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Applications of telemetry to fish habitat science and management

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Abstract: Telemetry has major potential for application to fish habitat science and management, but to date it is underutilized in this regard. We posit this is because (1) fish telemetry projects are often geared towards detecting fish movement, opposed to systematically sampling habitat selection, and (2) there are often differences in scale between telemetry data and management decisions. We discuss various ways in which telemetry can contribute to fish habitat science and present some considerations for improving its application to this field. To date, most fish telemetry studies have been descriptive (e.g., fish use area A more than area B); greater adoption of more inferential study approaches that assess causal ecological drivers of movement and space use would be of value and require more extensive measurement of environmental conditions. We conclude by presenting a conceptual framework for scaling from individual studies to broad applications in habitat management. Established telemetry networks can readily support synthesis activities, although fish tracking data and environmental data are rarely stored together, and current disconnects among repositories may constrain broad integration and scalability.

Résumé : Si le potentiel d'application de la télémétrie à l'étude et à la gestion des habitats du poisson est important, l'approche demeure sous-utilisée à ce jour. Nous postulons que les causes en sont (1) le fait que les projets de télémétrie appliquée au poisson sont souvent axés sur la détection des déplacements des poissons, par opposition à l'échantillonnage systématique de la sélection d'habitats et (2) les différences d'échelles fréquentes entre les données de télémétrie et les décisions de gestion. Nous abordons différentes approches par lesquelles la télémétrie peut contribuer à l'étude de l'habitat du poisson et certaines considérations permettant d'en améliorer l'application à ce domaine d'étude. La plupart des études télémétriques sur les poissons à ce jour sont descriptives (p. ex. les poissons utilisent plus la région A que la région B). Une adoption plus large d'approches plus inférentielles qui évaluent les facteurs écologiques causals des déplacements et de l'utilisation de l'espace serait utile et nécessiterait des mesures plus vastes des conditions environnementales. Nous concluons en présentant un cadre conceptuel pour passer de l'échelle d'études individuelles à celle d'applications plus larges en gestion des habitats. Des réseaux télémétriques établis peuvent aisément appuyer des activités de synthèse, mais les données de suivi des poissons et les données environnementales sont rarement conservées ensemble et le manque d'harmonisation des dépôts de données peut limiter l'intégration et l'extensibilité de ces dernières. [Traduit par la Rédaction]

Introduction

Effective management of fish populations requires careful consideration of their habitat requirements, including the physical/structural (e.g., substrate, macrophytes), chemical/limnological (e.g., water temperature, dissolved oxygen concentration), and biological (e.g., benthic invertebrate prey, predators) components (Minns 2001; Minns and Wichert 2005; Rice 2005; Rosenfeld and Hatfield 2006). Habitat requirements are complex, vary across life stages, and often must be characterized at multiple ecological scales (Johnson 1980). Further, ecosystems are exceedingly complex and highly interconnected and hence should be managed holistically using ecosystem-based management approaches (Slocombe 1993; Pikitch et al. 2004). While habitat is foundational for healthy and productive fish populations (Lapointe et al. 2014), habitat can be challenging to characterize and manage effectively.

Historically, fish–habitat associations have been characterized using sampling approaches involving direct in-person measurement (e.g., snorkeling) and (or) collection of fish distribution and abundance (e.g., through netting, electrofishing) and associated environmental conditions. These foundational approaches to fish habitat sampling still play important roles today (Bonar and Hubert 2002). However, such sampling is limited by logistic constraints and represents only a snapshot of the complex lives of fish. One obvious example of this is our more limited knowledge of fish winter ecology in temperate regions, given that most habitat work occurs in other seasons (Cunjak 1996; Block et al. 2018; Marsden et al. 2021). Meanwhile, new technologies are drastically increasing our capacity to measure the biotic and abiotic conditions of ecosystems either remotely or more continuously. For example, water surface temperature, vegetation composition and density, and ice cover can be quantified using satellite imagery (Schwab et al. 1992;

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Cavalieri et al. 1999; Marcaccio et al. 2021) or other tools (e.g., lidar, drones). Water temperature and dissolved oxygen can be measured in situ with loggers (store information on the device) or transmitters (transfer information remotely). Biological communities can be assessed visually with cameras (Harvey et al. 2007) or with hydroacoustics (Egerton et al. 2018) or bioacoustics (Lobel 2002; Lindseth and Lobel 2018). To remotely measure the position of fishes themselves, telemetry techniques, such as acoustic, radio, or satellite technology, have become highly popular (Hussey et al. 2015). Unlike conventional field-based sampling, these approaches can all provide more continuous and remote tracking that can be temporally and spatially integrated with the measurements of environmental conditions.

Data generated by satellite tracking, active radio or acoustic tracking, or fine-scale acoustic positioning are different than acoustic, radio, or passive integrated transponder monitoring at distinct receiver stations (Hussey et al. 2015). The former approaches produce estimates of animal positions (i.e., animal tracks), while the latter involves continuous monitoring of specific locations and is therefore more analogous with camera trap data (i.e., provides information on presence at a monitoring location) than satellite or active tracking data (Brownscombe et al. 2019*c*). Appropriate analytical techniques to generate insights on fish habitat use or selection therefore vary among tracking methods (Brownscombe et al. 2019*c*; Whoriskey et al. 2019). Here we discuss some of these conceptual differences, but mainly focus on station-based acoustic telemetry, as it has become the most popular and is generating a large and growing body of data (Hussey et al. 2015; Iverson et al. 2019). Station-based acoustic telemetry involves attaching or implanting transmitters in fish that emit acoustic signals (~60–400 kHz), which are detected by receivers placed throughout an aquatic system. This provides a general indication of fish position when in proximity to a receiver (which have ~10–1000 m ranges depending on conditions; Kessel et al. 2014; Klinard et al. 2019; Weinz et al. 2021). However, unless a fine-scale tracking receiver arrangement is used (e.g., Espinoza et al. 2011; Baktoft et al. 2017), specific locations within the detection range are unknown, as is the location of a tagged fish when it is not detected (although with sufficient detection frequencies modeling approaches can estimate locations; e.g., Simpfendorfer et al. 2012). Hence, acoustic telemetry generally provides continuous long-term monitoring of specific locations, but often discontinuous monitoring of individual fish positions, habitat use, movement patterns, and spatial connectivity. The degree of continuity of fish monitoring is directly related to the spacing of the individual receiver stations and the detection range of transmissions within the system (Kraus et al. 2018). In addition to space use, transmitters with integrated sensors enable remote measurement of fish behaviour (e.g., foraging), physiology (e.g., energy expenditure), and environmental experience (e.g., temperature; reviewed in Cooke et al. 2016*a*; Brownscombe et al. 2019*b*). These capabilities greatly expand our capacity to understand interactions between fish and environmental conditions and thus drivers of their space use. Further, the growing popularity of acoustic telemetry has resulted in extensive tracking networks that enable sharing of data among projects and researchers, expanding our capacity to track fish movement and space use at spatial and temporal scales never before possible (Iverson et al. 2019; Lowerre-Barbieri et al. 2019).

Despite the potential for telemetry to inform a variety of aspects of fish and fisheries management, it is considered underutilized in this regard (Crossin et al. 2017; Nguyen et al. 2018; Brownscombe et al. 2021). It has been recognized as being useful for characterizing fish habitat associations since its early conception (Winter and Ross 1982), and there are many relevant examples (e.g., Cooke et al. 2016*b*; Brooks et al. 2017, 2019*a*; Binder et al. 2018; Matley et al. 2020; Rudolfsen et al. 2021), some of which are discussed further below. Yet, it is our perspective that telemetry is still particularly underutilized for fish habitat science and management. Many existing applications use descriptive analyses, focusing on, for example, depth use across different embayments of the study area. Studies also often include a cursory characterization of habitat, focusing on a small number of factors relative to a fish's entire niche. Placed-based analyses with limited habitat characterization can provide valuable insights, but they enable limited inference and scalability — a key aspect for broad applicability of telemetry data in habitat management. Meanwhile, in the mainly terrestrial-focused field of landscape ecology, habitat selection and species distribution modelling based on animal tracking data are better developed and more widely applied (e.g., Millspaugh et al. 2006; Johnson et al. 2008; Kelly and Holub 2008; Sarmento et al. 2010; Trolliet et al. 2014). Yet, the near-continuous spatial and temporal nature of satellite- or GPS-based animal tracking data are very different from station-based acoustic telemetry, posing different challenges that require different approaches.

We posit two major reasons for a lack of widespread application of telemetry-based fish habitat science and management: (1) fish telemetry studies are most often designed to characterize fish movement (reviewed in Brownscombe et al. 2019*b*), which is fundamentally different from study designs focused on quantifying habitat selection, and (2) there are marked differences in spatial scale between telemetry data (i.e., individual fish in a specific ecosystem) and habitat management, wherein the latter involves making decisions about human activities on a range of scales from a single site to whole ecosystems or multiple watersheds and often in systems that have not been explicitly studied. In efforts to advance widespread application, we discuss the ways in which telemetry may be useful for enhancing fish habitat science and management, and then discuss the methodological and analytical considerations for doing so. We also present a general framework for synthesizing telemetry data repositories to explore generalizable patterns that may help to bridge the scale gap between telemetry studies and fish habitat decision making.

Applications

There are a variety of ways in which telemetry may inform fish habitat science and management (Table 1). Relatively simple and direct applications include questions such as the proportion of fish that successfully pass a barrier through a fishway, and hence, the availability of reaches above the barrier as fish habitat (reviewed in Bunt et al. 2012; Silva et al. 2018) or identification of important spawning habitats and their regional connectivity (e.g., Binder et al. 2016; Hayden et al. 2018; Brownscombe et al. 2019*a*). Although these are conceptually simple questions, they are challenging to address without the use of advanced tracking technologies, which require complex study design, data collection and analyses to be accomplished effectively. Despite presenting further challenges, it is also possible to gain greater insights into advanced spatial–temporal dynamics, habitat function and value, and complex biotic and abiotic interactions, which are key to enable scaling of fish telemetry data from individual studies to predictive models across broader ecosystems and landscapes. Below we further discuss a variety of applications of telemetry to habitat science (Table 1) organized under **Habitat suitability, Spatial scale and connectivity, Spatial–temporal patterns,** and **Biological community**. Further considerations and challenges to overcome to effectively accomplish robust fish habitat studies with telemetry are discussed in **Challenges and considerations**. Finally, considerations for scaling telemetry data to make predictions beyond individual studies are discussed in **Scaling for broader application**.

Habitat suitability

Perhaps the most fundamentally important information that fish habitat managers require is what exactly fish habitat is (i.e., its physical, chemical, and biological properties), its function, and the species it supports. This requires information about which habitat types, specific habitat features, or range of environmental

Table 1. Biological indicators and select metrics that can be derived from fish telemetry methods and their relevance to fish habitat management.

Biological indicator	Select relevant metrics	Application to fish habitat management
Habitat use or selection	• Habitat Suitability Index (HSI)	• Valuing fish habitat for protection, remediation, or creation • Assessing efficacy of remediation efforts
Habitat function	• Weighted HSI	• Valuing fish habitat for protection and offsetting
Spatial scale	• Home range size • Kernel utilization • Percent overlap	• Assess degree of impact on individuals/populations/ecosystems based on the scale of the impact relative to the scale of available fish habitat
Connectivity	• Network analysis, edge weight • Kernel utilization • Percent passage success/survival	• Identify important migration corridors • Determine spatial scale of metapopulation dynamics • Fish passage efficiency of dams or culverts
Spatial–temporality	• Seasonality • Daily or monthly percent use or occupation probability	• Provide guidance on timing windows (e.g., seasonal) for anthropogenic disturbance • Inform alternate standardized sampling efforts (e.g., netting, electrofishing)
Biological community	• Receiver Efficiency Index (REI; Ellis et al. 2019) • Index of Biological Integrity (IBI; Minns 1995) • Spatial–temporal overlap and time of arrival (Griffin et al., in press)	• Biodiversity hotspots • Multispecies habitat use • Species interactions

conditions that fish can tolerate, occupy, or select for. There is a key need to consider the spatial scale(s), ranging from regional space use and home range to fine scale selection of habitat features for a specific purpose, such as foraging (Johnson 1980; Manly et al. 2002); this is addressed further below in **Spatial scale and connectivity**. Habitat suitability index (HSI) models are often used by resource management agencies (reviewed by de Kerckhove et al. 2008) taking a range of forms from bivariate relationships between an environmental factor and fish presence, to multivariate models of fish habitat selection (see Ahmadi-Nedushan et al. 2006 for review of statistical approaches). These models are based on information from expert opinion (type I), direct measures of fish abundance in relation to habitat characteristics (i.e., habitat use: type II), or measures of fish abundance among the range of available habitat characteristics (i.e., habitat selection: type III). By this definition, habitat suitability generally refers to the capacity of a habitat to support fish populations and may take the form of habitat use, selection, or more broadly, relationships between environmental conditions and fish productivity (DFO 2014).

Telemetry provides an opportunity for a next-generation approach to generating comprehensive HSI models due to its capacity to measure fish space use near-continuously across extended temporal scales. For example, Brownscombe et al. (2021) used multivariate modeling techniques on presence/absence data at acoustic telemetry stations to develop HSI models integrating spatial–temporal interactions for largemouth bass (*Micropterus salmoides*) in Lake Ontario (Fig. 1A). Rudolfsen et al. (2021) used acoustic telemetry detection numbers to develop seasonal HSI models for structural fish habitats in Lake Winnipeg, including consideration of the amount of habitat being sampled to assess selection. Alternatively, Selby et al. (2019) and Griffin et al. (2020) applied resource selection function (RSFs) approaches to acoustic telemetry data to develop resource selection models for turtles in St. Croix, enabling prediction of relative habitat selection over space and time throughout their study area. Assessment of habitat selection is generally preferable to habitat use because a variety of factors (e.g., presence of predators, habitat degradation) may result in suboptimal habitat use, potentially leading to less generalizable fish habitat models or suboptimal fish habitat management targets. The RSF approach is exemplified here with horse-eye jack (*Caranx latus*) using a data subset from (Novak et al. 2020; Fig. 1B). This approach is typically applied to locations derived from "very high frequency" tracking or global positioning systems (Manly et al. 2002; Boyce 2006; Johnson et al. 2006), which produce data that are fundamentally different from typical stationary acoustic receiver studies, which produce data that are more analogous to camera trap surveys (Brownscombe et al. 2019*c*). From this perspective, mark–recapture models have been applied to stationary acoustic data, but more so to assess fish survival and abundance (Dudgeon et al. 2015; Melnychuk et al. 2017) or movement patterns (Hayden et al. 2014), opposed to habitat modeling, which may be a valuable focus of future applications. Importantly, although stationary acoustic telemetry generates animal presence/absence data, detections are limited to detection coverage and performance, both of which are imperfect and vary over space and time, and hence absences include some level of error that can be quantified (Brownscombe et al. 2020). Imperfect detection frequencies are also common in species occurrence data from nontelemetry sources, which is often dealt with using occupancy modelling approaches (e.g., Falke et al. 2010; Martin et al. 2013). We are not aware of any existing applications of occupancy modelling to fish telemetry data.

In addition to space use or selection, a growing suite of integrated sensors in telemetry technology (e.g., pressure/depth, temperature, acceleration) are enabling the remote measurement of animal behaviour, physiology, and ecological conditions and interactions (Hussey et al. 2015; Cooke et al. 2016*a*; Brownscombe et al. 2019*c*). This additional information can inform more in-depth aspects of fish ecology, such as habitat function (e.g., foraging or spawning) and potential energetic costs and gains (thus yielding information on habitat quality). It can also provide a mechanistic basis for fish space use. For example, Burnett et al. (2014) used telemetry to gain an understanding of fish physiological swimming capacity and measurement of fish behaviour (swimming

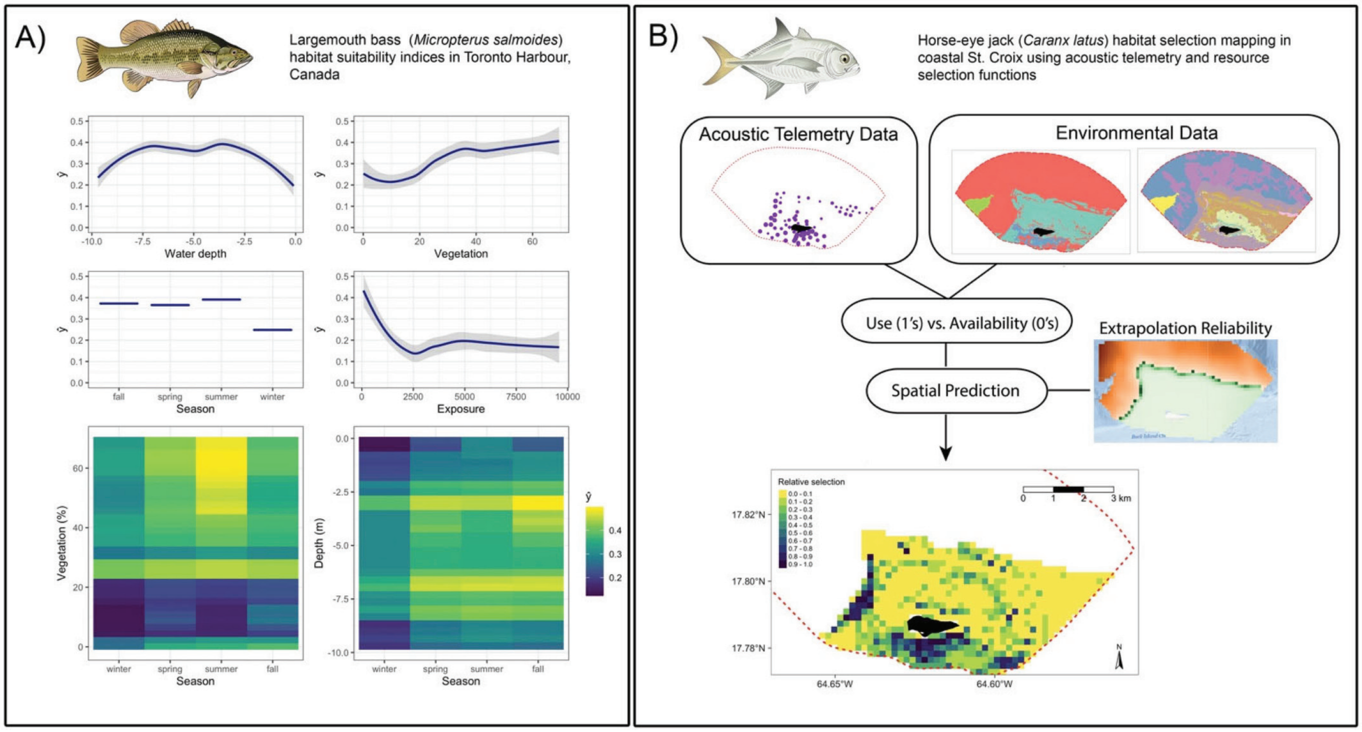


Fig. 1. (A) Habitat suitability indices (HSI) for largemouth bass generated from Toronto Harbour, Canada, using acoustic telemetry and random forests to generate marginal effects for individual factors (top) and interactions (bottom). Data from Brownscombe et al. (2021). (B) A resource selection function approach to model and predict horse-eye jack relative habitat selection using acoustic telemetry. Data subset from Novak et al. (2020) and A. Jordaan (UMass, personal communication), following methods from (Griffin et al. 2021). [Colour online.]

speeds) to determine the environmental constraints (i.e., temperature and water flow speed) on salmon dam passage success. Similarly, the metabolic capacity for exercise and digestion (i.e., aerobic scope) appears to be a strong predictor of bonefish foraging locations and timing (Brownscombe et al. 2017). Despite being more mechanistic and hence insightful and possibly generalizable, these more advanced approaches require more extensive methodologies (e.g., lab calibrations), which may not be as widely tractable with resource constraints.

Overall, the robust data that telemetry can provide on fish habitat suitability, use, selection, function, and drivers thereof should have an increasing role informing fish habitat decision making. This information enables a general assessment of the habitats that a given fish species/life stage rely upon and how any potential changes to these conditions by anthropogenic activities may affect habitat suitability and hence should be avoided, mitigated, or offset. Simpler assessments of habitat use/associations are valuable, but more robust estimates of selection, function, and mechanistic drivers integrating behaviour and physiology may enable more robust application across wider ecological scales. To accomplish this, it is essential to measure habitat variables at spatial and temporal scales comparable to the telemetry-derived positions (e.g., hourly or daily within the detection range of a tracking receiver) to ensure the data are usable for habitat science. This poses some challenges, as environmental conditions often vary considerably in four dimensions, including 3-dimensional space and time. One example of this is variation in submerged aquatic vegetation (SAV) density and height over space and time in freshwater ecosystems. To address this, Tang et al. (2021) used spatial–temporal sampling to develop a model of SAV density in a Lake Ontario marsh that can be applied across relevant spatial–temporal domains. Such estimates (along with others such as 4D temperature, light, turbidity, water flow) could be applied in concert with fish telemetry to develop fish habitat models.

Spatial scale and connectivity

The spatial scale and connectivity of fish habitat are also integral components of natural resource management. The success of aquatic protected areas (APAs), habitat restoration, fish passageways, population estimates, and place-based fisheries management zones all depend on understanding the movement behaviour of the fish species they intend to protect or restore. For example, when considering regulatory decisions around the alteration, destruction, or restoration of a portion of habitat, it is essential to consider the spatial scale of the affected area relative to the space use and distribution of the organism (Minns 1995). APAs (both marine and freshwater) are a rapidly growing conservation tool (Suski and Cooke 2007; Boonzaier and Pauly 2016; Acreman et al. 2019); their efficacy depends heavily on knowledge of animal space use patterns to ensure habitats are protected at a sufficient scale, including consideration of the connectivity among key habitats. Minns (1995) conducted an extensive synthesis of fish home range (i.e., the area encompassing the majority of their space use; often 95%) information and discussed its relevance to habitat management. At the time, however, Minns (1995) relied primarily on mark–recapture studies, which provide only a few data points on movements of fish from recaptures.

Telemetry is well suited to collect extensive information about the spatial scale of fish space use through long-term monitoring, and estimates of core and home ranges are perhaps the most common focus of telemetry studies (reviewed in Heupel and Webber 2012; Brownscombe et al. 2019*b*; Whoriskey et al. 2019). Telemetry is playing a key role in growing efforts to establish APAs as their efficacy depends heavily on understanding the scale of space use and habitat connectivity of aquatic organisms to plan their placement and orientation (Kramer and Chapman 1999; Lennox et al. 2019). Home ranges derived from telemetry (either from kernel utilization distributions, Brownian bridge movement models, or minimum convex polygons), and more recently network analyses (NA), have been used to understand the overlap between habitat a species of interest uses, and the area under protection, usually in the marine environment. Kramer and Chapman (1999) discussed coral reef species-specific home ranging behaviour (e.g., differences in mobility, fish size, levels of site attachment, density-dependent habitat distribution) to compare coverage and spillover effects of marine reserves. Lea et al. (2016) used acoustic telemetry and network analysis on several shark and turtle species to determine the efficacy of an APA in the Seychelles and found strong, species-specific habitat use and corresponding variation in APA use. Their proposed updated boundary increased the APA's coverage of marine predator movement by 34% and was accepted by the Seychelles government. Finally, Bellquist et al. (2008) tracked California ocean whitefish (*Caulolatilus princeps*) to generate home range estimates and determined that APAs can be an effective means of protecting populations of ocean whitefish and, based on their habitat associations, can be managed separately from reef fish. Collectively these examples demonstrate how telemetry can be used to inform the development or modification of protected areas to ensure they completely cover the core or home ranges of a target population.

Effective management and protection of fish species also relies on the connectivity of multiple habitat types that they may require throughout their life cycle and (or) on a seasonal basis. A single landscape or patches of habitat will have varying levels of connectivity, depending on the behaviour, habitat preferences, and dispersal abilities of the species being considered (Johnson and Gaines 1985; Calabrese and Fagan 2004). There are generally three classes of connectivity metrics: structural, potential, and actual (Calabrese and Fagan 2004). Structural is derived from the physical attributes of the landscape (size, location, shape), and potential considers these physical attributes and the species-specific dispersal abilities to predict the level of connectivity (including body size, energy budgets, mark–recapture distances). Actual connectivity relates to the observations of individuals moving in and out of focal patches and estimates of the linkages between various habitats (Grober-Dunsmore et al. 2009), which telemetry is well suited to measure. For example, Murray et al. (2018) tracked juvenile *Lichia amia* in two geographically separated estuaries in South Africa. Fish in both regions displayed high levels of connectivity among estuarine, port, and marine habitats. Similarly, acoustic tracking of lemon sharks (*Negaprion brevirostris*) in Florida by two independent research groups showed a popular migration corridor between a known nursery area and an adult aggregation site (reviewed in Brooks et al. 2019*b*). Movement data obtained from the FACT tracking network (Young et al. 2020) were used to update the federal Essential Fish Habitat zone boundaries for lemon sharks, and the connecting corridor was designated as a Habitat Area of Particular Concern. Connectivity is also a highly relevant metric in the context of fish passage of potential barriers (Wiens 2002; McKay et al. 2013) and a key consideration when animals move among delineated management zones, often requiring the cooperation of multiple management agencies (Griffin et al. 2018; Ogburn et al. 2018). As human activity reduces the area and continuity of aquatic habitats, understanding the species-specific degree of functional connectivity (potential and actual metrics) within the spatial context (structural metrics) becomes increasingly important in natural resource management and telemetry can provide users with these data (Lowerre-Barbieri et al. 2019).

Common approaches to develop estimates of fish space use and connectivity include kernel density estimates (KDE) and network analysis (NA). Lédée et al. (2015) compared these two approaches and found NA provides comparable information on activity space and core use areas to KDE, as well as more comprehensive information on actual movement paths within an acoustic array. Becker et al. (2016) found that KDE (including more advanced methods using Brownian bridges to estimate space use) were useful for identifying core use areas, whereas NA better identified movement corridors and key connections among core and peripheral use areas, which they suggested is important to assess and develop APAs. Indeed, NA has been used to assess reef shark species- and sex-specific movement behaviours and APA design (Espinoza et al. 2015). Kendall et al. (2017) used NA to show that the boundary of a protected area was also a natural barrier to fish movement because of the habitat characteristics of the area separating patches (sand and mud, between reefs and mangrove habitats). Understanding and identifying actual movement paths or unsuitable natural barriers to habitat connectivity could aid with boundary placements for APAs.

The ability to track movement of individuals over long time periods (often many years) and through different life stages also provides robust estimates of spatial scale and connectivity (e.g., for walleye (*Sander vitreus*) in the Great Lakes; Hayden et al. 2014; Raby et al. 2018; Matley et al. 2020). To date, perhaps the biggest constraint on assessing scale and connectivity with telemetry is due to limitations in the size and scale of tracking systems and battery life of tracking tags. With the continued development of telemetry studies, technology (miniaturization of transmitters and extended battery life), and cooperative tracking networks, we are developing a growing capacity to assess the scale of fish space use from small rivers to large open systems such as the Great Lakes and coastal ocean habitats. These telemetry networks are also increasing our capacity to conduct syntheses with these more advanced telemetry-based datasets (discussed further below under **Scaling for broader application**).

Spatial–temporal patterns

The capacity of telemetry to track fish space use near-continuously over multiple years provides more extensive temporal coverage than in-person sampling. As discussed above, this has value in generating comprehensive estimates of the scale of fish space use (e.g., home ranges; Simpfendorfer et al. 2012; Lédée et al. 2015), connectivity among regions, and interannual repeatability of habitat use, such as spawning sites (Binder et al. 2018; Hayden et al. 2018). It also allows for exploration of spatial–temporal interactions, for example, space use among seasons (Brooks et al. 2019*b*), and supports the examination of diverse and finer-scale spatial–temporal interactions in fish habitat use (e.g., Brownscombe et al. 2021; Fig. 1A). When regional habitat data are available, these types of models can be used to also make spatial–temporal predictions on animal distributions (Griffin et al. 2020, 2021; Bangley et al. 2020; Anderson et al. 2021). This capacity to integrate temporal variation is especially important in aquatic systems because they are often highly dynamic. In temperate freshwater systems, for example, entire beds of dense submerged aquatic vegetation can grow in the summer and then die away in the winter leaving near-bare substrate (Rooney and Kalff 2000). In some eutrophic systems, seasonal stratification and hypoxia can occur reducing the amount of suitable habitat available to many species (Flood et al. 2021). Rivers are inherently dynamic given natural flow variability (Puckridge et al. 1998). In coastal marine systems (including estuaries), tides cause dramatic variations in the amount of wetted area, water depth, and salinity, driving fish movements, species compositions, and habitat characteristics. Fishes and other animals may also be more vulnerable to human stressors during certain periods, such as spawning, necessitating dynamic spatial–temporal management actions (Pecl et al. 2006; Hobday et al. 2010; Brodie et al. 2021). Spatial–temporal habitat models would therefore be highly useful for decision making surrounding fish habitat, including the timing and location of anthropogenic disturbances (e.g., in-water works or activities), and could also guide alternative scientific sampling efforts (Larocque et al. 2020). There is major potential value in resource managers having access to models with such capabilities, although such applications are not common to date.

The capacity to translate telemetry data into usable spatial–temporal models of fish habitat and (or) distribution depends heavily on analytical techniques and the availability of comparable spatial–temporal information on habitat conditions. Often, stationary acoustic telemetry data are used to produce estimates of spatial connectivity or interpolated utilization distributions, which require some level of temporal data aggregation, often on monthly or seasonal level to provide sufficient data for the analytical approaches (e.g., Lédée et al. 2015; Brooks et al. 2019*b*). These approaches have the advantage of making inferences on space use and movements outside of the acoustic receiver locations, but they require assumptions about the nature of space use outside of detectable areas and constrain applications to broader temporal scales. Focusing on fish detection data within proximity of acoustic receiver stations, a growing number of studies are using these data to generate habitat models for fish and marine turtles, enabling finer-scale spatial–temporal habitat interactions, often at the day-scale (Selby et al. 2019; Griffin et al. 2020, 2021; Brownscombe et al. 2021; Rudolfsen et al. 2021). Theoretically, this presence/absence modeling approach could be applied at even finer scales (e.g., hourly at specific locations; Griffin et al. 2019); however, a major limitation is the ability to model highly zero-inflated data. An advantage of this approach is it requires no assumptions about where fish are located outside of detection periods; yet, we must consider the spatial scale of detection range in assessing habitat use, as fish may be located anywhere within a variable detection range, which can be 10 to 1000 m in radius (Kessel et al. 2014; Klinard et al. 2019; Weinz et al. 2021). Fine scale positioning systems overcome this challenge, providing up to sub-metre positioning accuracy, but are generally restricted to much smaller spatial scales due to limitations in receiver coverage (Espinoza et al. 2011; Baktoft et al. 2017; Binder et al. 2018). There is also a need to better integrate variation in acoustic receiver detection efficiency (i.e., the extent to which receivers can detect tagged animals in spatial proximity) to avoid biasing habitat models (this topic is discussed more below in **Challenges and considerations**).

Biological community

The increase in popularity and accessibility of acoustic telemetry for fish tracking, combined with advances in technology, has led to improved monitoring coverage (e.g., collaborative telemetry networks, longer battery life durations) and larger sample sizes. This has enabled researchers to scale from single-species to multispecies studies and garner new insights about biological communities and their habitats. For example, leveraging data from the iTAG tracking network, Friess et al. (2021) analyzed detection data from nearly 900 tagged individuals across 29 fish species to identify multispecies hotspots, functional movement classes, and seasonal movement pathways. To identify multispecies hotspots, Friess et al. (2021) calculated an array efficiency index (AEI), modified from a receiver efficiency index (REI) (Ellis et al. 2019), which computes the relative importance of a given location (or receiver) in terms of species detected and detection days, weighted by the array (or receiver) deployment period. Such methods that correct for unequal sampling efforts provide new ways to leverage multispecies datasets to identify potentially important habitats that support high levels of biodiversity. At a more localized scale, acoustic telemetry network analysis in combination with community detection algorithms have been used to explore how species aggregate and separate across habitats (Finn et al. 2014; Casselberry et al. 2020). For example, Casselberry et al. (2020) identified spatially explicit clusters of co-occurring shark species in a Caribbean APA to inform habitat function at the community level and across multiple life history stages. Such multispecies datasets on habitat use may contribute to the development and designation of APAs and to further ecosystem-based management by understanding species hotspots and interactions (Foley et al. 2010; Halpern et al. 2010; Ogburn et al. 2017; Lowerre-Barbieri et al. 2019, 2021). Considering APAs are often designed to protect multiple species and their habitats, applications of acoustic telemetry to evaluate space use are well positioned to provide measures of management efficacy (Lea et al. 2016; Crossin et al. 2017).

Multispecies acoustic telemetry approaches have also been effective in evaluating fish habitat restoration. For example, Rous et al. (2017), examining space use of four freshwater fish species in Toronto Harbor, determined site fidelity was higher for yellow perch (*Perca flavescens*) and northern pike (*Esox lucius*) in habitats that were restored compared to areas that were not restored, but lower for largemouth bass and common carp (*Cyprinus carpio*). In another example, Keller et al. (2017) found a designed artificial reef (habitat supplement) increased biomass production and increased connectivity to adjacent habitats. Similarly, Logan and Lowe (2018) found the addition of an artificial reef likely provided sufficient resources for game fishes compared to the adjacent natural habitats. Importantly, these studies not only monitored the focal habitats in question (e.g., restored habitats or artificial reefs) but also control habitats that were not restored or enhanced. While intuitive, this comparative approach is important to consider and often underutilized when evaluating the efficacy of management related habitat alterations (Taylor et al. 2019).

Despite the widely recognized influence of species interactions such as predation and competition on ecosystem processes, such interactions are challenging to measure at broad spatial and temporal scales (Grober-Dunsmore et al. 2009). Despite the often extensive spatial–temporal component to telemetry data, there are still challenges to translating these data to useful measures of biological interactions, which are increasingly being overcome with analytical approaches. For example, Griffin et al. (2021) used acoustic telemetry and RSFs to predict relative selection of tiger sharks (*Galeocerdo cuvier*) and eight corresponding prey species. The overlapping areas between tiger sharks and their potential prey helped identify areas of potential foraging success for sharks, predation vulnerability for prey, and ecological importance for managers. Summarizing spatially explicit habitat selection predictions across species could also provide managers information to maximize habitat protection, restoration, and monitoring efforts. Further, these methods produce interpretable maps on habitat selection that may help improve acceptance of study results and communications with diverse stakeholder groups (Brooks et al. 2019*a*; Nguyen et al. 2019).

Overall, consideration of habitat function and species interactions among the broader biological community is essential for habitat management, especially considering the now-predominant paradigm of ecosystem-based management. Advancing from species-specific studies to broader community analyses described above is therefore highly valuable. However, it is important to recognize that telemetry is limited to larger organisms, including relatively large fishes (Brownscombe et al. 2019*c*), and current technical and financial constraints do not allow for every animal in an ecosystem to be tracked. Continued advances will enable the tracking of a greater diversity and number of animals, but combined sampling and analytical approaches will likely always remain essential. There is a growing toolbox for ecologists, which now have the capacity to combine information from diverse sources, such as fish movement or presence/absence from tracking data, trophic interactions through tissue stable isotope sampling, structural habitat mapping through sonar, temperature and dissolved oxygen monitoring through stationary loggers, and fish community sampling through netting or electrofishing, or advanced environmental DNA methods.

Challenges and considerations

To effectively apply acoustic telemetry for fish habitat studies, there are some key challenges and considerations relating to study design, analysis, and synthesis that should not be overlooked. Receiver placement and detection coverage is perhaps the most fundamentally important aspect when exploring habitat use or management questions. Whether using an acoustic telemetry stationary grid, series of gates (sometimes referred to as curtains or fences), or a point-of-interest design differences (Heupel et al. 2006; Brownscombe et al. 2019*c*) in detection coverage across habitats may lead to sampling effort biases that could alter study results and ecological inferences (Kessel et al. 2014; Brownscombe et al. 2020). Considering the potential usefulness of pairing HSI models with acoustic telemetry data (discussed above in **Habitat suitability**), for these applications, receiver placement should include a random selection of available habitats (i.e., through random or systematic random designs), as opposed to selecting locations where researchers believe the species may be or selecting for locations with high detection efficiency to detect movement. Indeed, Kraus et al. (2018) showed that a grid receiver arrangement functions better at detecting space use and movement in Lake Erie than the previous receiver gate design, although it was not focused on habitat science per se and required a sufficiently large number of receivers to accomplish. Study designs often focus on achieving high detection rates, so far as to develop metrics such as the REI to guide receiver array design (Ellis et al. 2019). REI is useful for study designs focused on achieving high detection rates, as an aggregate metric weighting the number of species and individuals using locations, and may also be a useful metric for community space use and interactions (discussed above in **Biological community**). However, in the context of fish habitat studies, sampling seldomly used locations provides essential absence data and should be encouraged.

Incorporating detection efficiency into receiver placement should also be carefully considered during the design process. Detection range and efficiency vary drastically in aquatic ecosystems over space and time, often declining in shallow depths, and due to physical structure, wind, currents, thermal stratification, animal and anthropogenic noise (Gjelland and Hedger 2013; Huveneers et al. 2016; Selby et al. 2016; Klinard et al. 2019; Swadling et al. 2020; Wells et al. 2021; O'Brien and Secor 2021). For example, Weinz et al. (2021) found effective detection ranges could vary in a shallow freshwater system from 96.08 ± 51.89 to 6.85 ± 1.98 m depending on submerged aquatic vegetation (SAV) density. If ignored, this could have serious implications when evaluating space use relative to SAV since it would be much more likely to detect fish in non-SAV-dominated habitats compared to SAV dominated habitats. Detection range assessments are often applied to optimize receiver placement to achieve detectability (Clements et al. 2005; Heupel et al. 2006; Brownscombe et al. 2019*c*); this very process can be antithetical to habitat studies as it biases the habitats that are sampled. With some exceptions (i.e., extremely shallow or noisy environments), it is possible to track fish across a broad range of habitat conditions, assess variation in detection efficiency over space and time, and account for them through analytical techniques (e.g., Brownscombe et al. 2020).

Another common challenge with nearly all telemetry data are that it often contains spatial—temporal autocorrelation as the space use of individuals and (or) locations is continually tracked. Although often ignored, doing so may bias parameter estimates of habitat use or selection (Legendre 1993; Johnson et al. 2013; Fleming et al. 2015). Potential avenues to address autocorrelation with acoustic telemetry data are to model it explicitly (e.g., Griffin et al. 2019; Gutowsky et al. 2020) or to subsample detection data until the scale is no longer correlated (Swihart and Slade 1985). This is also relevant more broadly to study design, including the placement of tracking equipment (e.g., acoustic receiver stations) and locations of tagged animals. For example, if fish space use is characterized along a single habitat gradient, it can be difficult to untangle the spatial effects from that of habitat variation (Brownscombe et al. 2019*b*). In this cited example, fish space use had to be aggregated at broad spatial–temporal scales to overcome autocorrelation issues and assess habitat use, which is not ideal; it would be preferable to assess habitat use across multiple habitat gradients to provide more robust estimates.

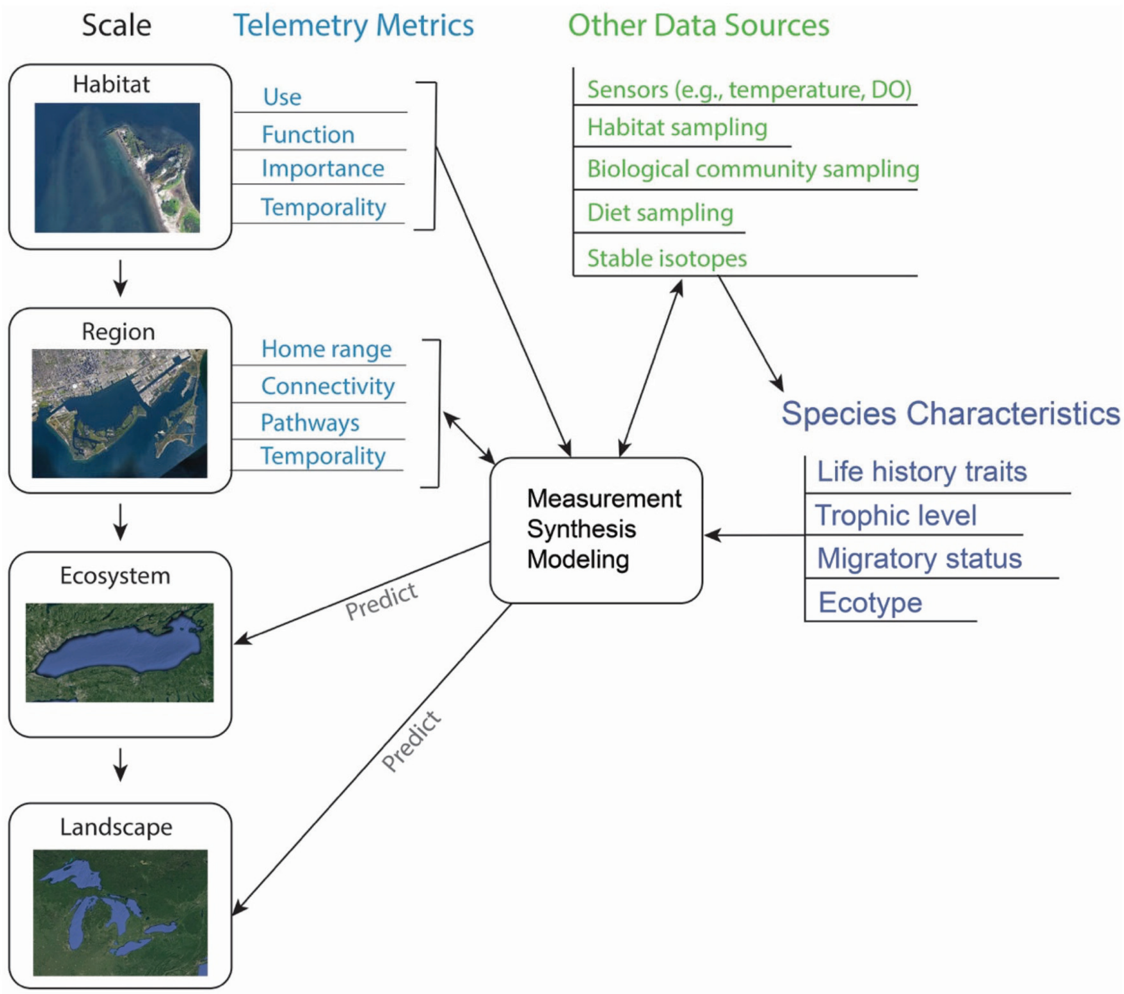
Analytical challenges can also arise because telemetry often samples a small number of individuals (a few dozen to hundred) relative to the population. This may cause biases in the derived data, especially if a particular sampling technique is used that targets a specific behavioural type or ecotype (Cooke et al. 2016*b*). Telemetry data are also often zero-inflated, especially when examined at a fine scale (e.g., at each receiver site every hour), which is challenging to model effectively. Depending on the question, researchers may mitigate issues with zero-inflation by aggregating detections at greater temporal or spatial scales or addressing zero-inflation explicitly in the modeling process (Zuur et al. 2009). Another approach is to apply weighted models that prioritize accurate prediction of rare presences (Brownscombe et al. 2021). Selection of the appropriate spatial scale for measurement and analysis is also of relevance — too fine scale may produce high levels of error, while too broad, fish–habitat relationships may be missed due to the need to produce general habitat types. In the context of station-based acoustic telemetry, detection range should play a large role in the selection of spatial scale to assign habitat characteristics to fish detections.

As acoustic telemetry continues to shed light on animal behaviour and habitat selection, it is important to recognize the limitations of extrapolating findings beyond a given study area. At a relatively simple level, predicting the space use of a species in unmeasured and unmodeled conditions may produce wildly unreliable results (Elith et al. 2010). More subtly, there may be unmeasured biological variation (at spatial, habitat, and (or) intra- and interspecies levels) that fundamentally alters animal–habitat relationships from one study area to another (Davis et al. 1998). To address this, individual studies must attempt to identify the biological confines within which their study findings may be applicable. Such approaches exist through model cross validation techniques with various subsampling regimes (Boehmke and Greenwell 2019) or through multivariate approaches to evaluate the similarity/dissimilarity of environmental conditions within the extrapolated area of interest (Mesgaran et al. 2014).

Scaling for broader application

Despite its advantages over in-person sampling in terms of logistical constraints, telemetry is still a resource intensive study approach— it typically costs hundreds of thousands of dollars to acquire equipment and implement a fish tracking project. Moreover, the analytical aspects take time and require a sophisticated understanding of quantitative biology and programming. As tracking studies scale in size and prevalence, these costs will continue to decline per study, but the reality is that logistical constraints will likely always limit the scope of telemetry studies to a proportion of ecosystems and species within a given management agency's domain. To be applicable across the entire domain, there is a need to scale telemetry-derived knowledge over space and time and across ecological conditions, as well as species and biological community characteristics. It is also important to do so in a timely manner to provide actionable information to resource managers. This is certainly a challenging task given the level of ecological complexity that exists, but is increasingly feasible as the amount of tracking data grows in organized, collaborative telemetry networks such as the Ocean Tracking Network (Iverson et al. 2019; https://oceantrackingnetwork.org). We are just now starting to have the capacity to engage in synthesis and metanalysis activities,

Fig. 2. Conceptual diagram outlining how data from telemetry studies and other data sources may inform fish habitat science and management across multiple spatial and ecological scales. Information at the habitat and regional scales, at which telemetry studies are typically conducted, may generate useful metrics that can be synthesized and modeled to make predictions at broader ecological scales by generating models of fish habitat based on comprehensive and causal predictors, which are often measured using complimentary habitat sampling methods. Integrating species characteristics into these models may also enable predictions of habitat suitability across diverse species and ecosystem types. [Colour online.]



with some great recent examples. Brodie et al. (2018) analyzed data from the IMOS tracking database in Australia to examine continental scale functional species movement classes. Friess et al. (2021) synthesized data from nearly 900 tagged individuals across 29 fish species to identify multispecies hotspots, functional movement classes, and seasonal movement pathways in coastal Florida. Lowerre-Barbieri et al. (2021) synthesized data within the iTAG and FACT tracking databases in the Florida Keys to examine "movescapes", which interface movement patterns with species characteristics (e.g., demographics, predators, aggregate spawners) and environmental data to understand ecological causes and implications of fish movement and space use.

The above examples highlight our ability to synthesize tracking data to explore broader ecological patterns, but to date this has not been accomplished by integrating any extensive habitat information beyond basic descriptors of general habitat types. This is essential to scale habitat science from individual studies to broader applications and to inform causal mechanisms underlying movement ecology. Woolnough et al. (2009) conducted a meta-analysis on home ranges of freshwater fish and found the size of the water body was a consistent predictor of a fish's home range, and therefore, the extrapolation of home ranges for a species obtained in a small water body to a larger one based on allometry alone would underestimate space use by orders of magnitude. As discussed above (**Challenges and Considerations**), a failure to capture the underlying drivers of biological variation may lead to extrapolation errors. This will continue to be a constraint unless more studies move from descriptive approaches (e.g., fish use area A more than area B) to inferential studies that measure related ecological conditions to identify mechanistic drivers of fish movement and space use. A more hypothesis-driven approach in acoustic telemetry studies is also warranted, to provide an a priori framework for linking movements to underlying mechanisms across a range of spatial and temporal scales. To advance broader syntheses efforts, we present a framework for integrating fish tracking data, environmental conditions, and species characteristics to produce broader ecosystem and landscape scale patterns and predictions (Fig. 2). Following this framework, data science projects may aggregate available fish tracking data from telemetry networks (or outside them as well), including tracking data from multiple ecosystems and (or) species. These telemetry data may be integrated with environmental/habitat measures from databases such as the Integrated Ocean Observing system, as well as assignment of system level characteristics such as ecosystem type or lake size. In multispecies projects, metadata may also be assigned to the species, such as their phylogeny, or their life history, reproductive, or foraging strategy. Advanced techniques such as multivariate models or machine learning algorithms will likely be required to model these datasets effectively, which should enable development of generalized models of fish habitat suitability and predictions of spatial–temporal distributions (Figs. 1, 2). By synthesizing information on fish habitat generated from numerous projects, models may be developed that enable prediction across broader spatial scales — this may provide inference for unstudied systems, or across broader space than has been studied (e.g., entire ecosystems). Further, syntheses activities that explicitly model how habitat associations vary among species characteristics (e.g., life history strategies, trophic levels) may enable broader biological inference about species habitat needs across lesser-studied species and systems. Effective implementation of such modeling activities will require consideration of both explanatory and predictive power (i.e., model accuracy in nontraining data), with extra caution applied in cases where extrapolation occurs to conditions not included in the model.

Major potential constraints to broader synthesis studies of fish habitat are that, firstly, telemetry studies often do not focus on comprehensive habitat science and therefore fail to collect extensive habitat information associated with their tracking study. Secondly, telemetry networks such as OTN, FACT, ACT, iTAG, IMOS, ATAP, ETN, and GLATOS generally do not store extensive habitat information. Even concurrent temperature data logger information is often not stored in association with the corresponding fish tracking detections in these networks. In a woeful number of cases, any related habitat information that does exist may only be on the computer of a single researcher. In some cases, there are databases of aquatic environmental characteristics available (e.g., through Integrated Ocean Observation System or Global Ocean Observation System) that may serve to provide valuable environmental data in combination with stored telemetry data (Sequeira et al. 2021). Yet, greater effort is required to combine data from multiple databases, and there is potential for issues related to data formats and scales. Indeed, great effort goes into data management and quality control in large-scale tracking databases (e.g., Udyawer et al. 2018; Sequeira et al. 2021), emphasizing that it would be ideal to develop a consistent framework of habitat metrics that researchers are encouraged to collect and store in direct association with fish telemetry data. There has been recognition of the need to integrate tracking data and environmental data for many years. For example, in the United States of America, the Animal Tracking Network aims to integrate aquatic tracking data from diverse ecosystems with environmental data collected through sources such as the Integrated Ocean Observation System (Block et al. 2013). These types of network integration will be essential for using tracking data for broader-scale habitat science.

Conclusions and recommendations

Telemetry is providing unprecedented insights into fish movement patterns and space use. Yet, despite some great examples, it is underutilized for habitat science. We posit this is because telemetry studies most often focus on characterizing fish movement patterns, opposed to comprehensive characterization of their habitat associations. There are also some key challenges for applying telemetry to fish habitat science related to tracking system design, variations in detection efficiency, and the scale of habitat/space use quantification and modeling. With some limitations (e.g., very shallow water), there are approaches available to readily overcome these challenges, as discussed above. These approaches often require more extensive effort and resources, but when feasible, are worthy of investment. There are a growing number of studies that serve as great examples of applications of telemetry to fish habitat science, including the scale of fish habitat requirements, behavioural and physiological mechanisms that limit habitat use, interactions of environmental conditions that influence space use, and spatial–temporal predictions of fish habitat distribution and selection. To date, telemetry studies have been mainly observational, which poses challenges for assessment of some aspects of fish ecology (e.g., habitat selection), because it is difficult to measure all of the abiotic and biotic factors that may be driving fish space use. There are opportunities to employ experimental study designs in cases where habitat is being manipulated through degradation or restoration projects (Veilleux 2014; Brooks et al. 2017). Such studies are valuable in that they can assess direct cause-and-effect relationships, yet there is a general scarcity of monitoring conducted in relation to the efficacy of fish habitat restoration projects, especially with telemetry (Lapointe et al. 2013). Such studies require replication and adequate controls, which are rarely used in studies of fish habitat restoration, albeit because it can be challenging to identify suitable control sites and sufficient replicates (Roni et al. 2018). More advanced approaches may also incorporate various physiological and behavioural endpoints can yield a mechanistic understanding of fish–environment relationships (Cooke and Suski 2008; Jeffrey et al. 2015), and this may provide an alternate or complementary approach to guide effective habitat restoration.

Notably, acoustic telemetry does have its limitations; it is financially costly, requires specific expertise, can only be applied to a subset of fishes (i.e., a subsample of a population, and generally larger-bodied animals), and only collects certain types of data that technologies have been developed to measure (Brownscombe et al. 2019*c*). Therefore, approaches that combine fish tracking with other measures such as direct characterization of habitat, fish community sampling, and stable isotope analysis are particularly powerful for fish habitat studies and may provide insights into fish niches, or the functional roles they play within the ecosystem. Further, fish tracking studies that assess multiple aspects of their ecology simultaneously are likely to be especially valuable. For example, characterizing the scale of space use (e.g., home range) and habitat selection indices within that area will indicate both the quantity and qualities of habitat for management targets.

In developing a telemetry study to address questions of interest, scientists should consider what data are already available from the many existing telemetry studies (often tracked in telemetry networks), as well as any potential tracking equipment already distributed in their study region that would aid in providing detection coverage (importantly, first coordinating with those research teams). It is also essential to consider the scale of the question and the ecology of the species relative to research capacity (i.e., number of tracking tags and receivers, funding for long-term equipment maintenance) to ensure questions are addressed effectively. For example, it would be difficult to assess the home range or multi-life stage habitat requirements of a long-lived highly migratory fish with one year of funding. Defining specific objectives and hypotheses at the outset of the study beyond "let us see where the fish go" will help to develop an effective study design, including the arrangement of tracking equipment and concurrent measurement of variables of interest such as water temperature, dissolved oxygen concentrations, water flow, structural habitat characteristics, or any other factors hypothesized to drive fish space use patterns. Overall, there is a very wide range in the types of telemetry studies and fish habitat questions they may address, with many considerations that are specific to study goals, as well as fish and ecosystem characteristics. For this reason, it is challenging to present a concise set of concrete recommendations for telemetry-based fish habitat studies. It is our hope that these general recommendations (e.g., development of hypotheses that guide the design of the tracking system, design of fish habitat measurement relative to telemetry system performance), combined with pointing to examples where certain methods have been applied effectively to specific ends (e.g., using resource selection functions to assess habitat selection; Griffin et al. 2021), will provide guidance for greater application of telemetry to fish habitat science.

There is no doubt that much of the above-mentioned information is of relevance to ecosystem and fish habitat management, guiding anthropogenic activities and the protection and restoration of key habitat quantities and qualities. Yet, the other major barrier to applicability is differences in scale between telemetry studies, which often focus on specific species and systems, and management, which often makes decisions across a broad array of systems and scales, many of which are not studied explicitly. To bridge this gap, synthesis activities may generate comprehensive models of fish habitat that enable accurate prediction across broad systems, species, and ecological conditions, while overcoming common issues related to extrapolation error. To do so, there is a need for individual studies to collect comprehensive and comparable habitat information. Cursory habitat quantification and descriptive analyses of fish space use and movement (e.g., fish used river A more than river B) limit broader inference and scalability of telemetry findings. However, there are opportunities to analyze existing telemetry databases, linking the available tracking data with other sources of habitat information stored in a variety of databases (e.g., Integrated Ocean Observing System or Great Lakes Observing System). Importantly, habitat conditions are constantly changing, so care should be taken to ensure relevant and timely data are used to assess current conditions and management goals. It may also be a laborious exercise to link disparate datasets, and it would be valuable for telemetry networks to store a standardized set of habitat information, making it readily accessible for synthesis (Sequeira et al. 2021). To accomplish this, acoustic telemetry networks could conduct workshops with their users to generate a set of useful and feasible standardized habitat variables that can be collected among studies. Standardized datasets analyzed through synthesis activities will help to generate robust models of fish habitat that are broadly applicable for fundamental movement ecology science (Nathan et al. 2008) and applied management and conservation of natural resources. Protection and restoration of fish habitat continues to be an important component of the fisheries management toolbox, and given that fish habitat is the basis for healthy and productive fish populations, addressing the issues raised here is both timely and necessary.

Competing interests statement

The authors declare there are no competing interests.

Data availability statement

All data used for this perspective piece were published in association with cited works.

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