanov & Lammers, 2014; Smith, 2000) and remote sensing methods (Cooley & Pavelsky, 2016; Pavelsky & Smith, 2004; Yang et al., 2020).

Globally, river ice breakup timing is highly correlated to air temperature, particularly the spring 0-degree C isotherm (Bonsal & Prowse, 2003; Lacroix et al., 2005; Prowse et al., 2002), and has predominantly been getting earlier within the past 150 years (Cooley & Pavelsky, 2016; Huntington et al., 2003; Janowicz, 2010; Magnuson et al., 2000; Prowse et al., 2007; Rokaya et al., 2018; Shiklomanov & Lammers, 2014; Smith, 2000). Earlier breakup dates are associated with more severe mechanical breakups, which have been correlated with increased flood risk (Rokaya et al., 2018). However, trends may not



be linear through time. For instance, as climatic extremes become more frequent (Landrum & Holland, 2020), river ice cover is primarily expected to get more variable with more frequent shifts from ice cover to open water both within and among years. This can lead to more frequent midwinter breakups as well as longer midwinter open water periods particularly within temperate and maritime regions, increasing ice jam flooding risk as the temperate region extends northward (Beltaos, 2002; Prowse & Beltaos, 2002; Rokaya et al., 2018).

Trends in breakup, however, differ in their magnitude geographically, within individual rivers, and across river orientations. For example, trends toward earlier breakup in Canadian rivers are strongest in Western and Southeast Canada, whereas areas of Central and Atlantic Canada have experienced slightly later breakups due to varying climate oscillation cycles across the region (Lacroix et al., 2005). River ice breakup trends have shown to be variable even along a single river profile (Cooley & Pavelsky, 2016). This variation highlights the need for ice trend observations along river profiles, instead of at discrete locations which may not reflect basin-wide patterns.

Freeze-up trends are less consistent than breakup trends, likely because freeze-up timing is less correlated to air temperatures and more related to geomorphology (Lacroix et al., 2005). While analyses of lake ice records document later freeze-up dates (Du et al., 2017; Magnuson et al., 2000), reviews of freeze-up dates in Canadian rivers found that patterns of freeze-up were spatially complex and were less important and consistent than breakup (Lacroix et al., 2005). Most existing studies show that freeze-up dates in river ice trend later (Magnuson et al., 2000), but some have found that freeze-up can occur earlier or has become more variable over time (Lacroix et al., 2005).

In general, ice cover duration on rivers is decreasing and becoming more variable, driven primarily by earlier spring break-up. The magnitude of this change depends on location, river orientation, and possibly on river size. Applying a temperature-based river ice model (Yang et al., 2020) for seven large northern rivers, we estimated the longitudinal ice duration gradient (i.e., the slope of estimated ice duration with downstream distance; see supporting information for detailed description). We found that, under RCP8.5 (Thrasher et al., 2012), all studied rivers, irrespective of orientation, were more likely to see reduced ice cover duration (Figure 3). However, due to amplified warming near high latitude regions, north-south oriented rivers were more likely to experience a reduction in surface air temperature gradient from headwaters to river mouth, which led to a reduced ice duration gradient along the river profile (Figure 4 and Table S1). In contrast, east-west flowing rivers show enhanced surface air temperature gradients (Figure 4 and Table S1). The ecological effect of these changes in temperature difference, thus ice cover, between headwaters and downstream, is unknown, but reduced temperature gradients are typically associated with thermal breakups and reduced ice-related flooding, indicating that riparian zones of the north-south rivers may experience decreased flood-associated nutrient inputs, while east-west rivers may see an increase in flooding (Beltaos, 2002; Beltaos & Prowse, 2009). Note that the air temperature-based ice prediction does not take into account landscape influences on river ice formation that have been found critical to accurately describing the complexity of river ice processes via its influence on water temperature (Fullerton et al., 2015; O'Sullivan et al., 2019, 2020). Further, anomalous ice conditions, like mid-winter breakups, are also projected to increase in frequency as the climate warms. In general, more variable ice conditions and more abrupt ice melt timing leads to more mechanical breakups. However, as rivers experience warmer winter temperatures, ice thickness will likely decrease favoring more thermal breakup, but this trend is poorly described (Prowse et al., 2010).

3. Ecological Processes

Winter is considered among the most critically challenging periods during the life cycle of stream organisms (Brown et al., 2011; Cunjak et al., 1998; Danks, 2007). Currently most of the understanding of winter ecology in rivers comes from particularly detailed studies on stream salmonids (Brown et al., 2011; Cunjak, 1996; Cunjak et al., 1998; Heggenes et al., 2018; Huusko et al., 2007) and fish communities more generally (Andrews et al., 2019; Bodensteiner & Lewis, 1992; Johnson et al., 1998; Knights et al., 1995). However, applicability of this work to other aquatic species and its generality within and across watersheds in different biomes is not well understood (Brown et al., 2010). In addi-





Figure 3. Modeled annual river ice duration along seven large rivers of different orientations from 2019 to 2099 using the 0-degree isotherm model developed by Yang et al. (2020). Of the rivers included, the Peace and Yukon Rivers run west to east, the Mackenzie, Lena, and Yenisey Rivers run south to north, while the Mississispip River runs north to south. The Missouri River starts west to east, but continues running southward after around 1,000 km. On each of the graphs, yellow represents the year 2099, while dark purple represents the year 2019; in every river case, as the years progress, ice duration decreases. Finally, in general, southern parts of the rivers have fewer days with ice than northern parts.

tion, despite the increasingly well-documented predicted change in ice cover, there are few quantitative studies relating ice dynamics to ecological and food web processes in rivers (Blackadar et al., 2020; Elser et al., 2020; Honeyfield & Maloney, 2015; Hood et al., 2018; Junker et al., 2020; Prowse, 2001). The presence of ice and snow can dramatically alter the physical river template on which ecological processes occur. We hypothesize that changes to ice processes primarily influence ecological processes through altering available space, flow velocity, temperature, and light availability (Figure 2). In this section, we review what is known regarding how ice processes affect physical habitat availability, explore patterns in winter ecosystem energetics and community dynamics, and discuss how these responses may differ from headwaters to the largest rivers.





Figure 4. Annual gradient of ice duration along downstream direction and their trend (represented by the blue line). Gray shading indicates 95% confidence interval of the trend line. The gradient values (represented by the points) were estimated as the slope of the linear regression between ice duration and downstream distance (days/1000 km).

3.1. Habitat

The presence of ice within a river channel alters several aspects of the physical river template, which has important implications for habitat for the biotic community during winter. Ice cover modifies the type and distribution of habitat through reducing space and limiting movement of species, altering local flow dynamics, and reducing light availability (Figure 2; e.g., Cunjak & Randall, 1993). Frazil ice, accumulating underneath an ice sheet, can transform a summertime low turbulence pool into a torrent during winter, rendering it unsuitable overwintering habitat (Figure 2; e.g., Caissie et al., 1997). In general, there is a more robust understanding of how these factors affect habitat for fish than for other lower trophic level organisms. This work has shown that fish tend to choose winter habitats to minimize energy expenditure and avoid adverse conditions such as ice jams, high flows, and low oxygen (Cunjak et al., 1998; Huusko et al., 2007), which is likely the case for other riverine biota as well (e.g., Danks, 2007). Ice can also reduce the availability of and migration to better habitat through physical space limitation (e.g., off-channel areas filled with frazil ice) or through altering flow conditions (Cunjak, 1996). Ice formation deflects and concentrates water current (Prowse, 1994) toward midstream (thalweg). The concentration of thalweg flow also induces heat energy gains from fluid friction (Newbury, 1968), thereby reducing the suitability of these areas for fish and altering stream substrate conditions for benthic organisms. Limited movement can further reduce access to prey, limit long-distance migrations to desirable winter habitat, and affect fish behavior (Cunjak, 1996; Linnansaari & Cunjak, 2013; Whalen et al., 1999). Therefore, the availability of refugia, either as in-stream features such as large wood or in some deep pools (depending on frazil ice accumulation; Caissie et al., 1997), accessible off-channel areas, early winter access to migratory corridors, deeply sourced groundwater tributaries (O'Sullivan et al., 2019), or even the ice itself, are particularly important for winter



survival of fish and likely macroinvertebrates and periphyton (Huusko et al., 2007). However, the presence of surface ice may also be beneficial to biota, as it offers insulation from extreme weather events (Andrews et al., 2019, 2020) and acts as a stable substrate for colonization in turbulent or scouring environments (Figure 1b; Katz et al., 2015; Twiss et al., 2012). Finally, in rivers of all sizes, ice can reduce water column and benthic light availability during the winter thereby limiting suitable habitat for photosynthetic organisms or visual predators, but the degree to which this occurs depends on the spatial extent, thickness, and clarity of ice and snow cover (Sharma et al., 2020).

The effect of ice on physical habitat is likely to differ with channel/river size and across biomes. Ice has greater potential to interact with the substrate in small, shallow, groundwater-limited rivers (e.g., more likely to freeze completely or form anchor ice), whereas ice tends to form above the aquatic community as surface ice in larger rivers (Turcotte & Morse, 2013). Therefore, in small to medium sized rivers, ice is more likely to have a direct, physical effect upon biota. For example, the formation of anchor ice encases benthic habitats in ice, forcing benthic invertebrates to the water column (Danks, 2007). Similarly, stream fish migrate out of the main channel to avoid direct interactions with ice, increasing the occupation of backwaters (Huusko et al., 2007). In contrast, in deeper areas of larger rivers, the effect of ice is often more similar to that seen in lakes, whereby surface ice does not reach the riverbed and water close to the riverbed is too warm to facilitate the formation of anchor ice (Prowse, 2001). This can depend on channel morphology, however (Caissie et al., 1997). On large river edges, a build-up of anchor and frazil ice often encases the benthos and water column, though direct evidence of how biota respond to these changes in river habitat is lacking; it is likely that similar to lakes, invertebrates will migrate to deeper water as ice develops on lake shorelines (Danks, 2007). The effect of ice on habitat will also vary substantially with latitude. For example, in Arctic rivers, shifts from bedfast to floating ice cover as winters warm (Prowse et al., 2011) may increase benthic macroinvertebrate survival and increase rates of productivity in early spring (Kendrick & Huryn, 2015). Additionally, hydrogeological features in Arctic rivers, such as rock glacier springs (Harrington et al., 2017), can provide flow, light, and thermal refuges and thereby ecological niches (Füreder, 1999). Similarly, in high altitude regions, such as Alpine rivers, ice formation conditions vary depending on surface water-groundwater interactions (Harrington et al., 2017). For instance, kyral reaches (glacial meltwater fed) can run dry, freeze to the substrate, or run beneath snow cover, while krenal reaches (groundwater fed) can remain ice free (see Ward, 1994).

Ice breakup can be a major disturbance for stream habitat, but the degree to which breakup alters or resets habitat conditions will depend on the nature of the breakup. Mechanical breakup is associated with substantial ice scouring and jamming events that dislocate some biota while creating habitat for others (Peters et al., 2021). Though few studies directly explore the effects of ice scour on stream habitats (Blackadar et al., 2020), ice scour may have positive or negative effects, increasing habitat and species diversity in some cases and disrupting spawning habitat affecting developing eggs or juvenile stages in others (Cunjak et al., 1998; Prowse, 2001). Detailed studies of how ice cover, ice duration, and ice breakup dynamics influence habitat availability and use by benthic organisms during the winter will be particularly important in understanding how the structure and function of these communities may change as river ice cover is lost (Blackadar et al., 2020; Kendrick & Huryn, 2015; Uehlinger & Naegeli, 1998).

3.2. Ecosystem Energetics

Ecosystem metabolism-the sum of gross primary production (GPP) and ecosystem respiration (ER) - is generally understood to increase with river size as a result of physical and chemical changes that occur across the longitudinal continuum from headwaters to large rivers (Finlay, 2011; Koenig et al., 2019; McTammany et al., 2003; Savoy et al., 2019). However, annual productivity regimes vary substantially among and within watersheds based on climate, geomorphology, riparian vegetation cover (light availability), temperature, and groundwater connectivity (Bernhardt et al., 2018). As such, watersheds will likely experience winter differently depending on where they are located, making generalizing how streams will respond to ice cover difficult. Further, because ice formation and breakup depend on several physical aspects of the river channel (e.g., depth, size, slope), how ice processes affect river metabolism are likely to vary substantially across a river network. For example, small headwater streams are more likely to be completely shaded by snow, covered in thick layers of ice, and may be more prone to rapid changes in snow cover than larger



rivers because of their size (Casson et al., 2012). In addition, rain on snow events may cause more frequent ice-breakups or anchor ice events in headwater streams than in larger rivers that have greater mechanical and thermal inertia. Further, groundwater makes up a greater portion of flow for many non-permafrost dominated small streams and therefore could keep water from freezing and provide opportunities for production or habitat during winter months.

We hypothesize that four major factors mediate how ice interacts with winter ecology in rivers of all sizes: grade, thermal regime, hydraulic connectivity (with the groundwater, hyporheic zone, floodplain), and light availability (Table 1). First, the slope of the river affects the function of river ice in the system. For instance, in high gradient rivers, river ice and snowmelt both scour biota and suspend sediment depending on the underlying geology (Fenoglio et al., 2014; Myrstener et al., 2020; Ulseth et al., 2018). Temperature and hydraulic connectivity interact to determine the type of ice breakup (thermal vs. mechanical) and formation. In mild temperature regimes, ice freezes from top to bottom, and under-ice warm refugia are enabled by warm groundwater connections (Barrineau et al., 2005; Marsh & Prowse, 1987; Prowse, 2001) or higher water residence time. In contrast, in Arctic, or extreme cold regions, cold groundwater driven by permafrost causes ice to freeze from bottom to top, prohibiting ecological activity in the benthos (Huryn et al., 2014; Shogren et al., 2020). In both cases, variability in temperature causes more freeze and thaw cycles, disrupting flow stability under ice (Prowse, 1994). Finally, the light regime of controls the timing of productivity. For example, small streams are often shown to have a late winter or early spring peak in productivity (Bernhardt et al., 2018; Savoy et al., 2019; Ulseth et al., 2018), which is related to the timing of snowmelt and leafout in the spring for deciduous catchments (Lutz et al., 2012; Roberts & Mulholland, 2007), summer flow instability in alpine regions (Myrstener et al., 2020; Ulseth et al., 2018), and low winter light availability in Arctic regions (Hauer et al., 2007; Huryn et al., 2014).

Annual productivity patterns also differ with river hydromorphology and connectivity, often peaking in river areas or during periods with longer residence time and varying with groundwater or floodplain connectivity (Hein et al., 1999; Houser et al., 2015). Thus, it is important to consider how the hydrogeomorphic setting of river channels influences how ice develops on that template and influences underlying productivity patterns (e.g., relative balance of benthic vs. pelagic productivity). For instance, ice tends to form and break up later in larger, deeper channels as a result of their thermal inertia (Buffin-Bélanger et al., 2013; Turcotte et al., 2012) and lateral variation of ice duration across the channel is common, as ice tends to form earlier and break up later in shallow, higher residence time locations like off-channel areas, backwaters, or channel margins (Blackadar et al., 2020; Brown et al., 2011; Danks, 2007). Therefore, typically productive channel margins and backwaters will have limited light for longer periods during the winter, while along the thalweg or the main channel, the flow may be too turbulent for primary producer communities to establish (Uehlinger, 2006; Uehlinger & Naegeli, 1998; Figure 2).

Given this variation, it is difficult to provide general predictions as to how changes in ice cover will influence ecological processes. There may be more predictable patterns by biome, thus we summarize what is known regarding ecological responses from each stream type (Table 1) separately below with a focus on headwater streams where we currently have the most information.

Temperate, forested headwater streams are characterized by spring peak in GPP, linked to the timing of snowmelt-delivered nutrients and canopy closure (Mulholland et al., 2009; Roberts & Mulholland, 2007). ER in these systems is tied to leaf litter inputs and often mirrors GPP (Mulholland et al., 2009). Winter values of metabolism are often not reported either due to total ice cover (resulting in sensor malfunction), or other physical constraints. However, seasonal studies that do include winter report that winter generally has the lowest rates of nutrient uptake (Hoellein et al., 2007), standing stocks of biomass and organic matter (Honeyfield & Maloney, 2015), and metabolism values of all the seasons with some exceptions (Blackadar et al., 2020; Mejia et al., 2019; Ostrofsky et al., 1998). Though metabolism may be low during the winter months, either due to low temperature or light impediment from ice, annual productivity and metabolism often depend on the timing and length of the snow-covered season (Casson et al., 2012; Mulholland et al., 2009). In addition, winter ice breakup and freeze-up were shown to be a driving force in maintaining "good quality" algal biomass and subsequent insect diversity throughout the year (Blackadar et al., 2020).



Table 1

Proposed Effects of the Light Regime, Temperature Regime, Slope Grade, and Degree and Degree of Hydraulic Connectivity (e.g., With the Groundwater, Hyporheic Zone, Floodplain, or the Catchment) on Wintertime Ecological Processes and How These Drivers Differ Among Major Winter Biome Types

	Light regime	Air Temperature regime	Grade	Hydraulic connectivity
Proposed winter effect relevant to ecological processes	Affects timing of productivity relative to ice on/off	Determines timing and thickness of ice Temperature anomalies could cause mechanical breakup of ice, which alters the opacity and thickness of ice	Determines ice function (e.g., scouring biota for steep catchments or ice rafting for low-gradient catchments) Determines ice opacity (steeper grades are associated with more opaque ice due to ice jams)	Determines ice type and depth Warm groundwater creates warm habitat refugia; cold groundwater supports complete freezes Floodplain or catchment connectivity affects availability of warmer off-channel habitat
Forested, deciduous catchment	High stream light in the spring and fall due to canopy shading during the terrestrial growing season	Variable (range = - 10°C to 30°C)	Variable	Warm groundwater input; catchment connectivity depends on geomorphology
Alpine catchment	Open canopy, uniform light	Cold (range = -15°C to 20°C)	Steep	Warm groundwater input; High hyporheic connectivity; catchment connectivity depends on geology
Arctic tundra catchment	Open canopy, summer light only due to winter "dark months"	Cold (range = -30°C to 10°C)	Shallow	Cold groundwater input High hyporheic connection but floodplain connectivity depends on freezing
Agricultural catchment	Dependent on riparian vegetation cover	Variable	Shallow	Warm groundwater input; overflow/ tile- drainage dominated Limited connectivity with hyporheic zone and floodplain
Urban- suburban catchment	Dependent on riparian vegetation cover	Variable	Shallow	Limited connectivity; overflow dominated; channelized



In contrast to the milder winters of deciduous headwater catchments, Arctic streams (above the Arctic Circle) experience long winters and are likely to completely freeze due to low sustained winter temperatures and reduced flow (Huryn et al., 2014; Shogren et al., 2020). Additionally, these streams have limited to no-light during the dark months, reducing the potential for winter productivity (Huryn et al., 2005, 2014). Because of the lack of light availability, bedfast ice, and their remote nature, winter metabolism is often not measured in Arctic streams. However, under current warming scenarios, more Arctic streams may have perennial flow, rather than intermittent, and have "dark-season" respiration exceeding that of deciduous catchments (Huryn et al., 2014). Similar to forested headwaters, productivity is limited in the winters, and the snowmelt period in Arctic rivers constitutes a majority of annual biogeochemical exports (Shogren et al., 2020). Shifts in the timing, magnitude, and form of snowmelt will invariably affect how winter fits into the rest of the year for Arctic streams (Beel et al., 2007; Myrstener et al., 2020; Shogren et al., 2020).

Alpine streams differ from forested and Arctic streams in that they typically contain no overhanging canopy, have a high slope, and do not uniformly experience dark months. As such, Alpine streams are incredibly variable in their ecological reliance on winter. Some Alpine headwater streams are hydrologically stable in the winters because of reduced rain-induced runoff (Myrstener et al., 2020; Ulseth et al., 2018). This stability promotes peak productivity during the winter, rather than in early spring due to spring-summer turbidity and turbulence (Myrstener et al., 2020; Ulseth et al., 2018). Greater hydrologic stability during the winter can also promote higher biomass of organic matter, algae, and insects that contribute to both primary and secondary productivity of these streams (Fenoglio et al., 2014). In addition, the snowmelt pulse in alpine regions resets the algal resource base through physical scour, determines availability of coarse particulates, and contributes substantially to the nutrient regimes in downstream reaches, underscoring winter's importance (Fenoglio et al., 2014).

Interestingly, studies of winter are relatively more common in anthropogenically influenced, low-gradient streams. These studies show that high flow events modulate the production response to winter (Beaulieu et al., 2013; Griffiths et al., 2012). In agricultural streams, winter nutrient uptake rates and metabolism tend to be lowest compared to other seasons; these low values coincide with increased winter discharge events driven by fallow fields (Griffiths et al., 2012). Intense winter storms rapidly transport nutrients downstream due to these low rates of uptake and the channelized nature of most agricultural streams (Griffiths et al., 2012). As mid-winter precipitation changes, increased winter streamflow events due to more snowmelt pulses could alter the amount of nutrient runoff in snow-covered agricultural streams. In contrast, in midwestern suburban streams, GPP was highest during ice-free winter days and dropped rapidly in the summer due to increased flow and turbidity (Beaulieu et al., 2013). The presence of ice and snow substantially altered the timing and magnitude of productivity by altering the number of days with high-light (ice-free) and low turbidity in the winter and spring months.

The measurement of metabolism is generally rare in larger rivers (Hall et al., 2016; Hotchkiss et al., 2015; Hosen et al., 2019), but even more so during the winter in cold regions or under ice (Mejia et al., 2019), making it difficult to assess variation among rivers in different biomes. Within the published literature, very few studies have specifically reported rates during the winter or early spring from larger rivers (e.g., Escoffier et al., 2018; Marcarelli et al., 2010; Mejia et al., 2019; Uehlinger, 2006; Uehlinger & Naegeli, 1998; Uehlinger et al., 2000), but similar to headwater streams, most were not collected with the intent of exploring winter metabolism. Seasonal metabolism studies in large rivers tend to either occur in regions with infrequent or no ice cover during the winter season (e.g., Dodds et al., 2013; Hall et al., 2016; Hart, 2013; McTammany et al., 2003; Ochs et al., 2013; Roach et al., 2014; Smith & Kaushal, 2015; Sobotka & Phelps, 2017; Val et al., 2016) or exclude winter (e.g., O'Connor et al., 2012; Snyder & Minshall, 2005). Like for headwaters, studies that report winter metabolic rates in large rivers typically show that wintertime GPP is lower than other seasonal values (Hosen et al., 2019; Marcarelli et al., 2010; Uehlinger, 2006; Uehlinger & Naegeli, 1998). In some cases, however, rates of both GPP and ER in larger rivers start to increase in late winter (February-March; e.g., Savoy et al., 2019; Uehlinger, 2006), depending on their location and hydrology (Uehlinger, 2006; Uehlinger & Naegeli, 1998). Rates were higher during winter than the rest of the year in the temperate Seine River near Paris, France (Escoffier et al., 2018) and in larger reaches of the Methow River (Mejia et al., 2019) located in a higher elevation area of Washington state. In both cases, the winter peaks in productivity were associated with low and stable streamflow conditions, low turbidity, and incomplete ice



cover thereby creating high light and stable conditions in the water column for growth of more cold-adapted species (Escoffier et al., 2018). Thus, as winters warm and ice off becomes earlier, this late winter/early spring period may increasingly contribute to annual productivity in rivers of all sizes Jankowski et al. (2021) and could have implications for the development of primary producer communities throughout the rest of the growing season. Evaluating how these seasonal connections play out within and across rivers in different biomes, across years with differing winter ice and discharge conditions, and in years with thermal versus mechanical ice breakups will be important avenues of investigation for understanding how winter fits into the annual productivity regimes of watersheds.

3.2.1. Scaling Winter Metabolism

Given the scarcity of measured data during the winter, there remain several unanswered questions, such as whether the longitudinal pattern of increasing GPP remains during winter, whether the contribution of winter productivity to annual productivity varies with river size, and whether spatial patterns in productivity during the winter mirror those that occur during the growing season. To address these gaps in knowledge and quantitatively compare the magnitude of winter productivity across gradients of river size, we used the annual time series of stream metabolism from a national-scale database (Appling, Hall, et al., 2018; accessed at https://data.streampulse.org).

Although this database has dramatically increased seasonal metabolism data availability, winter remains underrepresented in most systems, and especially in both the largest and smallest rivers (Figure 5). In addition, information remains biased toward rivers that are not consistently frozen during the winter, with only 25 sites with a mean winter air temperature between 0 and 2°C (supporting information), further emphasizing the need for more metabolism measurements in snow-covered areas. Nevertheless, we used these available data to assess how the role of the winter period changed among smaller streams (<10 m³ s⁻¹) mean daily streamflow), midsize (10–100 m³ s⁻¹), and larger rivers (>100 m³ s⁻¹) by comparing mean and max winter GPP, winter GPP as a percentage of annual GPP ("percent winter"), and the ratio of mean daily winter GPP to mean daily annual GPP ("winter: annual").

On average, we found that both percent winter and winter:annual GPP ratios were greatest in small streams and declined in mid and large size rivers (Figure 5). Percent winter reached nearly 40% in some small streams, but only 25% in larger rivers and mean daily winter GPP occasionally exceeded average annual GPP in some small streams (maximum = 1.2) but never in larger rivers. These results indicate that daily winter GPP is approximately equivalent to half of GPP in the other seasons on average, which is likely related to both cold temperatures and lower levels of light reaching the water surface (Kirk et al., 2020; Koenig et al., 2019; Savoy et al., 2019), caused by ice and as a result of lower solar irradiance during winter months.

We then evaluated factors that could influence winter GPP across all sites, including river size (as mean annual streamflow), latitude, winter temperature, and annual GPP using multiple regression models. All metabolism metrics were most strongly and positively associated with annual mean GPP, moderately positively associated with warmer mean winter temperature, but negatively related to river size (Table 2). Interestingly, our ability to explain variation in the scale of winter metabolism differed among metabolism metrics: we explained the most variation in mean and max winter GPP ($R^2 = 0.87$ and 0.77, respectively), some variation in winter: annual GPP ($R^2 = 0.25$), but very little variation in percent winter ($R^2 = 0.07$) among rivers. The latter is likely sensitive to variables describing winter duration and phenology (e.g., ice on and off), data for which are generally hard to find (or generate) for rivers of many sizes and were not available for the rivers in this data set.

Our results highlight several important features of winter productivity. First, sites with the highest annual productivity remained among the most productive sites during the winter (Table 2) indicating spatial patterns in productivity may carry over into the winter season (i.e., eutrophic rivers are still eutrophic in the winter). In addition, and not surprisingly, higher winter GPP occurred in areas with warmer winter air temperatures, indicating that winter river productivity is likely to increase as winter temperatures warm and ice cover decreases (Table 2). Last, the negative relationship of winter GPP with annual streamflow (i.e., river size) was strongest for the percent winter and winter: annual variables, supporting our general finding that winter was a smaller component of annual productivity in larger rivers (Table 2; Figure 5). This aligns with previous work showing that large rivers tend to have summertime peaks in metabolism whereas smaller





Figure 5. Variation in wintertime gross primary productivity (GPP) among rivers varying in size. (a) Map shows sites from StreamPulse database (Appling, Hall, et al., 2018) where annual metabolic data were available and which sites had sufficient winter data relative to where snowfall is most likely to occur in North America. Snow type information generated from MODIS imagery (Chamberlain, 2020; Wrzesien et al., 2019); (b) Distribution of values for winter and annual GPP in smaller streams (<10 m³ s⁻¹ mean daily streamflow), midsize (10–100 m³ s⁻¹), and larger rivers (>100 m³ s⁻¹). Data from Appling, Hall, et al. (2018); and (c) Table summarizing sample size, river streamflow, and metabolism metrics among small, midsize, and larger rivers.

streams tend to peak in early spring prior to canopy closure (Savoy et al., 2019), indicating a potentially greater importance of the winter period for metabolism in smaller systems. Together, our results indicate that the productivity of smaller rivers may be more sensitive to shortening winters than that of larger rivers (Figures 5b and 5c). Further, although GPP is generally higher in larger rivers, the cumulative productivity contributed by headwaters to network-scale production can be substantial as a result of their collective surface area within watersheds (Koenig et al., 2019). Thus, this difference in the reliance of rivers on winter productivity will have important implications for ecosystem and food web processes across river networks as winters change.



Table 2

Results of Multiple Regression Analysis Evaluating Controls on Several Aspects of Winter Metabolism Across Rivers: Percent Winter, Mean Winter Gross Primary Production (GPP), Maximum Winter GPP, and the Ratio of Mean Daily Rates of Winter to Summer GPP (See Text for Full Description of How Variables Were Calculated)

	Term	Coefficient	SE	<i>p</i> -value	R^2
Percent winter	Intercept	0.15	0.07	0.03	0.07
	Annual GPP	0.19	0.06	0.003	
	Winter temp	0.18	0.06	0.003	
	Annual streamflow	-0.19	0.06	0.001	
Mean Winter GPP	Intercept	0.55	0.03	0.001	0.87
	Annual GPP	0.95	0.02	0.001	
	Winter temp	0.14	0.02	0.001	
	Annual streamflow	-0.09	0.02	0.001	
Max Winter GPP	Intercept	0.89	0.42	0.04	0.77
	Latitude	-0.02	0.01	0.05	
	Annual GPP	0.89	0.03	0.001	
	Winter temp	0.14	0.05	0.004	
	Annual Streamflow	-0.04	0.03	0.16	
Winter GPP: Summer GPP	Intercept	0.0003	0.06	0.99	0.25
	Annual GPP	0.33	0.05	0.001	
	Winter Temp	-0.20	0.06	0.001	
	Annual Streamflow	-0.21	0.06	0.001	

Note. Covariates were standardized (Z-score) prior to analysis for easier comparison of model coefficients.

3.3. Communities and Food Webs

Winter food webs in ice-covered rivers differ fundamentally from summer food webs due to seasonal changes in habitat, food availability, and trophic interactions. Ice causes disruptions in species' habitats through altering water velocity and reducing access to habitat (Prowse, 2001), creating increased organismal stress as a result of unfavorable habitat conditions (e.g., low dissolved oxygen, Knights et al., 1995) and altering the space for foraging and species interactions. Further, in winter, resource availability from both autochthonous and allochthonous sources is also limited (Figure 6) because of reduced GPP, decomposition, and reduced inputs from a frozen catchment to ice-covered rivers (Prowse, 2001). Therefore, the models typically used to understand river food webs in summer are unlikely applicable in winter (Weber et al., 2013). A model by Humphries et al. (2017) highlights how trophic interactions among terrestrial species are likely to differ during winter because of differences in resource availability. They classify individuals either as seasonal specialists, i.e., species which are best adapted to summer or winter conditions, or aseasonal generalists, which continue to grow and forage throughout the year. They suggest that trophic position and body size are key predictors of where species fall on this gradient of specialization, where small-bodied, low-trophic position organisms such as benthic macroinvertebrates are primarily seasonal specialists, whereas larger-bodied carnivores are primarily seasonal generalists owing in part to their ability to forage over a wider area and on a wider variety of high-quality prey.

The degree to which lotic consumers are seasonal "specialists" or "generalists" is not well understood, and there are contrasting expectations regarding the degree to which lotic consumers continue to feed during winter months (Cummins et al., 1989; Humphries et al., 2017). For example, in forested systems, distinct guilds of invertebrate shredders, associated with tree litter that break down at fast, medium, and slow rates, result in seasonal peaks in the abundance and activity of certain macroinvertebrate guilds (Cummins et al., 1989). McMeans et al. (2020) detail seasonal specialization in a temperate lake fish community, whereby smallmouth bass are the most active predator in summer months but are replaced by lake trout in winter. Both species occupy positions close to the top of the lake food web, but their trophic behavior, growth, and





Figure 6. Conceptual model of seasonal variation in nutrient resources and invertebrate functional feeding groups in lotic systems, after Merritt and Cummins (2008). Altered terrestrial-delivered materials and light availability in temperate, deciduous systems promote distinct seasonally coupled food webs.

condition differ among seasons. In contrast, seasonal generalists, such as brown trout and Chinook salmon, continue foraging on seasonally abundant prey, primarily feeding on Chironomidae throughout the winter to maintain growth (French et al., 2017; Levings & Lauzier, 1991). The degree to which stream communities include seasonal generalists or specialists likely varies with ice cover and the degree to which winter food and habitat are available to support winter communities (Whalen et al., 1999).

Pronounced seasonal changes in resource availability and production within cold-season rivers drive substantial seasonal change in the resource use of stream and river consumers (Figure 6). Energy and nutrients that fuel river food webs are derived from allochthonous and autochthonous production pathways (Figure 6), and the relative importance of both pathways shifts among seasons, driving changes in the functional assemblages of seasonal specialist macroinvertebrates (Humphries et al., 2017). For example, small to moderate-sized forested rivers receive a large influx of terrestrial energy in the fall as the leaf pack falls resulting in a large pulse of coarse particulate organic matter (leaf litter, etc.) entering the river (Compson et al., 2018). During winter months, shredders break this material down to fine particulate organic matter that is fed on by collectors and filter feeders and ultimately mineralized by fungi and bacteria within river biofilms (Cummins et al., 1989). The terrestrial input drives a shift from autochthonous fueled food web in spring and early summer to one driven by allochthony in winter. Following ice-off in spring, the availability of nutrients through mineralization and increasing light, especially in the period between ice-off



and leaf-out, drives a shift back to autochthonous reliant food web through the summer months. Because macroinvertebrates are often prey for larger-bodied generalists, the seasonal food web could therefore be decoupled by shifting dominance of seasonal specialists that capitalize on these changes but coupled by seasonal generalists that retain nutrients among seasons. Evidence linking this seasonal shift in productivity patterns to ice cover or duration is sparse, but supporting evidence is available from several studies of non-ice enclosed temperate streams and rivers. In an investigation of seasonal variation in production in Icelandic streams, Junker and Cross (2014) report a shift from autochthonous driven food web in summer to an allochthonous one in winter. In similar investigations of stream meiofauna communities, Schmid-Araya et al. (2020) and Majdi and Traunspurger (2017) used stable isotopes to reveal seasonal shifts in consumers' trophic niches to incorporate greater amounts of allochthonous material during winter.

The consideration of aquatic consumers as seasonal specialists and seasonal variation in food web processes raises concerns regarding the effects of climate change on organism physiology (Blackadar et al., 2020; Elser et al., 2020; Honeyfield & Maloney, 2015; Hood et al., 2018; Junker et al., 2020; Prowse, 2001) and community phenology in seasonally frozen streams and rivers. For example, the life cycle of winter specialists is timed to coincide with the presence of suitable food and absence of predators (Cummins et al., 1989). Changes in the timing of ice formation and break up may disrupt these processes, with consequences for overall ecosystem productivity patterns. Such a breakdown in the phenology of ecological processes is a widely acknowledged consequence of climate change (e.g., Cohen et al., 2018). This process has received considerable attention in the terrestrial (Henden et al., 2017; Thakur, 2020) and marine (Tedesco et al., 2019) literature but comparatively few studies have examined its effect on stream food webs. Furthermore, the increased prevalence of mid-winter melt and rainfall events poses a direct threat to winter specialists relying on ice covered conditions for their preferred habitat. The absence of data to test these hypotheses was noted by Weber et al. (2013), and few studies have emerged following their call for more work on this topic. However, Weber et al. (2013), propose a conceptual model whereby increases in rain and snow and mid-season melt events influence river ecosystem function by disrupting winter habitat and modifying production pathways by introducing large amounts of terrestrial material into the river channel (2013). For example, Lamberti et al. (1991) estimated that it took three years for the stream ecosystem to recover following a catastrophic landslide resulting from an extreme mid-season rain on snow event caused in the U.S. Rocky Mountains.

The association between river size and the relative contribution of allochthonous materials to the food web has been widely studied (Vannote et al., 1980), but few studies have attempted to account for how winter resource shifts or the effect of ice cover affect food web productivity. The examples outlined above primarily relate to small- and medium-sized forested rivers with questions regarding this process in large rivers and rivers in other biomes remaining unanswered. Our metabolism analysis (Figure 5) indicates that winter productivity is a more substantial portion of annual productivity in smaller rivers, indicating that the degree to which food web pathways will shift seasonally will depend at least somewhat on river size. How these spatial differences in seasonal river productivity are translated into river food webs is a topic that would benefit greatly from careful study in the coming years.

4. Discussion

Despite these gaps in our understanding of the winter ecology of rivers of different sizes, several points emerge from synthesizing existing literature. The interaction of climate, river hydrogeomorphology (flow, size, and slope), and surface water-groundwater connectivity determine ice cover type and formation. In contrast, ice breakup timing and form are primarily temperature-driven: rapid fluctuations in temperature favor mechanical breakup while slow temperature changes favor thermal breakup. Differences in breakup types can influence ecological factors such as the extent of instream productivity due to ice scour and the exchange of nutrients with the floodplain via ice jam flooding common to mechanical breakups. The timing of winter ice conditions is projected to vary as winter temperatures increase and this aspect of winter climate change poses the greatest uncertainty in a river's ecological response.

Ice can act as both a beneficial and disruptive force in river ecosystems. Under stable ice conditions, ice can allow light penetration and increase flow heterogeneity (Figure 2). In rivers with warm groundwater connectivity, ice can insulate habitats, providing a refuge for winter specialists, primary producers, and other



dependent organisms. In small rivers especially, ice jams reduce flow and form pools that can provide temporary habitat for organisms, where turbulent frazil ice does not accumulate. However, under disrupting conditions (ice formation, freeze-thaw cycles, and breakup), ice and snow can scour or rearrange habitats, impede light, and alter riverine flow paths. The duration of time that ice-covered rivers spend in either stabilizing conditions or disrupting conditions varies by river size, orientation, and will likely change as winter temperatures continue to rise and winter whiplash events become more frequent (e.g., Casson et al., 2019).

4.1. Future Research Directions and Conclusions

The literature on the winter ecology of rivers is represented widely across disciplines from hydrology and engineering to fish and invertebrate ecology but is only in-depth in a few areas. Work on ice processes in large rivers and fish habitat in small streams represent the largest suite of available literature, with the largest gaps in our knowledge focused on winter dynamics of ecosystem energetics and food webs (Table 3). Most of the studies in this review pull either from the ice literature or ecological studies, exclusively, and few have attempted to link these fields. Thus, there is a pressing need to integrate studies of ice and ecological dynamics (e.g., Blackadar et al., 2020; Whalen et al., 1999) and quantify these linkages across river types (e.g., Turcotte & Morse, 2017).

Several additional avenues of research could improve our understanding of how ice dynamics influence river ecology both within the winter season and throughout the rest of the year (Table 3). For ice process, there is a lack of empirical studies quantifying how patterns and controls of ice formation vary with river size. Although long ice-cover records exist for some rivers (Benson et al., 2013; de Rham et al., 2020; Magnuson et al., 2000), more empirical data across rivers of all sizes, especially small rivers, that quantify multiple aspects of ice cover (e.g., ice characteristics, ice spatial extent and duration, frequency of mid-winter breakups) are needed to inform ecological studies and develop models that quantify ice processes at ecologically relevant scales. Further, our understanding of ice dynamics in larger rivers has advanced much more quickly than for small streams. Historically, research and modeling focus has been centered on larger rivers because of how ice threatens river infrastructure (e.g., Rokaya et al., 2018). In addition, satellite remote sensing of ice is much more feasible for the largest rivers (i.e., channel width >90 m; Yang et al., 2020) than for small streams that remain difficult to detect. Thus, there remains a particular need for studies of ice dynamics and trends in smaller rivers that can now be detected using finer-resolution satellites (e.g., Planet, Sentinel) or on-the-ground instruments (e.g., game cameras, drones, citizen science networks).

Better quantifying ice cover across watersheds would enable an improved understanding of its ecological role both during the winter and throughout the year. More studies of the physical-chemical role of ice cover, such as the effects of ice on light and flow conditions, the role of ice as a substrate (Figures 1 and 2), and how the timing and characteristics of breakup influence sediment/nutrient transport, are needed to better link ice cover to ecological processes. Although there is a comparatively large literature on winter habitat for stream organisms (Brown et al., 2011; Danks, 2007; Huusko et al., 2007; Whalen et al., 1999), it is predominantly focused on salmonids (e.g., Brown et al., 2011; Cunjak, 1996; Hedger et al., 2013; Linnansaari & Cunjak, 2013; Mejia et al., 2016; Whalen et al., 1999); studies of more diverse fish assemblages, as well as other aquatic organisms (e.g., macroinvertebrates), are needed during the winter in both small and large rivers.

Studies linking ice conditions to ecological dynamics such as nutrient cycling, productivity, or food web dynamics are particularly rare in rivers of all sizes (Blackadar et al., 2020). Specifically, there is a need for annual scale studies of metabolism and food web dynamics in rivers with perennial ice cover (e.g., Myrstener et al., 2020). Recently published information on stream metabolism fills some of that gap (Figure 5), but even the largest publicly available data set of stream metabolism on which we based our analyses (Appling, Hall, et al., 2018) is skewed toward streams that do not have seasonal ice cover. Comparative studies of annual ice and metabolic regimes within a river basin (e.g., Mejia et al., 2019) would be useful in understanding how changing ice cover would affect watershed phenology and annual productivity (Brentrup et al., 2020; Koenig et al., 2019; Savoy et al., 2019). Although the use of sensors to measure metabolism and nutrient dynamics under ice is increasingly common, more fully understanding the role of winter ice on the ecology in river networks will take creativity and interdisciplinary approaches (Sharma et al., 2020) given their scale, complexity, and unique logistical challenges (e.g., ice jams, ice flows). While a significant challenge, it is also an exciting opportunity to expand the field of river ecology.



Table 3

Knowledge Gaps and Research Needs Identified for Understanding River Ice Dynamics and Winter Ecology in Small Rivers (First to Third Order), Large Rivers (Greater Than Sixth Order), or Among River Networks

Торіс	River types	Unknown areas	Study directions
Ice formation	Small	Ability to use remote sensing of ice phenology is limited in small channels; therefore, detecting ice has been difficult across different small river types	Need empirical studies of ice formation across a broader set of ecosystems/biomes (e.g., alpine)
	Large	Limited knowledge of ice formation in areas outside of the main channel	Expand and improve remote sensing methods for quantifying ice phenology which are currently limited by complexity of formation processes as well as cloudiness and low light conditions during freeze-up
	River network	Very few studies that link upstream processes to downstream ice processes (e.g., at the watershed scale)	Need empirical studies of patterns and controls of ice formation across entire watersheds, including evaluations of synoptic weather patterns on ice formation
Ice Breakup	Small	Ability to use remote sensing of ice phenology limited in small channels	Need empirical studies of ice breakup that evaluate: (1) drivers and resistors of thermal vs mechanical breakup, (2) likelihood of ice jam flooding during mechanical breakup; (3) water temp and nutrient/ sediment transport during ice mechanical vs thermal breakups, (4) frequency of mid-winter breakups
	Large	Limited knowledge of ice breakup in areas outside of the main channel or the frequency of mid-winter breakups	Development and use of remote sensing (satellite, UAV), hydraulic models to evaluate ice processes in off- channel areas
	River network	Limited knowledge of how breakup upstream impacts downstream reaches	Empirical studies of patterns and controls of ice breakup across entire watersheds
Effects of Climate Change on Ice cover	Small	Limited information from remote sensing or <i>in situ</i> studies	Need <i>in situ</i> data to develop empirical models for ice dynamics (ice on, off, ice types, and thickness) that represent diverse hydrological, morphological, and climatological conditions
	Large	Coarse understanding of cover types changing via temperature models, but lack more robust ice characteristics	Need improvements in temperature-based river ice cover models to (1) consider effects from ice type and precipitation type (rain or snow), and (2) develop algorithm to retrieve variables beyond ice cover (thickness, ice type, etc.)
	River network	Lack information on river ice dynamics associated with other landscape changes (e.g., thawing permafrost);	Need more studies on rivers with varying groundwater types and connectivity
Energetics	Small	Limited measurements of winter/ annual metabolism in high gradient rivers with ice cover, in temperate forests and arctic catchments	More studies that specifically target winter/ cold-season energetics
	Large	Limited winter/annual measurements of stream metabolism in rivers with perennial ice cover, rivers at high latitudes	Need more comparison of winter productivity in rivers with benthic vs pelagic productivity; in areas outside of the main channel
	River network	Limited study of variation in winter metabolism or its drivers within a stream network/watershed, and with corresponding ice/snow cover	Need comparisons of the prevalence and timing of late winter/early spring productivity peak across stream types and sizes. Need studies that evaluate upstream- downstream effects of ice phenology and spatial, extent on productivity



Table 3	
Continued	

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Торіс	River types	Unknown areas	Study directions
Food webs	Small	Limited number of studies of non- salmonids or lower trophic level organismsLimited knowledge of feeding patterns of lotic consumers during winter, including seasonal responses to availability of prey	Need studies linking patterns in ice cover to resources supporting upper trophic levels across seasons (autochthonous vs. allochthonous)
	Large	Limited number of studies of food webs on larger rivers	Increased studies with more aquatic organisms (e.g., more than salmonids) during winter
	River network	Limited number of studies of food webs among many rivers in one network	Increased studies with more aquatic organisms (e.g., more than salmonids) during winter across rivers of different sizes

Note. We color coded the river types to indicate areas where there have been a greater number of studies (green), a moderate number of studies (yellow), and limited number of studies (red), based on this review.

These types of data are missing from the broader literature not only because of a historical focus on the growing season but also as a result of the difficulty required to obtain them (Block et al., 2018; Hampton et al., 2017). Furthermore, the challenges of winter sampling are distinct between larger and smaller rivers making designing and implementing a study across the entire continuum challenging and expensive. Although ice dynamics in larger rivers can now more easily be quantified from space (e.g., Kääb et al., 2019; Yang et al., 2020), large rivers can be difficult and dangerous to sample in the winter without expensive or specialized equipment such as snowmobiles or air boats thereby limiting the capacity to obtain more ecological information. Thus, the inclusion of the winter period in existing long-term monitoring programs would be beneficial and potentially feasible if the necessary equipment to sample larger rivers is already available. In addition, researchers may benefit from using large publicly available datasets (i.e., Water Quality data portal; https://www.waterqualitydata.us/) or remote sensing options available for larger rivers to detect river conditions such as turbidity and chlorophyll (Gardner et al., 2021; Kuhn et al., 2019; Olmanson et al., 2013; Topp et al., 2020) to explore these patterns more thoroughly during the winter. In contrast, although many small rivers and streams are more easily accessible for ecological sampling through conventional means (i.e., walking or driving; excepting those in high alpine or exceptionally remote locations), it is difficult to detect large scale differences in ice dynamics in small rivers. Thus, in situ data collected manually or with unmanned aerial vehicles (UAV) are currently the best means to increase our understanding of ice dynamics on extremely small rivers; therefore, researchers working in small streams during the winter may wish to incorporate information on ice and snow cover and phenology into their sampling plans.

Despite the multiple impacts of ice and snow cover on river ecosystems, we lack a general understanding of their influence on river ecology during the winter and throughout the year. Particularly important questions exist around how changing ice and winter duration may influence species habitat availability and migration, the timing and magnitude of ecosystem metabolism and nutrient cycling, and seasonal food web dynamics. Rapid and persistent physical changes in ice type and duration as a result of climate change not only affects ecosystems, but also can change the way humans recreate, utilize, and benefit from ice-covered rivers (Contosta et al., 2019; Sharma et al., 2020). Increased understanding of the magnitude of and responses to this change would assist future management and conservation of these ecosystems.

Data Availability Statement

All data supporting analyses in this review are accessible on online repositories. For the future river ice analysis (methods in supporting information), the Future River Ice Duration data set can be accessed from https://doi.org/10.5281/zenodo.4470153. The metabolism across the continuum analysis leveraged metabolism data (Appling, Hall, et al., 2018; Appling, Read, et al., 2018), MODIS-derived snow cover data (Wrzesien et al., 2019), and NOAA air temperature data (Chamberlain, 2020). Datasets for metabolism analyses were accessed at https://data.streampulse.org/ and provided by the StreamPULSE Network.



Supplemental MODIS snow cover data were accessed from https://doi.org/10.5281/ZENODO.2626737. Air temperature data for each StreamPULSE site were accessed from NOAA's Land Climatological Data (LCD) at https://www.ncdc.noaa.gov/data-access/land-based-station-data/land-based-datasets/quali-ty-controlled-local-climatological-data-qclcd and processed using R Core Programming language package, "rnoaa" (Chamberlain, 2020).

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