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REVIEWS

Using untapped telemetry data to explore the winter biology of freshwater fish

J. E. Marsden · P. J. Blanchfield · J. L. Brooks · T. Fernandes · A. T. Fisk · M. H. Futia · B. L. Hlina · S. V. Ivanova · T. B. Johnson · N. V. Klinard · C. C. Krueger · S. M. Larocque · J. K. Matley · B. McMeans · L. M. O'Connor · G. D. Raby · S. J. Cooke

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Abstract Winter is a challenging period for aquatic research—weather is uncomfortable, ice is hazardous, equipment fails, and daylength is short. Consequently, until recently relatively little research on freshwater fishes has included winter. Telemetry methods for tracking fish and observing movement behavior are an obvious solution to working in harsh conditions because much of the data can be collected remotely, and passive methods collect data year-round without winter maintenance. Yet, many telemetry studies do not collect data during winter or, if they do, only report data from the ice-free seasons while the remaining data are unused. Here, we briefly summarize the advantages and limitations of using telemetry methods in winter, including acoustic and radio telemetry and passive integrated transponder technology, then review the range of questions related to fish ecology, behavior, bioenergetics, and habitat use that can be addressed in winter using telemetry. Our goals are to highlight the untapped potential of winter fish biology

J. E. Marsden (✉) · M. H. Futia
Rubenstein Ecosystem Science Laboratory, University of Vermont, 3 College St., Burlington, VT 05401, USA
e-mail: ellen.marsden@uvm.edu

P. J. Blanchfield
Freshwater Institute, Fisheries and Oceans Canada, 501 University Cres, Winnipeg, MB R3T 2N6, Canada

P. J. Blanchfield
Department of Biology, Queen's University, 116 Barrie St., Kingston, ON K7L 3N6, Canada

J. L. Brooks · B. L. Hlina · S. J. Cooke
Fish Ecology and Conservation Physiology Laboratory, Department of Biology and Institute of Environmental and Interdisciplinary Science, Carleton University, 1125 Colonel By Dr, Ottawa, ON K1S 5B6, Canada

T. Fernandes · B. McMeans
Department of Ecology and Evolutionary Biology, University of Toronto, Mississauga Campus, 25 Willcocks St., Toronto, ON M5S 3B2, Canada

A. T. Fisk · S. V. Ivanova · N. V. Klinard · S. M. Larocque · J. K. Matley
Great Lakes Institute for Environmental Research, University of Windsor, 401 Sunset Ave., Windsor, ON N9B 3P4, Canada

T. B. Johnson
Glenora Fisheries Station, Ontario Ministry of Natural Resources and Forestry, 41 Hatchery Lane, Picton, ON K0K 2T0, Canada

C. C. Krueger
Department of Fisheries and Wildlife, Center for Systems Integration and Sustainability, Michigan State University, 115 Manly Miles Building, 1405 S. Harrison Rd., East Lansing, MI 48823, USA

L. M. O'Connor
Great Lakes Laboratory for Fisheries and Aquatic Sciences, Fisheries and Oceans Canada, 1219 Queen St East, Sault Ste. Marie, ON P6A 2E5, Canada

and to motivate scientists to revisit their four-season telemetry data and incorporate objectives specific to winter biology in future study plans.

Keywords Telemetry · Acoustic · Techniques · Tracking · Movement · Behavior

Introduction

Winter is a critical season for freshwater fishes that affects survival, bioenergetics, community structure, spawning, and recruitment (Shuter et al. 2012; Farmer et al. 2015; McMeans et al. 2020). Cold temperatures reduce metabolic rates, digestion, swimming capacity, and cell membrane fluidity (Fry 1947; Brett and Groves 1979). Because winter is a logistically challenging season for aquatic research due to cold, snow depth, ice cover, and safety issues (Brown et al. 2011; Shuter et al. 2012), even cold-adapted fishes are, perhaps conveniently, assumed to be quiescent in winter, with suppressed energy intake and expenditure - basically they are not doing anything of interest (Crawshaw 1984). Most fish research in temperate regions of the northern hemisphere occurs during the ice-free periods, and generally in summer, when seasonal staff and summer students are available to help conduct such research (Block et al. 2019; Fernandes and McMeans 2019). However, in temperate regions of the world the winter season is a predictable event that may comprise over 30% of the year. Currently, much of what we know about fish in the winter is derived only from anecdotes and a small body of empirical laboratory and field studies. Research focused on winter is needed to understand annual energy budgets, improve bioenergetics modelling, predict factors that affect recruitment, and anticipate the effects of global climate change. While winter telemetry cannot fully address many climate change effects on fishes such as changes in growth, mortality, diet, and energetics, the effects of shorter winters, less ice, less snow cover, and more frequent thaw periods will undoubtedly affect winter behavior of fishes and be documented in telemetry studies.

G. D. Raby
Department of Biology, Trent University, 1600 West Bank Dr., Peterborough, ON K9J 7B8, Canada

Among fish species with disparate thermal ranges, winter may simply be an interval between growth and reproductive seasons or a period of opportunity. In extreme cases, seasonal activity is reversed; for example, summer is the stressful, quiescent period for burbot (*Lota lota*) while winter is the period in which predation, growth, and reproduction occur (Grabowski et al. 2020). For cold-water species, cooling of the epilimnion and de-stratification opens a significant volume of habitat that is unfavorable for them in summer. Cold temperature is only one of many aspects of winter that affect fish. Dynamic ice conditions (e.g., anchor ice, frazil ice, hanging dams, ice flows, and high-water conditions associated with snowmelt in early spring) represent formidable challenges for fish and can lead to physiological stress, stranding, and mortality (Brown et al. 2011). Reduced sunlight due to low sun angle, shorter daylength, ice, and snow cover may reduce primary productivity (Greenbank 1945; Hampton et al. 2017). In lentic systems, winter hypoxia is common and can exacerbate the severity of winterkill events (Magnuson et al. 1985). Despite the challenges of winter, shorter, warmer winters under a changing global climate have been linked to reduced reproductive success in some fishes (Farmer et al. 2015). Studying fish behaviors during winter, particularly movement, foraging, energetics, and habitat use that influence growth and reproduction in other seasons, therefore remains a crucial research agenda.

Conducting research on fish biology in winter involves difficulties for people and operation of equipment for sampling, and unique logistical considerations. Cold exposure can cause hypothermia and frostbite, equipment is subject to freezing and battery life can be severely shortened, samples can freeze, and removing fish from the water may cause cold injury or mortality. Boat access to rivers and lakes may be limited by ice, and working on ice requires specialized safety training, such that some organizations restrict winter-weather work entirely. Many traditional approaches used to study fish during ice-free seasons do not easily translate to efficient, effective, and safe winter work. Routinely-used sampling tools such as electrofishing and netting (of all sorts) have limited utility in the winter, particularly after ice formation. Winter snorkeling and scuba require specialized training and equipment. The advent of underwater video and remotely operated underwater vehicles

(ROVs) have expanded the toolbox for studies (Mueller et al. 2006) but still can be logistically challenging to employ during the winter season and can only provide limited information on the distribution and behavior of fish (e.g., O'Malley et al. 2018).

In contrast to traditional fish research methods, passive telemetry provides unique opportunities to circumvent many of the challenges of winter work. The development of passive telemetry methods (i.e., where receivers deployed in the field automatically detect transmissions from tagged fish) for tracking and monitoring fish behavior has dramatically improved our ability to observe and quantify fish movements. Telemetry can be used to track individual fish at fine temporal scales (seconds between detections) in three dimensions year-round for multiple years. With sufficient numbers of tagged individuals, data can then be used to characterize populations. In freshwater systems, passive telemetry receivers are often left in place year-round. However, individual studies tend to focus on one or two particular questions and seasons, and ignore data from other seasons, particularly winter. Some researchers deploy tags that turn off in winter and back on in the spring so as to not waste valuable battery life during a period when fish are apparently "being boring". For example, the Great Lakes Acoustic Telemetry Observation System (GLATOS, a collaborative research network and database established in 2010; Krueger et al. 2018) has generated close to 400×10^6 detections of telemetry-tagged fish and 65 scientific publications within 10 years of its inception; however, "winter" does not appear in the titles of any of those papers and only four papers focus on seasonal comparisons based on their titles (https://glatos.glos.us/). The relatively few studies that use data from electronic tags to provide cross-seasonal comparisons of fish behavior and habitat serve as inspiration for the enormous untapped potential in existing telemetry datasets (e.g., Blanchfield et al. 2009; Brooks et al. 2019a; Colborne et al. 2019; Ivanova et al. in press). The strength of telemetry is the potential to examine temporal within-individual changes in behavior and habitat use, among-individual variation, and quantify behaviors and habitat use in winter when it would otherwise often be impossible to do so with traditional fishery surveys. In particular, winter telemetry can be used to understand anthropogenetic changes to climate, habitat, nutrients, and aquatic communities.

Here, we review potential uses of telemetry and develop research questions and priorities for winter data collection and analyses. Many of these questions can be addressed using existing data rather than starting new studies. The paper is focused on freshwater (lotic and lentic) work in temperate latitudes (approximately 23.5°–66.5°) where extensive studies of fishes have occurred, but winter has largely been overlooked. We begin by defining winter and providing a brief overview of the technical aspects of acoustic, radio, and passive integrated transponder (PIT) telemetry with specific reference to their deployment and performance in winter. We then review aspects of the importance of winter for fishes, highlighting the opportunities to study winter fish ecology, behavior, and bioenergetics using telemetry. We finish by presenting research questions and opportunities that span across the research topics and can be addressed with telemetry data. This paper is a stimulus/call for researchers to revisit their four-season datasets and incorporate objectives that include winter in future studies. We hope that this paper will inspire more researchers to consider how they can contribute to understanding the winter biology of fish and in doing so contribute to their conservation and management. The U.S. Endangered Species Act and Canadian Species at Risk Act both define and protect critical habitat, but winter critical habitat is poorly defined for most species; telemetry is one of most powerful tools to fill that information need. Note: we use 'telemetry' herein defined as remote data collection, whereas 'biotelemetry' specifies biological data (energetics, movement and behavior, physiology) that are inherent in some telemetry studies.

Defining 'winter'

Winter can be defined astronomically, thermally, or meteorologically (i.e., based on extent of ice and snow cover). Astronomically, winter is the period between the winter solstice and vernal equinox, with short daylengths and a low sun angle. However, the length, severity, impacts, and benefits of winter are dependent on latitude and elevation, so an astrological definition is not as relevant as a thermal definition for fish across latitudinal scales. Thermally, aquatic habitat during winter is a period of either isothermal conditions or reverse stratification, with the coldest water (< 4 °C) near the surface overlying the densest water (4 °C). Meteorologically, winter is the cold season which can range in the northern hemisphere from a few months to as many as nine months in the Arctic. From a practical standpoint, researchers often define winter as the period when ice is present (e.g., Shuter et al. 2012). However, frequency, extent, depth, and duration of ice cover are related to lake size and fetch and can show considerable variation among years. Climate change is also altering lake ice dynamics, generally reducing the duration of lake ice coverage and increasing interannual variability (Magnuson et al. 2000; Woolway et al. 2020). In extreme latitudes, 'winter' is the dominant season and ice-free periods are short. Thus, no simple definition of winter exists that is useful for all studies.

A simple working definition for winter studies in temperate regions where winter is less than half a year long is to use the contrast of coldwater conditions that are usually isothermal or reverse-stratified (winter) versus warmwater, stratified conditions (summer), in which spring and autumn are transitional intervals, while recognizing that spring and fall are distinct seasons for fish ecology and behaviors. To highlight winter studies, we use the term 'warmwater season' herein to contrast between the understudied winter season and seasons that are typically entirely ice-free. For studies in small lakes and rivers or in areas where water temperatures rarely exceed 15 °C, an alternative contrast may be between the ice-covered and open-water seasons. In groundwater-dominated streams that do not freeze, winter may be better defined using some meteorological definition such as when 24-h air temperatures average 5 °C.

Overview of telemetry methods: issues with working and tracking in winter

Here, we briefly outline the array of telemetry methods, with specific attention paid to the unique advantages and challenges of working in winter (Table 1). More in-depth reviews of telemetry methods and relative advantages and costs have been published by Cooke et al. (2012, 2013), Hussey et al. (2015), and others, and the logistical issues of working in cold water and on ice have been reviewed extensively elsewhere (e.g., Block et al. 2019). However, winter offers unique challenges and opportunities for telemetry studies, many of which are common to all methods. On one hand, ice provides a stable platform to access offshore sites, and to mount and deploy equipment underwater (Fig. 1; Barkley et al. 2018). For acoustic and radio telemetry, which are affected by turbulence or noise, the under-ice environment is mostly quiet until the ice begins to form and to break up; these periods of ice instability can reduce detection ranges of tags (Klinard et al. 2019a). In rivers, in contrast, unstable and moving ice can be extremely hazardous to personnel and to gear such that winter field work and overwinter deployment of stationary receivers may be ill-advised (Brown et al. 2011). At any season, small lakes and rivers can be too shallow for acoustic telemetry but ideal for radio or PIT tags, whereas deep and offshore areas are better suited for acoustic telemetry that does not require overwinter maintenance of equipment (Fig. 1). Snow on ice, and on solar panels, presents a set of challenges that are familiar to terrestrial biologists but rarely encountered in aquatic work. In addition, some equipment does not operate well in sub-freezing conditions. For example, batteries have shorter operating lives and can perform more poorly in cold than in warm conditions. Cost and logistics such as winter access to shorelines are also critical variables when considering the optimum method to select for a particular project to be conducted during the winter.

Acoustic telemetry

Acoustic telemetry relies on the transmission and receipt of individually coded acoustic signals detected by underwater receivers (Hussey et al. 2015). Tags as small as 0.3 g are typically attached externally or surgically implanted into the body cavity, using methods described in an extensive and growing body of literature (e.g., Klinard et al. 2018; Walton-Rabideau et al. 2019; Hubbard et al. 2020). An acoustic signal unique to an individual is emitted at variable set intervals from seconds to hours, over several months to over 10 years, that is detected by passive or mobile receivers (Cooke et al. 2012; Table 1). Passive receivers with a georeferenced location record the identity and time of any tagged fish passing within the range of the receiver, typically 0.5–4 km. Mobile receivers can be used to expand area covered by passive receivers. Receiver arrays in which tag detection ranges overlap allow signal triangulation and can be used to pin-point fish

Table 1 Comparison of telemetry methods (modified from Cooke et al. 2012) and challenges associated with their use in winter. Minimum tag size is not included as all tag types are evolving rapidly to allow tagging of very small fishes

Characteristic	Acoustic	Radio	PIT
Typical environments	Lakes and large rivers	Streams and shallow areas of lakes	Shallow streams, shallow lake embayments
Transmission mode	Active	Active	Passive
Detection range	250 m, up to 4 km	To 1 km	To 1 m
Tag longevity	Weeks to > 10 yrs	To 3 yrs	Indefinite
Common sensors	Temperature, pressure (depth), acceleration	Temperature, pressure	Temperature
Cost per tag	\$150–500	\$100–400	\$2–5
Winter maintenance	None	Access to land-based power/solar power; snow removal	Access to land-based power/solar power; snow removal
Detection efficiency issues in winter	Effects of surface ice and ice breakup/movement	Effects of ice breakup/movement	No change
Physical/logistical issues in winter	None	Hazards of ice movement, access to sites	Hazards of ice movement and damage to antennae
Cold temperature issues	Decreased battery life	Decreased battery life	No change for tags; decreased battery life for detection antennae
Advantages for winter telemetry	No field work or maintenance needed during winter data collection	Ice can be used as a platform for tracking	Potential for low-maintenance winter detections

locations (Roy et al. 2014). These positioning arrays can produce fine-scale movement data to evaluate time spent resting and moving, and behaviors such as feeding and spawning can be inferred from changes in speed or proximity to other tagged conspecifics (Binder et al. 2018; Dorazio and Price 2019). Tags with temperature and pressure (depth) sensors add the capacity to detect responses to temperature changes and to yield three-dimensional movement of fishes (e.g., Gallagher et al. 2019). Tags can also be equipped with tri-axial accelerometer sensors, allowing for robust estimates of fish activity, however these sensors greatly diminish tag life (Cruz-Font et al. 2019). Tags and receivers are relatively expensive as up-front capital equipment costs, but receivers operate constantly throughout the year, require no labor costs beyond deployment and retrieval for battery changes and data downloads (typically every 6–18 months), and can acquire data from tagged fish across multiple studies simultaneously. Thus, there is a high benefit:-cost ratio, particularly for winter telemetry.

Signal detection range is a particular concern, and is influenced by ambient noise, bubbles, temperature, and macrophytes (Huveneers et al. 2016); thermal stratification can influence the speed, reflection, refraction, and attenuation of transmissions (Voegeli and Pincock 1996; Heupel et al. 2006; Gjelland and Hedger 2013). Surface ice layers can reflect or distort acoustic signals, and ice movement during formation and break-up creates acoustic noise that lowers detection ranges (Klinard et al. 2019b); after ice formation, ambient noise from boats and waves is reduced. Range testing, i.e., determining the proportion of transmissions detected relative to distance from a receiver, is necessary to make corrections to fish detection data and account for variable detection range (Kessel et al. 2014). If fish move less at low temperatures, detection probability could decrease. In addition, fish resting within a receiver range may be presumed to be dead until movement resumes in spring (Klinard and Matley 2020).

Acoustic receiver arrays are currently deployed in the Laurentian Great Lakes (https://glatos.glos.us/) and other temperate and northern freshwater lakes year-round, yet much of the winter data collected remains unused (Binder et al. 2017a). Most of our knowledge on the function and efficiency of acoustic telemetry is derived from studies conducted during

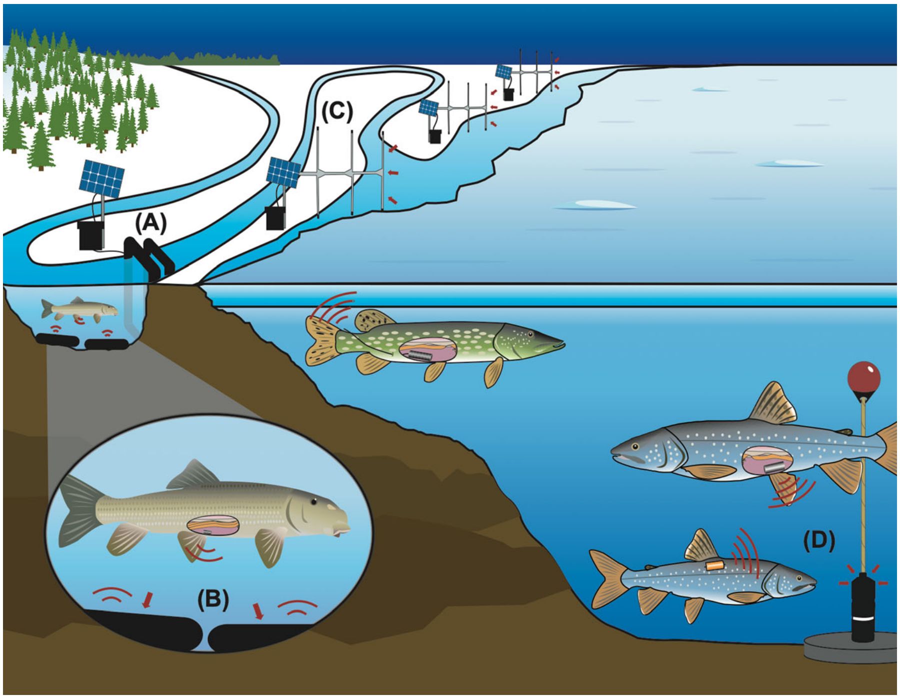


Fig. 1 Cross-section of an ice-covered lake and tributary stream with a schematic of passive (unattended) use of telemetry technology deployed in the field. **a** Swim-through antennae encircling a stream bed to detect PIT-tagged fish; paired antennae indicate direction of movement of tagged fish. **b** Swim-over antennae for detection of PIT tagged fish. **c** Antennae for detection of radio-tagged fish in a stream or nearshore lake area. **d** Acoustic telemetry receiver mounted on an anchor with retrieval buoy. PIT tag and radiotelemetry antennae are shown powered by solar power panels, with boxes to house batteries and data storage equipment. Location and relative size of surgically implanted tags are indicated in 'windows' on each fish; radiotelemetry tag includes an antenna inserted through the skin of the fish. Illustrations created by J. Knuth (white sucker) and J. Tomelleri (northern pike, lake trout) were used as reference material when creating digital fish illustrations

warm seasons (Kessel et al. 2014). Relatively few telemetry studies have explored winter data (e.g., Blanchfield et al. 2009; Matley et al. 2020) and even fewer have investigated detection efficiency during winter (e.g., Klinard et al. 2019b). For example, loss of macrophytes due to winter dormancy may substantially increase detection ranges (AT Fisk, unpublished data). Considering acoustic telemetry permits near-continuous spatial and temporal monitoring and can offer insights into three-dimensional movements and predation (Halfyard et al. 2017; Klinard et al. 2020), greater effort is needed to understand changes in the acoustic environment in winter to improve interpretation of fish behavior data acquired from acoustic telemetry (Hayden et al. 2016).

Radio telemetry

Radio transmitters for fish telemetry emit electromagnetic energy in the radio frequency (RF) range (Cooke et al. 2012). The smallest tags are similar to acoustic telemetry tags (0.25 g) and are implanted internally with an attached antenna extending externally from the fish. Because radio signals are attenuated with increasing water depth and in waters with high conductivity, radio telemetry is best suited for work in shallow (usually < 5 m) water with low conductivity (usually < 500 µS cm-1). Signals are generally unaffected by issues such as entrained air (e.g., in shallow rapids; Velle et al. 1979).

Challenges associated with use of radio telemetry in winter are limited only to the power requirements for fixed antennas and thus require access to make battery changes or remove snow from solar panels. Receiver antennas can take several forms including loop, Yagi, H, or omnidirectional, and can even be placed underwater (Kenward 2000). An added benefit of radio telemetry is that fish tags can be tracked on land if they are removed from the aquatic system by a predator (e.g., human, otter, bird; Patterson and Blanchfield 2013).

Radio telemetry signals can be detected through ice such that fish can be tracked using shore-based, solar-powered, automated listening stations or manual tracking fish on the ice by snowmobile or foot, or from small aircraft. The methods for radio tracking fish in the winter, including when ice is present, have been perfected over the years (e.g., Favrot and Jonasson 2020). Unlike acoustic telemetry which locates fish in two dimensions automatically, radio telemetry is more effective when used to assess fish passage past a given location in a linear system (Cooke and Thorstad 2012). Direction of movement is detectable by using paired or multiple antennas (e.g., Bryant et al. 2009). The most comprehensive studies of winter fish biology using radio telemetry, especially in fluvial systems, have used extensive manual tracking (e.g., Brown and Mackay 1995; Lindstrom and Hubert 2004) and have contributed substantially to our understanding of how fish respond to winter in fluvial systems, including under ice (Huusko et al. 2007). Relatively little winter work on fish has used passive radio telemetry.

PIT telemetry

Passive integrated transponders (PIT tags) are small (< 4 mm diameter, 8–32 mm long, < 11 mg), cylindrical tags encoded with a unique identification code (ID) for identification of individual animals (Cooke et al. 2012). These tags do not require batteries and transmit their ID when activated by an antenna/tag scanner emitting a low frequency radio signal (Boarman et al. 1998). PIT tags have a number of advantages for studying the movement of fish, mainly related to their small size, including: (1) ease of use in very small fish (< 10 g), including juveniles (Simard et al. 2017); (2) use in shallow water such as small streams where acoustic telemetry would not work; (3) easy implantation via hypodermic injector or minor surgery; (4) high tag retention rates (Acolas et al. 2007; Larsen et al. 2013; Simard et al. 2017; D'Arcy et al. 2020); (5) low cost (approximately $2/tag), allowing a large number of animals to be tagged (1000 to 10,000 individuals); and (6) longevity—tags remain active for the life-span of the tagged individual (Table 1).

PIT tags have some significant drawbacks; in particular, they have a low detection range (< 1 m distance from antenna) which effectively limits their use to shallow water, mainly streams and rivers (Zydlewski et al. 2001). Antennas used for tag detection and recording require power, either direct or off-the-grid power source (e.g., batteries, solar, wind, or a combination). The power requirement can limit locations where antennas can be used. Shore-based equipment also requires vandal-proof infrastructure. As with other types of telemetry, ice, ice movement, and structurally complex habitat may limit PIT tag detection (Brown et al. 2011; Weber et al. 2016). Swim-through and swim-over antennas mounted on the substrate may also be impacted by debris and ice at high flow rates in lotic systems (Connolly et al. 2005). Consequently, many studies remove or turn off stationary radio receivers during the winter. Development of deep water, internal battery-powered antennae may address several of the PIT tag limitations.

Historically, PIT tags have been used extensively in lotic systems during the open-water seasons. PIT tag arrays are often only used to monitor specific life-history events, such as the migration of salmonid smolts (Achord et al. 1996), and often are not left in the system over the entire year. Technology is available that allows for extended deployments (Johnston et al. 2009), and PIT tagging has been used during winter months to address winter ecology of some species (Stickler et al. 2008; Linnansaari et al. 2009; Linnansaari and Cunjak 2010). Even so, PIT tags remain an under-used technology for the study of the winter ecology of stream and river fishes.

A note on biologging

Fish biologists now routinely deploy animal-borne data loggers that are equipped with a diversity of sensors (reviewed in Cooke et al. 2016) that record depth and temperature (e.g., Bergstedt et al. 2016; Raby et al. 2020), and (less commonly) tri-axial acceleration or heart rate. The latter two measurements are particularly rare for fish released into the wild (but see Brownscombe et al. 2014; Broell et al. 2016). Biologging is similar to passive telemetry insofar as both technologies could be used to collect data on the winter biology of fish with no additional effort, amassing heretofore unused data. Unless programmed to stop recording, animal-borne loggers are unaffected by winter and can continue recording data at the same frequency as in summer. Thus, we anticipate that as with telemetry (but to a lesser extent) numerous datasets may already exist on winter depth and temperature occupancy from biologger studies that could be probed with questions about winter biology.

Research topics

Environmental drivers

Many environmental variables that influence the movement of fish are as relevant in the winter months as they are in other seasons. Temperature is an important driver of fish metabolism and behavior and has been called the ecological master variable for fish (Brett 1971; Magnuson et al. 1979). Other abiotic factors are inherently linked to water temperature: dissolved oxygen and water density both increase at lower temperatures. Winter involves low light conditions due to short day length, low penetration of light below the surface, presence of ice, and addition of snow cover.

How fish respond to summertime thermal stratification and hypoxia has been studied using telemetry in fresh water (Baldwin et al. 2002; Guzzo et al. 2017; Gorman et al. 2019), while little has been done to explore how fish respond to inverse stratification and hypoxia during winter. For example, movement patterns may differ between years with and without ice coverage. In lotic ecosystems, fish may be further impacted by freshet timing and water flows, directly related to winter severity. For example, black crappie (*Pomoxis nigromaculatus*) and bluegill (*Lepomis macrochirus*) have been shown to use different temperatures and dissolved oxygen in winter depending on the current speed they experience (Knights et al. 1995). Dynamic ice processes in streams affect habitat availability and use by cutthroat trout (*Oncorhynchus clarkii)* and brook trout (*Salvelinus fontinalis*) (Lindstrom and Hubert 2004). Temperature apparently mediates seasonal use of rivers by lake trout (*Salvelinus namaycush*) in the Flathead Lake drainage (Muhlfeld and Marotz 2011). Groundwater inputs provide winter warmwater refuges as well as summer cold-water refuges (Baird and Krueger 2003; Mackenzie-Grieve and Post 2011). Variability in temperatures experienced by fish influence the timing, behaviors, and success of spawning (e.g., Bondarev et al. 2019). Acoustic telemetry used in an estuary system in the southeast USA revealed that winter severity influenced spotted sea trout (*Cynoscion nebulosus*) mortality (Ellis et al. 2017). Previous telemetry research has described variability in spring spawning behavior, yet how behavioral decisions and habitat use in the cold months leading up to spring dictate spawning behavior is unknown. Telemetry data can assist with determining the influence of environmental variables on fish ecology in winter as well as carry-over effects into other seasons.

Migration and movements

Research on fish movements and migration is vital for fishery management, conservation of imperiled species, and understanding basic fish biology (e.g., Landsman et al. 2011). Fish migrations include daily, seasonal, and ontogenetic changes in habitat use. Diel vertical migrations may involve foraging at night in pelagic waters and seeking refuge near the substrate during the day (Hasler and Villemonte 1953); horizontal movements may be daily or seasonal as fish move between nearshore foraging or refuge areas and offshore zones (Nowak and Quinn 2002; Říha et al. 2015). Seasonal migrations are usually associated with movement towards or away from spawning or feeding areas, but may involve complex interactions between temperature, predation, energy budgets, individual variability, and boldness (Brodersen et al. 2008, 2012; Chapman et al. 2011). Seasonal migrations may be triggered by changing thermal environments, or inter-individual variation in activity and habitat preference (Ivanova et al. in press). Ontogenetic migrations occur when fish transition from spawning sites to juvenile and then adult feeding habitats, and back to spawning locations. The breakdown of summer thermal stratification expands habitat for coldwater fishes (Ivanova et al. in press) and removes optimal thermal habitat for warmwater fishes, potentially changing the frequency and amplitude of vertical and nearshore-offshore movements and seasonal range sizes for all thermal guilds. Based on thermal preferences, coldwater species may continue to forage in winter but use more of the water column and potentially littoral habitats, whereas warmwater species may forage less or not at all in winter (Block et al. 2020; McMeans et al. 2020) and thus may move less and potentially have a small winter home range. At a fine spatial scale, foraging and quiescent periods may be affected by light availability due to changes in ice cover, ice opacity, and snow cover (Keyler et al. 2019).

Fish movements and available thermal habitats are affected by scale. For example, shallow lakes may not have a hypolimnion in summer, and large lakes with a long fetch may not become fully ice-covered in winter due to wind disturbance of the surface or volume of water to cool. Behavioral differences may occur between predictably ice-covered lakes and intermittently frozen lakes. For both lentic and lotic systems, fish home-range size and daily movement increase with increasing fish size (Minns 1995; Rosten et al. 2016) and size of the ecosystem (Woolnough et al. 2009). Summer home-range for lake fish is approximately 20 times larger than for similar-sized river fish (Minns 1995). Telemetry can be used to define home ranges and depth ranges, determine changes in activity, and contrast these parameters among seasons and among thermal guilds (Penne and Pierce 2008; Blanchfield et al. 2009; Watson et al. 2019; Brooks et al. 2019b; Cote et al. 2020). In particular, winter telemetry can address applied questions such as: (1) Which species remain active and in pursuit of food during winter and which become quiescent? (2) For winter-active species, do feeding areas differ among seasons? (3) For both winter-active and winter-quiescent fish, how much among-individual variation exists in activity levels and range of movements? (4) Does stock structure and mixing among stocks change between winter, summer, and spawning seasons? Numerous studies have focused on identification of spawning habitats and movements towards and away from spawning sites, or movement to 'traditional' summer feeding sites, but migrations to overwintering sites are relatively understudied compared to migrations that occur in the rest of the year (Marsden et al. 2016; Binder et al. 2016, 2017b; Ivanova et al. in press). Fidelity to particular sites for winter feeding or winter quiescence has particular management implications related to habitat protection and identification of seasonal fishing refuges. Evaluation of post-stocking movements has been used to determine post-stocking survival and stock structure and inform future stocking (Landsman et al. 2011).

Habitat use

Habitat encompasses multiple dimensions, including substrate type, vegetation, bathymetry, dissolved oxygen, temperature, predation threat, prey, and water flow. Quantifying species-specific habitat use (and intraspecific variation) also has fundamental value for understanding community dynamics (McMeans et al. 2020). Assessing habitat use in winter relative to other seasons across species and populations can reveal large-scale trends, such as patterns among trophic or thermal guilds, or across lotic and lentic systems of varying size. Telemetry has been used to identify critical seasonal habitats, as repeated measurements of individuals over extended periods can be used to define habitat area and patterns of habitat use (Landsman et al. 2011). Winter habitat use has been thoroughly studied in lotic systems (see reviews by Cunjak 1996; Brown et al. 2011) due to high accessibility relative to large lakes for PIT and radiotelemetry studies, while there is a paucity of studies on winter habitat use in lentic systems. However, in both systems, published studies examining winter habitat use with telemetry have been primarily focused on salmonids (e.g., Cunjak 1996; Brown et al. 2011; Watson et al. 2019; Blanchfield et al. 2009; Cote et al. 2020), other top predators (e.g., Brooks et al. 2019a; Walton-Rabideau et al. 2020), and invasive species (e.g., Lechelt and Bajer 2016; Pfauserova et al. 2019), with fewer papers focused on suckers, cyprinids, and centrarchids (e.g., Cunjak and Power 1986; Karchesky and Bennett 2004; Brown et al. 2001). Consequently, we have a limited understanding of fish habitat use in winter relative to other seasons (McMeans et al. 2020).

Seasonal fish movements are constrained by the size of aquatic systems (the area and depth available for fish movement), by thermal stratification and hypoxic layers in lentic systems, and by flow and connectivity in lotic systems. Most of what we know of fish habitat use across a gradient of water body sizes is from the warmwater season. Fish ranges in winter may be either expanded or contracted by loss of stratification and presence of ice (Ivanova et al. in press). Fish home ranges are reduced for some species in temperate lakes during the winter relative to

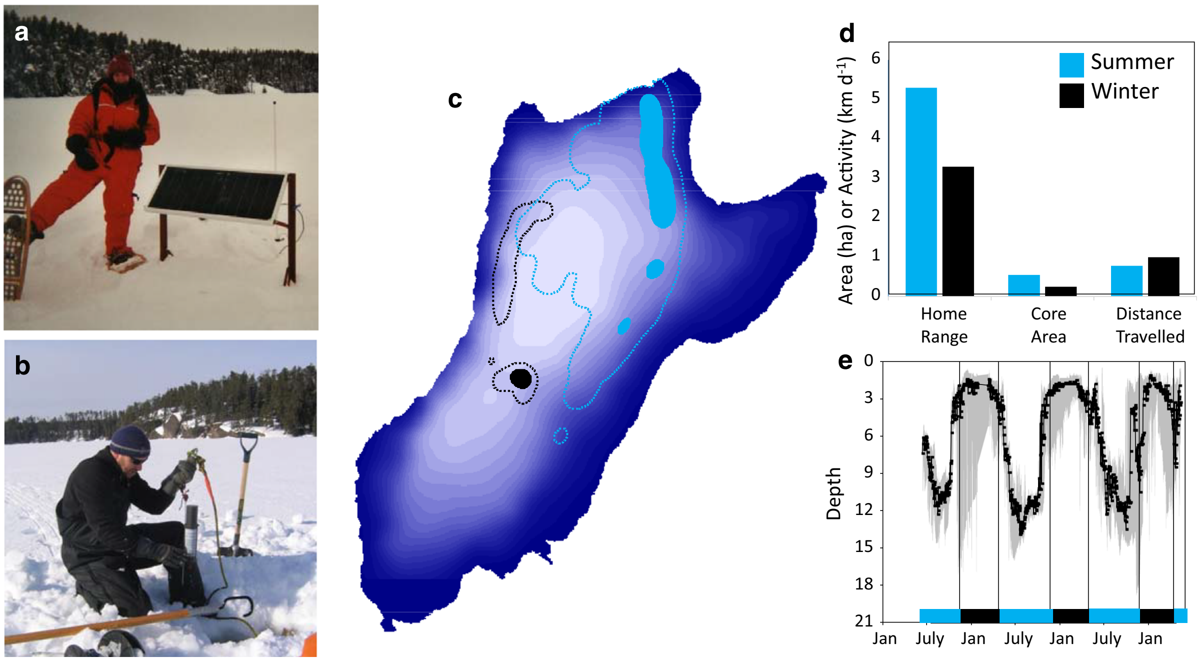


Fig. 2 Winter monitoring of lake trout in a small boreal lake using acoustic telemetry (**a**, **b**) revealed (**c**, **d**) reductions in home ranges (95% Kernel; dashed line) and core areas (50% Kernel; solid area) relative to summer (June-Aug.), **d** with similar movement rates between seasons. Lake trout showed distinct seasonal depth preferences (**e**), occupying shallow and deep water in winter and summer, respectively. In panel e, the black line = median daily depth of all tagged lake trout, grey shading = associated daily 95% CI. For study details see Blanchfield et al. (2009)

summer (Fig. 2; Penne and Pierce 2008; Blanchfield et al. 2009; Taylor et al. 2012a; Watson et al. 2019; Cote et al. 2020), which conforms to predictions (and physiological principles) about fish activity during the winter season. Yet, considerable interspecific variation has been documented, even within thermal guilds. Brook trout and rainbow trout (*Oncorhynchus mykiss*), for example, have been reported to reduce activity in winter (Cote et al. 2020; Watson et al. 2019), while lake trout had some increased activity but with variation from year-to-year (Blanchfield et al. 2009). Home ranges can be constrained or expanded in winter by changes in abiotic variables (e.g., dissolved oxygen and temperature) and biotic factors such as distribution and abundance of predators or prey. For example, some species appear to occupy greater depths more frequently during winter, when water is colder nearer the surface, than in summer (Penne and Pierce 2008; Gorsky et al. 2012; Cote et al. 2020); in lakes with limited deepwater areas, this behavior may reduce habitat range. However, lake trout have also been found to use shallower depths in winter than in summer (Fig. 2; Blanchfield et al. 2009; Gallagher et al. 2019; Ivanova et al. in press), potentially suggesting differences in response to winter conditions based on temperature guild.

In addition to loss of thermal stratification in winter, lakes experience depth-related changes in dissolved oxygen content. Data on vertical movement behavior during winter in lakes equipped with dissolved oxygen loggers could provide new insights into species-specific physiological performance windows. Fishery assessment programs have provided ample data on species- and life-stage-specific depth use (among other habitat variables), but few of those data are collected in winter (e.g., Elrod et al. 1996; Stewart and Bowlby 2009). Electronic tags equipped with pressure/depth sensors can fill these data gaps. Depth sensors provide data on the vertical dimension of movement and are more valuable than temperature sensors in winter because lakes become isothermal as temperatures decline in fall. If fish reduce their horizontal movement in winter so that they are only detected on one or two acoustic receivers, depth sensing tags can be used to identify which species remain active vs. becoming dormant (Speers-Roesch et al. 2018). For fishes that remain active in winter (e.g., coldwater species and piscivores, for whom food availability may be similar across seasons), data on vertical behaviors may provide clues about which prey they are targeting. Vertical movements in summer can be associated with diel vertical migrations that may disappear or reverse in winter because of physiochemical changes in lakes and changes in forage distributions (Ahrenstorff and Hrabik 2016; Gallagher et al. 2019).

Predation

Predation plays a key role in structuring aquatic ecosystems as it influences patterns of energy flow, species abundance and distribution, and both competitive and non-competitive interactions. Foraging activities are influenced by seasonal changes in accessible habitat, prey composition, day length, light intensity, and metabolic rate (Guzzo et al. 2017; Keyler et al. 2019). Conversely, the threat of predation can alter habitat use and activity patterns of potential prey (Plumb et al. 2014). Pharmaceutical exposure changes predation risk and habitat use (Klaminder et al. 2016). Understanding foraging generally involves direct methods such as diet analysis, including biochemical methods, and observational data (Clarke et al. 2005; Happel et al. 2015). Telemetry permits more detailed investigation of predation through active and passive monitoring of individual predators and prey (Hockersmith et al. 2003; Lidgard et al. 2014). Acoustic telemetry studies have attempted to quantify predation via ancillary sensor data (e.g., pressure and accelerometer data; Thorstad et al. 2011), qualitative assumptions based on known predator and prey behavior (Perry et al. 2010), and quantitative post hoc methods such as clustering and multivariate mixture models (Romine et al. 2014; Gibson et al. 2015). However, winter predation remains greatly understudied. Telemetry provides an opportunity to investigate hypothesized seasonal and species-specific differences in predation rates based on thermal guild.

The recent advent of an acoustic transmitter that can detect predation events (i.e., predation tag) has enabled easier identification and quantification of predation (Halfyard et al. 2017; Weinz et al. 2020). Predation tags in prey are triggered by digestion of a biopolymer tag coating; however, digestion time will be slowed at winter temperatures and will lengthen the signal lag (time for tag to switch coding after consumption) of predation tags. Published studies that have used predation tags remain limited but have reported longer signal lags with cold than warm temperatures (Halfyard et al. 2017); however, testing of tags has yet to occur at temperatures below 12 °C. Klinard et al. (2019a) observed predation of tagged forage fish 5.5 ± 5.2 days after release in Lake Ontario when the lake was isothermal (5–8 °C); thus, predation tags work at low temperatures but a need exists for quantified signal lags at these temperatures. Alternative methods for identifying predation events have been developed based on movement, e.g., changes in speed or habitat use (Gibson et al. 2015; Schultz et al. 2015; Daniels et al. 2018), and these methods can be used to confirm predation events inferred from predation tags (Weinz et al. 2020).

Daily variation in ice and snow cover and their effects on light may influence predation and foraging, especially for visual predators. Species such as walleye (*Sander vitreus*) that have high visual acuity in low light (Lester et al. 2004) may benefit from periods of ice and snow cover. Keyler et al. (2019) used modeling to demonstrate substantial seasonal differences in the maximum depths and time available for foraging in response to light levels by siscowet, a morph of lake trout. Arctic charr (*Salvelinus alpinus*) overwintering in fresh water appear to select a narrow temperature range to reduce energy expenditure and metabolism to accommodate reduced feeding (Mulder et al. 2018). Predation rates are also affected by the influence of temperature on metabolic rates, which are specific to thermal guilds. Therefore, sorting out the relative effects of daylength, light intensity, temperature, metabolic rate, and thermal guild on foraging is a challenge that can be addressed only partially by telemetry data.

Bioenergetics

During peak prey production pulses, fish are able to capture and store energy that can be mobilized during times of limited resource availability or increased energy demand (Hayes and Taylor 1994; Berg et al. 2011; Shuter et al. 2012; Fernandes and McMeans 2019). However, annual lipid maxima can occur during winter periods in both cool- and cold-water species (Stockwell et al. 2014; see Fig. 5, Fernandes and McMeans 2019). These bioenergetic outcomes support recent telemetry findings that suggest winter is not a period of biological stasis. Across freshwater systems, the temporal dynamics of seasonal energy storage and depletion appear to be most strongly mediated by spawning and winter phenology (Medford and Mackay 1978; Tanasschuk and Mackay 1989; Shuter and Post 1990; Finstad et al. 2004; Berg et al. 2011). Regardless, little work has been done to identify how winter energetics interact with activity and movement patterns. For example, Plumb et al. (2014) integrated telemetry observations with behavioral and bioenergetics modelling to assess the probability that lake trout could acquire sufficient resources to spawn in the fall, and demonstrated that climate and predation can influence habitat use and reproductive growth. Winter telemetry data may allow us to better resolve mechanisms that drive rates of energy depletion or accumulation during winter that in turn influence spawning, mortality, and carry-over effects during other times of the year.

Sensor-based tags are increasing the ways in which we can now estimate several aspects of fish energetics in the field. For example, Brown et al. (2000) used radio transmitters with electromyography (EMG) to reveal how hanging ice dams altered swimming energetics of brown trout (*Salmo trutta*) and common carp (*Cyprinus carpio*) while Taylor et al. (2012b) used similar technology to explore the energetic costs of living downstream from a peaking hydropower facility for mountain whitefish (*Prosopium williamsoni*). Cooke and Schreer (2003) used EMG radio transmitters to assess common carp responses to widely fluctuating water temperatures in the discharge canal of a coal-fired thermal generating station. Although other bioenergetic measures can be obtained from fish using electronic tagging tools (see Cooke et al. 2016), we are unaware of any attempts to use acceleration or heart rate sensors in free-swimming fish in winter. Clearly many opportunities are available to refine annual energy budgets and better understand the extent to which fish rely on pre-winter nutritional state versus winter foraging to survive winter and be prepared for the coming spring and summer months. We anticipate rapid growth in this research area over the next decade as smaller and more reliable sensors are developed and potentially incorporate additional measures (e.g., glucose, cortisol). Also a strong potential exists for synergistic research between physiology/respirometry work in controlled laboratory conditions and observed behaviors using telemetry in free-ranging fish.

Cold-water species are assumed to be more physiologically capable of remaining active in winter than cool- or warmwater species (Shuter et al. 2012). Telemetry can be used to describe activity budgets to partition behaviors into time spent moving, foraging, and being inactive at each season. Seasonal differences in rate and frequency of movement can be quantified using accelerometer tags, acoustic telemetry positioning arrays, and biologging. Seasonal movement data are of particular value for informing bioenergetics models. These models provide an important and widely accepted tool for fishery managers and serve a variety of roles, not the least of which are the determination of the numbers of fish for stocking and determination of harvest quotas. However, incorporation of empirical data to inform these models has been limited with respect to fish habitat use and prey consumption during winter.

Contrasts among thermal guilds

The range limits of warmwater fish are defined by the duration of northern winters (Shuter and Post 1990; Giacomini and Shuter 2013). Conversely, recent evidence from seasonal telemetry data suggests that long winters promote the persistence of cold-water fishes when in sympatry with warmwater species (McMeans et al. 2020). Existing seasonal telemetry data from a broad diversity of fish species can be leveraged to identify overlapping seasonal strategies and highlight critical species interactions that may be associated with explicit population- or community-level outcomes. For example, divergent seasonal activity levels in lake trout and smallmouth bass (*Micropterus dolomieu*) are thought to be critical for mediating species coexistence (McMeans et al. 2020). Seasonal telemetry data can be used to identify similar coexistence or exclusion mechanisms that may depend on seasonal fluctuations. In both cool- and cold-water species, regardless of divergent life histories (e.g., spring vs. fall spawning), warming winters may decrease reproductive output and likely annual production, as demonstrated for brook trout and yellow perch (*Perca flavescens*: Robinson et al. 2010; Farmer et al. 2015). However, our understanding of what mediates decreased production and how changing environmental conditions influence carry-over effects across time is poor. The general prediction that outcomes of warmer winters than in the past will be negative is likely overly simplistic. We may expect that sensitivity to similar seasonal perturbations will vary predictably across thermal guilds (e.g., increased summer length and intensity may benefit warmwater species through increased opportunity for spawning, while increasing mortality/spawning omission in coldwater fish: Robinson et al. 2010; Plumb et al. 2014); however, the relative importance of thermal and physical habitat availability for species-specific reproductive output and production is unclear. Seasonal telemetry data has the potential to better resolve species interactions and requirements for seasonal habitats and how deviations from 'optimal' seasonal habitat use may influence reproduction and production dynamics.

Low movement rates in winter, particularly for warm- and coolwater species, may result in large temporal gaps in telemetry data for each animal, whereas biologgers continue to generate data at the same frequency as in summer. For example, depth loggers have been used year-round for salmonids in the Great Lakes and seem to indicate that depth use and vertical movement by fish is relatively restricted in summer compared to other seasons (Fig. 2; Bergstedt et al. 2016). In Lake Ontario, Chinook salmon (*Oncorhynchus tshawytscha*) used a dramatically wider range of depths in winter, whereas lake trout retained a similar range of depth use across seasons (Raby et al. 2020). For non-piscivores, these patterns may be reversed. Lake whitefish (*Coregonus clupeaformis*), an invertivore, changed from feeding on pelagic to benthic invertebrates from summer to winter, and had reduced vertical movements in winter (Gorsky et al. 2012). Telemetry could be used to establish trophic and thermal guild 'norms' for seasonal patterns of diel vertical activity.

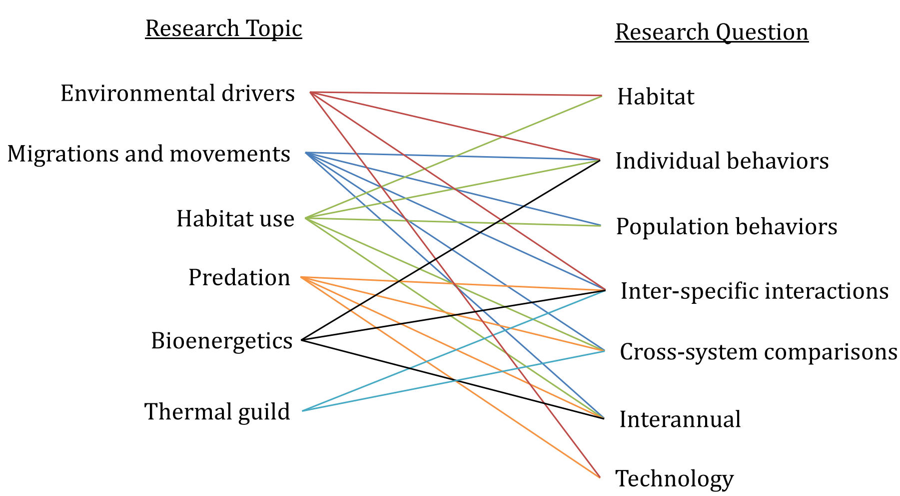
Research questions and opportunities

Based on the forgoing review, we outline key questions about fish behavior, ecology, and physiology that can be addressed using existing winter telemetry data or integrated into future studies (Fig. 3), and link them to specific research topics (in parentheses). Some of these topics have been examined previously in one or more species, but all of these questions can be expanded to additional species and more geographic areas. We note that the potential for climate change to affect the duration and severity of winter should be considered as a factor in research that addresses most if not all of these questions.

Habitat (environmental drivers, migration and movement, habitat use)

- Do fish home ranges change in winter relative to warmwater seasons?
  - Where do fish of a particular species spend the winter?
  - What is their preferred winter temperature, relative to the range of temperatures available in winter?
- Does vertical habitat use change in winter?

Fig. 3 Flow chart of linkages between research topics outlined in this review and the categories of research questions that can be addressed with winter telemetry



- Does winter home range change in relation to winter duration and severity, e.g., extent of ice cover, snow cover, light levels, median low temperature?

Individual behaviors (migration and movement, habitat use, predation, bioenergetics)

- Does behavior of individuals change in winter, relative to the warmwater seasons, including:
  - the average rate of movement
  - amount of time spent moving
  - distance travelled per day, per month
  - nocturnal vs. diurnal movements?
  - frequency and amplitude of vertical movements
- How do the above metrics change with ice conditions that affect light penetration, i.e., ice thickness, ice clarity, snow cover, and no ice?
- Does winter severity (duration, temperature extremes, ice thickness) change individual behaviors?

Population behaviors (migration and movement, habitat use, bioenergetics, contrasts among thermal guilds)

- Does winter duration and severity affect post-winter behaviors such as timing of migration, timing of spawning for spring-spawning species, likelihood of spawning in species that skip-spawn?
- Do thermal habitat preferences vary among populations or strains of a given species?
- Does species composition of communities change or overlap differently in winter?

Inter-specific comparisons (predation, bioenergetics, contrasts among thermal guilds)

- What is the role of winter activity and feeding on annual energy budgets among species with different habitats and thermal preferenda?
- What data can telemetry provide from winter to revise biogenetics models?
- How do individual behaviors vary among species based on:
  - thermal guild,
  - habitat type (benthic, demersal, pelagic; lotic vs. lentic), and
  - trophic level.

Across-system comparisons (environmental drivers, migration and movement, habitat use, predation, contrasts among thermal guilds)

- Do winter behaviors of fish vary depending on the size, bathymetry, shape, and fetch of lakes and size, discharge, sinuosity of rivers, and how do lakes and rivers differ?
- How do fish in systems of similar sizes differ in winter at different latitudes and altitudes?

Interannual comparisons (environmental drivers, migration and movement, habitat use, individual behaviors, bioenergetics)

- How much do foraging, movement, and reproductive behaviors vary among winters with different severity and duration?
- Does interannual variation in winter conditions affect post-winter activity such as foraging and reproduction?
- Does interannual variation in winter conditions affect mortality?

Technology issues (all research topics)

- What variables in winter affect the detection range of telemetry signals?
- How much data is lost during ice breakup, conditions with frazil ice, etc.?
- What power options can be developed or improved for winter radiotelemetry and PIT systems (e.g., solar, wind)?

Summary

Winter is an under-explored season for conducting fish research, in part due to logistical challenges of field operations. Telemetry tools overcome many obstacles of cold-water data collection, and yield high temporal frequency, data-rich, spatially extensive data. A wealth of existing but currently neglected seasonal telemetry data likely already exists and could be mined to address a broad suite of questions highlighted here. These data present a valuable opportunity to document the current status of winter activity and behavior in freshwater fishes prior to the anticipated rapid alteration of winter phenology and severity that will occur with climate warming. Changes in winter conditions have been associated with reduction of optimal oxythermal habitat, decreased energy allocation to reproduction, decreased survival of young, and shifted spawning phenology (e.g., Farmer et al. 2015; Guzzo and Blanchfield 2017), but may also increase thermal habitat available to cool- and warmwater species and increase foraging success of visual feeders. However, documented changes in seasonal activity, depth and habitat use, and behavioral strategies after shifts in winter phenology are lacking. Combining spawning, bioenergetics, and foraging information with seasonal telemetry will better position us to understand and predict how seasonal habitat selection and activity (e.g., how habitat use or activity translate to the capacity for acquiring or maintaining adequate energy for spawning) translate to reproduction and recruitment outcomes (e.g., skipped spawning, spawning frequency). New and existing multi-year acoustic telemetry data that span seasonal timescales may be crucial for outlining longitudinal trends in seasonal strategies and designing future studies.

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Compliance with ethical standards

Conflict of interest The authors declare they have no conflict of interest.

References

Achord S, Matthews GM, Johnson OW, Marsh DM (1996) Use of passive integrated transponder (PIT) tags to monitor migration timing of Snake River Chinook salmon smolts. N Am J Fish Manag 16:302–313

Acolas ML, Roussel JM, Lebel JM, Baglinière JL (2007) Laboratory experiment on survival, growth and tag retention following PIT injection into the body cavity of juvenile brown trout (*Salmo trutta*). Fish Res 86:280–284

Ahrenstorff TD, Hrabik TR (2016) Seasonal changes in partial, reverse diel vertical migrations of cisco *Coregonus artedi*. J Fish Biol 89:1794–1809

Baird OE, Krueger CC (2003) Behavioral thermoregulation of brook and rainbow trout: comparison of summer habitat use in an Adirondack River, New York. Trans Am Fish Soc 132:1194–1206

Barkley AN, Fisk AT, Hedges KJ, Treble MA, Hussey NE (2018) Transient movements of a deep-water flatfish in coastal waters: implications of inshore-offshore connectivity for fisheries management. J Appl Ecol 55:1071–1081

Berg OK, Rød G, Solem Ø Finstad AG (2011) Pre-winter lipid stores in brown trout Salmo trutta along altitudinal and latitudinal gradients. J Fish Biol 79:1156–1166

Bergstedt RA, Argyle RL, Taylor WW, Krueger CC (2016) Seasonal and diel bathythermal distributions of lake whitefish in Lake Huron: potential implications for lake trout bycatch in commercial fisheries. North Am J Fish Manag 36:705–719

Binder TR, Riley SC, Holbrook CM, Hansen MJ, Bergstedt RA, Bronte CR, He JX, Krueger CC (2016) Spawning site fidelity of wild and hatchery lake trout (*Salvelinus namaycush*) in northern Lake Huron. Can J Fish Aquat Sci 73:18–34

Binder TR, Riley SC, Holbrook CM, Paige K, Hayden TA, Nate N, Paige K, Riley SC, Fisk AT, Cooke SJ (2017a) Acoustic telemetry observation systems: challenges encountered and overcome in the Laurentian Great Lakes. Can J Fish Aquat Sci 751:1755–1763

Binder TR, Marsden JE, Riley SC, Johnson JE, Johnson NS, He J, Ebener M, Holbrook CM, Bergstedt RA, Bronte C, Hayden TA, Krueger CC (2017b) Movement patterns and spatial segregation of two populations of lake trout *Salvelinus namaycush* in Lake Huron. J Great Lakes Res 43:108–118

Binder TR, Farha SA, Thompson HT, Holbrook CM, Bergstedt RA, Riley SC, Bronte CR, He J, Krueger CC (2018) Fine-scale acoustic telemetry reveals unexpected lake trout, spawning habitats in northern Lake Huron, North America. Ecol Freshw Fish 27:594–605

Blanchfield PJ, Tate LS, Plumb JM, Acolas ML, Beaty KG (2009) Seasonal habitat selection by lake trout (*Salvelinus namaycush*) in a small Canadian shield lake: constraints imposed by winter conditions. Aquat Ecol 43:777–787

Block BD, Denfeld BA, Stockwell JD et al (2019) The unique methodological challenges of winter limnology. Limnol Oceanogr-Meth 17:42–57

Block BD, Marsden JE, Stockwell JD (2020) Contributions of winter foraging to the annual growth of thermally dissimilar fish species. Hydrobiologia. https://doi.org/10.1007/s10750-020-04428-2

Boarman WI, Beigel ML, Goodlett GC, Sazaki M (1998) A passive integrated transponder system for tracking animal movements. Wildlife 26:886–891

Bondarev DL, Kunah OM, Fedushko MP, Gubanova NL (2019) The impact of temporal patterns of temperature and precipitation on silver Prussian carp (*Carassius gibelio*) spawning events. Biosystems Diversity 27:106–117

Brett JR (1971) Energetic responses of salmon to temperature. A study of some thermal relations in the physiology and freshwater ecology of sockeye salmon (*Oncorhynchus nerka*). Am Zool 11:99–113

Brett JR, Groves TDD (1979) Physiological energetics. Fish Physiol 8:280–352

Brodersen J, Nilsson PA, Hansson L-A, Skov C, Brönmark C (2008) Condition-dependent individual decision-making determines cyprinid partial migration. Ecology 89:1195–1200

Brodersen J, Nilsson PA, Chapman BB, Skov C, Hansson L-A, Brönmark C (2012) Variable individual consistency in timing and destination of winter migrating fish. Biol Lett 8:21–23

Broell F, Taylor AD, Litvak MK, Bezanson A, Taggart CT (2016) Post-tagging behavior and habitat use in shortnose sturgeon measured with high-frequency accelerometer and PSATs. Anim Biotelemetry 4:1–13

Brooks JL, Midwood JD, Gutowsky LFG, Boston CM, Doka SE, Hoyle JA, Cooke SJ (2019a) Spatial ecology of reintroduced walleye (*Sander vitreus*) in Hamilton Harbour of Lake Ontario. J Great Lakes Res 45:167–175

Brooks JL, Chapman JM, Barkley AN, Kessel ST, Hussey NE, Hinch SG, Patterson DA, Hedges KJ, Cooke SJ, Fisk AT, Gruber SH, Nguyen VM (2019b) Biotelemetry informing management: case studies exploring successful integration of biotelemetry data into fisheries and habitat management. Can J Fish Aquat Sci 76:1238–1252

Brown RS, Mackay WC (1995) Fall and winter movements of and habitat use by cutthroat trout in the Ram River, Alberta. Trans Am Fish Soc 124:873–885

Brown RS, Power G, Beltaos S, Beddow TA (2000) Effects of hanging ice dams on winter movements and swimming activity of fish. J Fish Biol 57:1150–1159

Brown RS, Power G, Beltaos S (2001) Winter movements and habitat use of riverine brown trout, white sucker and common carp in relation to flooding and ice break-up. J Fish Biol 59:1126–1141

Brown RS, Hubert WA, Daly SF (2011) A primer on winter, ice, and fish: what fisheries biologists should know about winter ice processes and stream-dwelling fish. Fisheries 36:8–26

Brownscombe JW, Gutowsky LFG, Danylchuk AJ, Cooke SJ (2014) Foraging behavior and activity of a marine benthivorous fish estimated using tri-axial accelerometer biologgers. Mar Ecol Prog Ser 505:241–251

Bryant MD, Lukey MD, McDonell JP, Gubernick RA, Aho RS (2009) Seasonal movement of dolly varden and cutthroat trout with respect to stream discharge in a second-order stream in southeast Alaska. N Am J Fish Manage 29:1728–1742

Chapman BB, Hulthén K, Blomqvist DR, Hansson L-A, Nilsson J-Å, Brodersen J, Nilsson PA, Skov C Brönmark C (2011) To boldly go: individual differences in boldness influence migratory tendency. Ecol Lett 14:871–876

Clarke LR, Vidergar DT, Bennett DH (2005) Stable isotope and gut content show diet overlap among native and introduced piscivores in a large oligotrophic lake. Ecol Freshwater Fish 14:267–277

Colborne SF, Hondorp DW, Holbrook CM, Lowe MR, Boase JC, Chiotti JA, Wills TC, Roseman EF, Krueger CC (2019) Sequence analysis and acoustic tracking individual lake sturgeon identifies multiple patterns of river-lake habitat use. Ecosphere 10:1. https://doi.org/10.1002/ecs2.2983

Connolly PJ, Jezorek IG, Prentice EF (2005) Development and use of in-stream PIT-tag detection systems to assess movement behavior of fish in tributaries of the Columbia River Basin, USA. 5th International Conference on Methods and Techniques in Behavioral Research. Wageningen, Netherlands, pp 217–220

Cooke SJ, Schreer JF (2003) Environmental monitoring using physiological telemetry–a case study examining common carp responses to thermal pollution in a coal-fired generating station effluent. Water Air Soil Poll 142:113–136

Cooke SJ, Thorstad EB (2012) Is radio telemetry getting washed downstream? The changing role of radio telemetry in studies of freshwater ichthyofauna relative to other tagging and telemetry technology. Am Fish Soc Symp 76:349–369

Cooke SJ, Hinch SG, Lucas MC, Lutcavage M (2012) Chapter 18—Biotelemetry and biologging. In: Zale AV, Parrish DL, Sutton TM (eds) Fisheries Techniques, 3rd edn. American Fisheries Society, Bethesda, pp 819–860

Cooke SJ, Midwood JD, Thiem JD, Klimley P, Lucas MC, Thorstad EB, Eiler J, Holbrook C, Ebner BC (2013) Tracking animals in freshwater with electronic tags: past, present and future. Anim Biotelem 1:5

Cooke SJ, Brownscombe JW, Raby GD, Broell F, Hinch SG, Clark TD, Semmens JM (2016) Remote bioenergetics measurements in wild fish: opportunities and challenges. Comp Biochem Physiol A 202:23–37

Cote D, Tibble B, Curry RA, Peake S, Adams BK, Clarke KD, Perry R (2020) Seasonal and diel patterns in activity and habitat use by brook trout (*Salvelinus fontinalis*) in a small Newfoundland lake. Env Biol Fish 103:31–47

Crawshaw LI (1984) Low-temperature dormancy in fish. Am J Physiol 246:R479–R486

Cruz-Font L, Shuter BJ, Blanchfield PJ, Minns CK, Rennie MD (2019) Life at the top: lake ecotype influences the foraging patterns, metabolic costs and life history of an apex fish predator. J Anim Ecol 88:702–716

Cunjak RA (1996) Winter habitat of selected stream fishes and potential impacts from land-use activity. Can J Fish Aquat Sci 53(Suppl. 1):267–282

Cunjak RA, Power G (1986) Winter biology of the blacknose dace, *Rhinichthys atratulus*, in a southern Ontario stream. Env Biol Fish 17:53–60

D'Arcy J, Kelly S, McDermott T, Hyland J, Jackson D, Bolton-Warberg M (2020) Assessment of PIT tag retention, growth and post-tagging survival in juvenile lumpfish, *Cyclopterus lumpus*. Anim Biotelem 8:1–9

Daniels J, Chaput G, Carr J (2018) Estimating consumption rate of Atlantic salmon smolts (*Salmo salar*) by striped bass (*Morone saxatiis*) in the Miramichi River estuary using acoustic telemetry. Can J Fish Aquat Sci 75:1811–1822

Dorazio RM, Price M (2019) State-space models to infer movements and behavior of fish detected in a spatial array of acoustic receivers. Can J Fish Aquat Sci 76:543–550

Ellis TA, Buckel JA, Hightower JE (2017) Winter severity influences spotted seatrout mortality in a southeast US estuarine system. Mar Ecol Prog Ser 564:145–161

Elrod JH, O'Gorman R, Schneider CP (1996) Bathythermal distribution, maturity, and growth of lake trout strains stocked in US waters of Lake Ontario, 1978–1993. J Great Lakes Res 22:722–743

Farmer TM, Marschall EA, Dabrowski K, Ludsin SA (2015) Short winters threaten temperate fish populations. Nat Commun 6:7724

Favrot SD, Jonasson BC (2020) Fall and winter movement dynamics of naturally produced spring chinook salmon parr in two neighboring interior Pacific Northwest natal rivers. Trans Am Fish Soc 149:532–551

Fernandes T, McMeans BC (2019) Coping with the cold: energy storage strategies for surviving winter in freshwater fish. Ecography 42:2037–2052

Finstad AG, Naesje TF, Forseth T (2004) The importance of ice cover for energy turnover in juvenile Atlantic salmon. Freshw Biol 49:1459–1467

Fry FEJ (1947) Effects of the environment on animal activity. Pub. Ontario Fish. Lab. No. 68. U. Toronto Studies. Biol. Ser 55:1–52

Gallagher CP, Guzzo MM, Dick TA (2019) Seasonal depth and temperature use, and diel movements of lake trout (*Salvelinus namaycush*) in a subarctic lake. Arctic Sci 5:71–89

Giacomini HC, Shuter BJ (2013) Adaptive responses of energy storage and fish life histories to climatic gradients. J Theor Bio. 339:100–111

Gibson AJF, Halfyard EA, Bradford RG, Stokesbury MJW, Redden AM (2015) Effects of predation on telemetry-based survival estimates: insights from a study on endangered Atlantic salmon smolts. Can J Fish Aquat Sci 72:728–741

Gjelland KO, Hedger RD (2013) Environmental influence on transmitter detection probability in biotelemetry: developing a general model of acoustic transmission. Meth Ecol Evol 4:665–674

Gorman AM, Kraus RT, Gutowsky LFG, Vandergoot CS, Zhao Y, Knight CT, Faust MD, Hayden TA, Krueger CC (2019) Vertical habitat use by adult walleyes conflicts with expectations from fishery-independent surveys. Trans Am Fish Soc 148:592–604

Gorsky D, Zydlewski J, Basley D (2012) Characterizing seasonal habitat use and diel vertical activity of lake whitefish in Clear Lake, Maine, as determined with acoustic telemetry. Trans Am Fish Soc 141:761–771

Grabowski T, Young SP, Cott PA (2020) Looking for love under the ice: using passive acoustics to detect burbot (*Lota lota*: Gadidae) spawning activity. Freshwater Biol 65:37–44

Greenbank J (1945) Limnological conditions in ice-covered lakes, especially as related to winter-kill of fish. Ecol Monog 15:343–392

Guzzo MM, Blanchfield PJ (2017) Climate change alters the quantity and phenology of habitat for lake trout (*Salvelinus namaycush*) in small Boreal Shield lakes. Can J Fish Aquat Sci 74:871–884

Guzzo MM, Blanchfield PJ, Rennie MD (2017) Behavioral responses to annual temperature variation alter the dominant energy pathway, growth, and condition of a cold-water predator. Proc Natl Acad Sci 114:9912–9917

Halfyard EA, Webber D, Del Papa J, Leadley T, Kessel ST, Colborne SF, Fisk AT (2017) Evaluation of an acoustic telemetry transmitter designed to identify predation events. Meth Ecol Evol 8:1063–1071

Hampton SE, Galloway AW, Powers SM et al (2017) Ecology under lake ice. Ecol Lett 20:98–111

Happel A, Creque S, Richard J, Hook T, Bootsma H, Janssen J, Jude D, Czesny S (2015) Exploring yellow perch diets in Lake Michigan through stomach content, fatty acids, and stable isotope ratios. J Great Lakes Res 41(3):172–178

Hasler A, Villemonte J (1953) Observations on the daily movements of fishes. Science 118:321–322

Hayden TA, Holbrook CM, Binder TR, Dettmers JM, Cooke SJ, Vandergoot CS, Krueger CC (2016) Probability of acoustic transmitter detections by receiver lines in Lake Huron: results of multi-year field tests and simulations. Anim Biotelem 4:19

Hayes DB, Taylor WW (1994) Changes in the composition of somatic and gonadal tissues of yellow perch following white sucker removal. Trans Am Fish Soc 123:204–216

Heupel MR, Semmens JM, Hobday AJ (2006) Automated tracking of aquatic animals: scales, design and deployment of listening station arrays. Mar Freshwat Res 57:1–13

Hockersmith EE, Muir WD, Smith SG, Sandford BP, Perry RW, Adams NS, Rondorf DW (2003) Comparison of migration rate and survival between radio-tagged and PIT-tagged migrant yearling chinook salmon in the snake and Columbia rivers. N Am J Fish Manage 23:404–413

Hubbard JAG, Hickie BE, Bowman J, Hrenchuk LE, Blanchfield PJ, Rennie MD (2020) No long-term effect of intracoelomic acoustic transmitter implantation on survival, growth, and body condition of a long-lived stenotherm in the wild. Can J Fish Aquat Sci. https://doi.org/10.1139/cjfas-2020-0106

Hussey NE, Kessel ST, Aarestrup K, Cooke SJ, Cowley PD, Fisk AT, Harcourt RG, Holland KN, Iverson SJ, Kocik JF, Flemming JEM, Whoriskey FG (2015) Aquatic animal telemetry: a panoramic window into the underwater world. Science 348(6240):1. https://doi.org/10.1126/science.1255642

Huusko ARI, Greenberg L, Stickler M, Linnansaari T, Nykänen M, Vehanen T, Koljonen S, Alfredsen K (2007) Life in the ice lane: the winter ecology of stream salmonids. River Res Appl 23:469–491

Huveneers CC, Simpfendorfer CA, Kim S, Semmens JM, Pederson H, Stieglitz T, Vallee R, Webber D, Heupel MR, Peddemors V, Harcourt RG (2016) The influence of environmental parameters on the performance and detection range of acoustic receivers. Meth Ecol Evol 7:825–835

Ivanova SV, Johnson TB, Metcalfe B, Fisk AT (In press) Spatial distribution of lake trout (*Salvelinus namaycush*) across seasonal thermal cycles in a large lake. Freshwater Biol. https://doi.org/10.1111/fwb.13665

Johnston P, Bérubé F, Bergeron NE (2009) Development of a flatbed passive integrated transponder antenna grid for continuous monitoring of fishes in natural streams. J Fish Biol 74:1651–1661

Karchesky CM, Bennett DH (2004) Winter habitat use by adult largemouth bass in the Pend Oreille River, Idaho. Am J Fish Manage 24:577–585

Kenward RE (2000) A manual for wildlife radio tagging. Academic Press, London. ISBN 0-12-404242-2

Kessel ST, Cooke SJ, Heupel MR, Hussey NE, Simpfendorfer CA, Vagle S, Fisk AT (2014) A review of detection range testing in aquatic passive acoustic telemetry studies. Rev Fish Biol Fish 24:199–218

Keyler TD, Matthias BG, Hrabik TR (2019) Siscowet lake charr (*Salvelinus namaycush siscowet*) visual foraging habitat in relation to daily and seasonal light cycles. Hydrobiologia 840:63–76

Klaminder J, Hellstrom G, Fahlman J, Jonsson M, Fick J, Lagesson A, Bergman E, Brodin T (2016) Drug-induced behavioral changes: using laboratory observations to predict field observations. Front Environ Sci. https://doi.org/10.3389/fenvs.2016.00081

Klinard NV, Matley JK (2020) Living until proven dead: addressing mortality in acoustic telemetry research. Rev Fish Biol Fish 1:1. https://doi.org/10.1007/s11160-020-09613-z1

Klinard NV, Halfyard EA, Fisk AT, Steward TJ, Johnson TB (2018) Effects of surgically implanted acoustic tags on body condition, growth, and survival in small, laterally compressed forage fish. Trans Am Fish Soc 147:749–757

Klinard NV, Matley JK, Fisk AT, Johnson TB (2019a) Long-term retention of acoustic telemetry transmitters in temperate predators revealed by predation tags implanted in wild prey fish. J Fish Biol 95:1512–2516

Klinard NV, Halfyard EA, Matley JK, Fisk AT, Johnson TB (2019b) The influence of dynamic environmental interactions on detection efficiency of acoustic transmitters in a large, deep, freshwater lake. Anim Biotelem 7:17

Klinard NV, Matley JK, Halfyard EA, Connerton M, Johnson TB, Fisk AT (2020) Post-stocking movement and survival of hatchery-reared bloater (*Coregonus hoyi*) reintroduced to Lake Ontario. Freshwater Biol 1:1

Knights BC, Johnson BL, Sandheinrich MB (1995) Responses of bluegills and black crappies to dissolved oxygen, temperature, and current in backwater lakes of the upper Mississippi River during winter. N Am J Fish Manage 15:390–399

Krueger CC, Holbrook CM, Binder TR, Vandergoot CS, Hayden TA, Hondorp DW, Nate N, Paige K, Riley SC, Fisk AT, Cooke SJ (2018) Acoustic telemetry observation systems: challenges encountered and overcome in the Laurentian Great Lakes. Can J Fish Aquat Sci 75:1755–1763

Landsman SJ, Nguyen VM, Gutowski LFG, Gobin J, Cook KV, Binder TR, Lower N, McLaughlin RL, Cooke SJ (2011) Fish movement and migration studies in the Laurentian Great Lakes: research trends and knowledge gaps. J Great Lakes Res 37:365–379

Larsen MH, Thorn AN, Skov C, Aarestrup K (2013) Effects of passive integrated transponder tags on survival and growth of juvenile Atlantic salmon *Salmo salar*. Anim Biotelemetry. https://doi.org/10.1186/2050-3385-1-19

Lechelt JD, Bajer PG (2016) Modeling the potential for managing invasive common carp in temperate lakes by targeting their winter aggregations. Biol Invasions 18:831–839

Lester NP, Dextrase AJ, Kushneriuk RS, Rawson MR, Ryan PA (2004) Light and temperature: key factors affecting walleye abundance and production. Trans Am Fish Soc 133:588–605

Lidgard DC, Bowen WD, Jonsen ID, Iverson SJ (2014) Predator-borne acoustic transceivers and GPS tracking reveal spatiotemporal patterns of encounters with acoustically tagged fish in the open ocean. Mar Ecol Prog Ser 501:157–168

Lindstrom JW, Hubert WA (2004) Ice processes affect habitat use and movements of adult cutthroat trout and brook trout in a Wyoming foothills stream. N Am J Fish Manage 24:1341–1352

Linnansaari T, Cunjak RA (2010) Patterns in apparent survival of Atlantic salmon (*Salmo salar*) parr in relation to variable ice conditions throughout winter. Can J Fish Aquat Sci 67:1744–1754

Linnansaari T, Alfredsen K, Stickler M, Arnekleiv JV, Harby A, Cunjak RA (2009) Does ice matter? site fidelity and movements by Atlantic salmon (*Salmo salar* L.) parr during winter in a substrate enhanced river reach. River Res Appl 1:1. https://doi.org/10.1002/rra.1190

Mackenzie-Grieve JL, Post JR (2011) Thermal habitat use by lake trout in two contrasting Yukon Territory lakes. Trans Am Fish Soc 135:227–238

Magnuson J, Crowder L, Madvick P (1979) Temperature as an ecological resource. Am Zool 19:331–343

Magnuson JJ, Beckel AL, Mills K, Brandt SB (1985) Surviving winter hypoxia: behavioral adaptations of fishes in a northern Wisconsin winterkill lake. Env Biol Fish 14:241–250

Magnuson JJ, Robertson DM, Benson BJ, Wynne RH, Livingstone DM, Arai T, Assel RA, Barry RG, Card V, Kuusisto E, Granin NG, Prowse TD, Stewart KM, Vuglinski VS (2000) Historical trends in lake and river ice cover in the northern hemisphere. Science 289:1743–1746

Marsden JE, Binder TR, Johnson J, He J, Dingledine N, Adams J, Johnson N, Krueger CC (2016) Five-year evaluation of habitat remediation in Thunder Bay, Lake Huron: comparison of characteristics of constructed reefs that attract spawning lake trout. Fish Res 183:275–286

Matley JK, Faust MD, Raby GD, Zhao Y, Robinson J, MacDougall T, Hayden TA, Fisk AT, Vandergoot CS, Krueger CC (2020) Seasonal habitat-use differences among Lake Erie's walleye stocks. J Great Lakes Res 46:609–621

McMeans BC, McCann KS, Guzzo M, Bartley TJ, Bieg C, Blanchfield PJ, Fernandes T, Giacomini H, Middel T, Rennie M, Ridgway M, Shuter BJ (2020) Winter in water: differential responses and the maintenance of biodiversity. Ecol Lett. https://doi.org/10.1111/ele.13504

Medford BA, Mackay WC (1978) Protein and lipid content of gonads, liver, and muscle of northern pike (Esox lucius) in relation to gonad growth. J Fish Res Bd Can 35:213–219

Minns CK (1995) Allometry of home-range size in lake and river fishes. Can J Fish Aquat Sci 52:1499–1508

Mueller RP, Brown RS, HopH Moulton L (2006) Video and acoustic camera techniques for studying fish under ice: a review and comparison. Rev Fish Biol Fish 16:213–226

Muhlfeld CC, Marotz B (2011) Seasonal movement and habitat use by subadult bull trout in the upper Flathead River system, Montana. N Am J Fish Manage 25:797–810

Mulder IM, Morris CJ, Dempson JB, Fleming IA, Power M (2018) Overwinter thermal habitat use in lakes by anadromous Arctic char. Can J Fish Aquat Sci 75:2343–2353

Nowak GM, Quinn TP (2002) Diel and seasonal patterns of horizontal and vertical movements of telemetered cutthroat trout in Lake Washington, Washington. Trans Am Fish Soc 131:452–462

O'Malley BP, Dillon RA, Paddock RW, Hansson S, Stockwell JD (2018) An underwater video system to assess abundance and behavior of epibenthic *Mysis*. Limnol Oceanogr-Methods 16:868–880

Patterson K, Blanchfield PJ (2013) *Oncorhynchus mykiss* escaped from commercial freshwater aquaculture pens in Lake Huron, Canada. Aquacult Env Interac 4:53–65

Penne CR, Pierce CL (2008) Seasonal distribution, aggregation, and habitat selection of common carp in Clear Lake, Iowa. Trans Am Fish Soc 137:1050–1062

Perry RW, Skalski JR, Brandes PL, Sandstrom PT, Klimley AP, Ammann A, MacFarlane B (2010) Estimating survival and migration route probabilities of juvenile Chinook salmon in the Sacramento-San Joaquin river delta. N Am J Fish Manage 30:142–156

Pfauserova N, Slavik O, Horky P, Kolarova J, Randak T (2019) Migration of non-native predator asp (*Leuciscus aspius*) from a reservoir poses a potential threat to native species in tributaries. Water 11:1306

Plumb JM, Blanchfield PJ, Abrahams MV (2014) A dynamic-bioenergetics model to assess depth selection and reproductive growth by lake trout (*Salvelinus namaycush*). Oecologia 175:549–563

Raby GD, Johnson TB, Kessel ST, Stewart TJ, Fisk AT (2020) Pop-off data storage tags reveal niche partitioning between native and non-native predators in a novel ecosystem. J Appl Ecol 57:181–191

Říha MRD, Vašek M, Prchalová M, Mrkvička T, Jůza T, Cech M, Draštik V, Muška M, Kratochvíl M, Peterka J, Tušer M, Seda J, Blabolil P, Bláha M, Wansenböck J, Kubecka J (2015) Patterns in diel habitat use of fish covering the littoral and pelagic zones in a reservoir. Hydrobiologia 747:111–131

Robinson JM, Josephson DC, Weidel BC, Kraft CE (2010) Influence of variable interannual summer water temperatures on brook trout growth, consumption, reproduction, and mortality in an unstratified Adirondack lake. Trans Am Fish Soc 139:685–699

Romine JG, Johnston SV, Fitzer CW, Pagliughi SW, Blake AR (2014) Identifying when tagged fishes have been consumed by piscivorous predators: application of multivariate mixture models to movement parameters of telemetered fishes. Anim Biotelem 2:3. https://doi.org/10.1186/2050-3385-2-3

Rosten CN, Gozlan RE, Lucas MC (2016) Allometric scaling of intraspecific space use. Biol Lett 12:20150673. https://doi.org/10.1098/rsbl.2015.0673

Roy R, Beguin J, Argillier C, Tissot L, Smith F, Smedbol S, De-Oliveira E (2014) Testing the VEMCO positioning system: spatial distribution of the probability of location and the positioning error in a reservoir. Anim Biotelemetry 2:1. https://doi.org/10.1186/2050-3385-2-1

Schultz A, Kumagai K, Bridges B (2015) Methods to evaluate gut evacuation rates and predation using acoustic telemetry in the Tracy Fish Collection Facility primary channel. Anim Biotelem 3:13. https://doi.org/10.1186/s40317-015-0034-y

Shuter BJ, Post JR (1990) Climate, population viability, and the zoogeography of temperate fishes. Trans Am Fish Soc 119:314–336

Shuter BJ, Finstad AG, Helland IP, Zweimüller I, Hölker F (2012) The role of winter phenology in shaping the ecology of freshwater fish and their sensitivities to climate change. Aquat Sci 74:637–657

Simard LG, Sotola VA, Marsden JE, Miehls S (2017) Assessment of PIT tag retention and post-tagging survival in metamorphosing juvenile sea lamprey. Anim Biotelem 5:18–24

Speers-Roesch B, Norin T, Driedzic WR (2018) The benefit of being still: energy savings during winter dormancy in fish come from inactivity and the cold, not from metabolic rate depression. Proc R Soc B Biol Sci 285:20181593. https://doi.org/10.1098/rspb.2018.1593

Stewart TJ, Bowlby JN (2009) Chinook salmon and rainbow trout catch and temperature distributions in Lake Ontario. J Great Lakes Res 35:232–238

Stickler M, Enders EC, Pennell CJ, Cote D, Alfredsen K, Scruton DA (2008) Stream gradient-related movement and growth of Atlantic salmon parr during winter. Trans Am Fish Soc 137:371–385

Stockwell JD, Yule DL, Hrabik TR, Sierszen ME, Isaac EJ (2014) Habitat coupling in a large lake system: delivery of an energy subsidy by an offshore planktivore to the nearshore zone of Lake Superior. Freshwater Biol 59:1197–1212

Tanasschuk RW, Mackay WC (1989) Quantitative and qualitative characteristics of somatic and gonadal growth of yellow perch (Perca flavescens) from Lac Ste. Anne. Alberta. Can J Fish Aquat Sci 46:989–994

Taylor AH, Tracey SR, Hartmann K, Patil JG (2012a) Exploiting seasonal habitat use of the common carp, *Cyprinus carpio*, in a lacustrine system for management and eradication. Mar Freshw Res 63:587–597

Taylor MK, Cook KV, Hasler CT, Schmidt DC, Cooke SJ (2012b) Behaviour and physiology of mountain whitefish (Prosopium williamsoni) relative to short-term changes in river flow. Ecol Freshw Fish 21:609–616

Thorstad EB, Uglem I, Arechavala-Lopez P, Økland F, Finstad B (2011) Low survival of hatchery-released Atlantic salmon smolts during initial river and fjord migration. Boreal Environ Res 16:115–120

Velle JI, Lindsay JE, Weeks RW, Long FM (1979) An investigation of the loss mechanisms encountered in propagation from a submerged fish telemetry transmitter. In: Proceedings of 2nd International Conference Wild. Biotelemetry 1979. Univ. Wyoming, Laramie, WY pp 228–237

Voegeli FA, Pincock DG (1996) Overview of underwater acoustics as it applies to telemetry. In 'Underwater Biotelemetry'. (Eds E Baras, JC Phillipart) pp. 23-30. University of Liege: Liege, Belgium

Walton-Rabideau SE, Newell M, Jeanson AL, Lédée EJI, Farrell JM, Cooke SJ (2019) Evaluation of tag retention, healing, growth, and behavior in age-0 muskellunge following acoustic transmitter implantation. N Am J Fish Manage 39:652–663

Walton-Rabideau SE, Lédée EJI, Leblanc JP, Szekeres P, Midwood JD, Gallagher AJ, Farrell JM, Cooke SJ (2020) Spatiotemporal ecology of juvenile muskellunge (*Esox masquinongy*) and northern pike (*Esox lucius*) in upper St Lawrence River nursery bays during their inaugural fall and winter. Ecol Freshw Fish 1:346–363

Watson BM, Biagi CA, Northrup SL, Ohata MLA, Charles C, Blanchfield PJ, Johnston SV, Askey PJ, van Poorten BT, Devlin RH (2019) Distinct diel and seasonal behaviours in

rainbow trout detected by fine-scale acoustic telemetry in a lake environment. Can J Fish Aquat Sci 76:1432–1445
Weber C, Scheuber H, Nilsson C, Alfredsen KT (2016) Detection and apparent survival of PIT-tagged stream fish in winter. Ecol Evol 6:2536–2547
Weinz AA, Matley JK, Klinard NV, Fisk AT, Colborne CF (2020) Identification of predation events in wild fish using novel acoustic transmitters. Anim Biotelemetry 8:28. https://doi.org/10.1186/s40317-020-00215-x
Woolnough DA, Downing JA, Newton TJ (2009) Fish movement and habitat use depends on water body size and shape. Ecol Freshw Fish 18:83–91
Woolway RI, Kraemer BK, Lenters JD, Merchant CJ, O'Reilley CM, Sharma S (2020) Global lake responses to climate change. Nat Rev Earth Env 1:388–403
Zydlewski GB, Haro A, Whalen KG, McCormick SD (2001) Performance of stationary and portable passive transponder detection systems for monitoring of fish movements. J Fish Biol 58:1471