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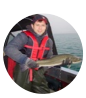

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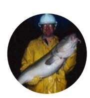

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A moving target—incorporating knowledge of the spatial ecology of fish into the assessment and management of freshwater fish populations

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Abstract Freshwater fish move vertically and horizontally through the aquatic landscape for a variety of reasons, such as to find and exploit patchy resources or to locate essential habitats (e.g., for spawning). Inherent challenges exist with the assessment of fish populations because they are moving targets. We submit that quantifying and describing the spatial ecology of fish and their habitat is an important component of freshwater fishery assessment and management. With a growing number of tools available for studying the spatial ecology of fishes (e.g., telemetry, population genetics, hydroacoustics, otolith microchemistry, stable isotope analysis), new knowledge can now be generated and incorporated into biological assessment and fishery management. For example, knowing when, where, and how to deploy assessment gears is essential to inform, refine, or calibrate assessment protocols. Such information is also useful for quantifying or avoiding bycatch of imperiled species. Knowledge of habitat connectivity and usage can identify critically important migration corridors and habitats and can be used to improve our understanding of variables that influence spatial structuring of fish populations. Similarly, demographic processes are partly driven by the behavior of fish and mediated by environmental drivers. Information on these processes is critical to the development and application of realistic population dynamics models. Collectively, biological assessment, when informed by knowledge of spatial ecology, can provide managers with the ability to understand how and when fish and

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their habitats may be exposed to different threats. Naturally, this knowledge helps to better evaluate or develop strategies to protect the long-term viability of fishery production. Failure to understand the spatial ecology of fishes and to incorporate spatiotemporal data can bias population assessments and forecasts and potentially lead to ineffective or counterproductive management actions.

Keywords Habitat use · Movement ecology · Behavior · Fisheries · Telemetry · Hydroacoustics · Sampling strategy · Trophic ecology

Introduction

Biological assessment of inland fish populations is a fundamental component of a science-based approach to freshwater fishery management (Cowx 1996; Krueger and Decker 1999; King 2013). Key components of biological assessment include knowledge of the production potential of a given water body, fish-habitat relationships, habitat quality and quantity, population size and trends, demographic parameters (e.g., natural mortality rates, population age, growth, and sex structure), and community assemblage composition (Cowx 1996; Power 2007; Hilborn and Walters 2013). Moreover, in systems with fishing pressure, knowing the distribution of effort, catch (relative to what is available to be caught), and harvest (i.e., fishing mortality) in time and space is necessary for effective fishery management (Hilborn and Walters 2013). Information about fish, their habitat, and the behavior of humans involved in exploitation represent the triad of knowledge components needed to ensure that biological assessment can inform fishery management (Krueger and Decker 1999).

Biological assessment of inland fishes is not a simple task. Beyond financial, human, and technical resource limitations, it is difficult to study freshwater fish in the wild due to low visibility and habitat complexity. Moreover, many freshwater fishes are highly mobile, moving vertically and horizontally through the aquatic landscape (Lucas and Baras 2001). Fish move for a variety of reasons, such as to find and exploit patchy resources or to locate essential habitats (e.g., for spawning; Lucas and Baras 2001). Fish movements determine demographic characteristics such as immigration and emigration (and thus potential exchange of genetic material), define population boundaries, and drive population and ecosystem-level processes (e.g., material and process subsidies; Flecker et al. 2010).

Spatial ecology (i.e., processes that influence the spatiotemporal abundance and distribution of populations and communities; Legendre and Fortin 1989) is fundamental for understanding the structure and function of populations (Tilman and Kareiva 1997), linking animals to each other and their environment (Lima and Zollner 1996), and influencing the ways in which humans interact with them. The abundance and distribution of fish in space and time provides the information necessary to (A) identify critical habitats, (B) understand inter-specific interactions, (C) develop effective assessment techniques, (D) understand how human activities (e.g., development, water use, fishery exploitation) influence fish populations, and (E) effectively manage and conserve fish populations. Failure to understand the spatial ecology of fish, therefore, can bias population assessments and potentially lead to ineffective or counterproductive management actions. For example, consider the erroneous conclusions that would be made if assessment gears were only deployed in areas occupied by fish of a given sex or life stage. Consider the consequences if one failed to identify critical habitats needed for reproduction and did not protect such habitats from degradation. What would be the effect if one placed a barrier on a river that confined the population to short reaches lacking critical habitats? Poor management decisions can also arise when the spatial dynamics of fisher behavior is not understood.

At times, consideration of the spatial ecology of fish appears to be an afterthought in assessment and monitoring programs. We know of few examples where knowledge of spatial ecology is fully integrated into biological assessment programs in freshwater (noting that some exceptions exist in the marine realm; Cooke et al. 2014), perhaps because the recent maturity of advanced technologies has not been widely recognized and to integrate new methods and information into standard assessment protocols takes time. In past decades, a number of important technological innovations have enabled scientists and resource managers to effectively study the spatial ecology of fish (Lucas and Baras 2000; Cooke et al. 2013). Indeed, spatial ecology can now be studied at a variety of spatial (e.g., from micro-habitats to macrohabitats) and temporal (e.g., from seconds to millennia) scales. This expanding toolbox provides opportunities for unprecedented understanding and has great potential to improve fishery assessment and management.

The objective of this paper is to elucidate how knowledge of the spatial ecology of freshwater fish can inform biological assessment and identify pathways to improve management decision making and outcomes. This understanding is particularly relevant and timely because opportunities exist within the design of new programs for biological assessment within fishery management programs of developing countries and emerging economies. Thus, the time is right to ensure that spatial ecology concepts are considered. We have organized the paper by breaking down common elements of assessment and management, and then consider how spatial ecology knowledge has contributed, or could contribute to improving assessment and management. We note that the maintenance and restoration of connectivity (linking organisms to each other and their environment in space and time) is a spatially explicit management theme that is inherently critical to core ecological processes (Taylor et al. 1993; Sheaves 2009) and is covered to some extent in all sections of this paper. We have attempted here to minimize repetition of this concept but if the incorporation of this concept was further constrained an artificial compartmentalization would occur of this fundamental ecological concept essential to the functioning of freshwater ecosystems (Lapointe et al. 2014) and that underpins assessment and management strategies (McRae et al. 2012).

A primer on the toolbox for studying fish spatial ecology

Historically fishery assessment and management often did not include key elements of the spatial ecology of fish. Although mark-recapture (Gerking 1950, 1953) and visual census (Allen 1966) methods have been employed for many decades, the resolution of the information they can yield was not well-matched to the resolution required for many ecological processes (see Gowan et al. 1994). The development of electronic tags (especially radiotelemetry, acoustic telemetry, and passive integrated transponders (PIT)) has provided scientists with a much improved capacity to collect fine-scale spatiotemporal information on fish, thus, revolutionizing our understanding of freshwater fish ecology (Lucas and Baras 2000; Cooke et al. 2012, 2013; Hussey et al. 2015). In response to this availability, hundreds of studies have used electronic tags to study fish ecology (see Cooke and Thorstad 2012). Fish can now be tagged across a variety of sizes (including as small as several grams) and life stages in habitats as diverse as headwater streams to the largest lakes in the world, with monitoring covering all seasons (including under ice; Cooke et al. 2013). Tagged fish can be coarsely positioned as they swim past receivers or can yield high-resolution positions through manual tracking or the use of algorithms that position the fish in two-dimensional receiver networks (Donaldson et al. 2014). Pressure sensors in electronic tags enable the positioning of fish in the water column and in three dimensions when combined with positional telemetry and high-resolution bathymetry (Martins et al. 2014). Satellite tags are being explored for use on a variety of large freshwater fish, but we are unaware of any published studies that have reported such data. New modeling techniques have also been developed to identify behaviors and environmental correlates of behaviors and habitat use (Goodwin et al. 2014; Gurarie et al. 2015).

Hydroacoustics (including traditional split-beam approaches and Dual-Frequency Identification Sonar (DIDSON) acoustic cameras) can provide detailed information on fish distribution, abundance, and behavior on a fine time scale in discrete locations (Arrhenius et al. 2000; Belcher et al. 2002; Melegari 2015). Various videography and camera techniques (especially novel digital action cameras) can be used to observe fish behavior, including timing and extent of movements in relation to environmental conditions with high temporal and spatial resolution (Struthers et al. 2016). Use of these technologies is expanding with miniaturization of cameras and availability of autonomous and remotely operated sampling platforms (e.g., gliders, AUVs, ROVs, fish wheels), but large, complex datasets necessitate concurrent development of algorithms and software to efficiently extract useful information from those data.

In addition to the above methodologies that generate spatiotemporal data, a range of other tools have recently emerged for addressing questions associated with the spatial ecology of fishes. For example, studies of population genetics using markers such as microsatellites and mitochondrial DNA provide information on population connectivity and spatial structure over intergenerational to evolutionary time scales (Hughes et al. 2009). With the rapid advancement of genomic approaches (Seeb et al. 2011; Shafer et al. 2016), such as transcriptomics, the utility of genetic analyses for providing information on the spatial ecology of fishes is likely to increase dramatically in the coming years. Otolith chemistry is another burgeoning technique in fisheries research that has been used to examine population structure, trace individual migration histories, and estimate connectivity among sub-populations (Starrs et al. 2016). Stable isotope analyses (e.g., Jardine et al. 2011) and biological tags (e.g., parasites; Catalano et al. 2014) have also been used to examine various aspects of the spatial ecology of fish. Although the emphasis of the rest of this paper is directed towards techniques that yield spatiotemporal information for biological assessment, we strongly advocate for their integration with other techniques to develop a thorough understanding of the processes that ultimately drive the movements and distributions of fishes (see also Crook et al. 2015).

Spatial ecology in the assessment and management cycle

Fishery assessment and management (especially adaptive management (Walters and Holling 1990) or an ecosystem approach framework [Garcia and Cochrane 2005; Beard et al. 2011]) are best described as an interconnected cycle of various feedbacks (see Fig. 1; Cowx 1996; Krueger and Decker 1999; King 2013). Spatial ecology is fundamental to being able to design, implement, and interpret biological assessment, to develop models (e.g., habitat and environmental models) to inform management, and to evaluate various fishery management and conservation strategies. We have organized material under a thematic structure that fits within the assessment and management cycle.

Development of assessment protocols

To develop an effective assessment protocol, information on the spatial ecology of fish across the life history is needed to determine when (e.g., season, time of day), where (e.g., habitat types, movement corridors), and how (e.g., gear types, replication) sampling should be undertaken. Because inland fisheries typically involve multiple species—often at different life stages—and multiple gears, one cannot adopt a "one size fits all" approach to sampling (Jackson and Harvey 1997; Welcomme et al. 2010). Timing and location of assessments and gear types must be tailored to the specific species or life stage of interest to accurately represent the underlying population. In the Laurentian Great Lakes, assessments of walleye (*Sander vitreus*) year-class recruitment are often performed for early life history stages (i.e., prior to becoming vulnerable to a fishery). For larval walleye, assessments require unique gears (e.g., ichthyoplankton trawls, light traps), knowledge of habitat requirements (Roseman et al. 2005), the timing of large-scale water movements that influence the distribution of larval walleye (Höök et al. 2006), and necessitate a completely different sampling strategy to that for the population segment vulnerable to fishing. Given the complexity of fish movements in inland

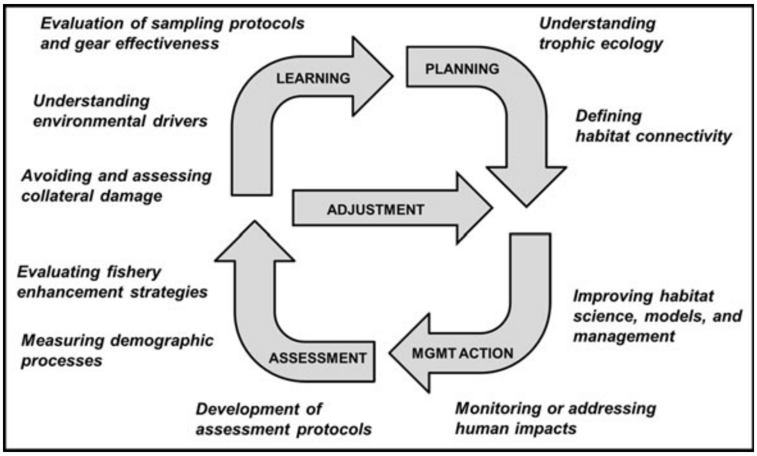

Fig. 1 A conceptual diagram of the fisheries management cycle with relevant aspects of spatial ecology (and components of this paper—in *italics*) mapped onto the cycle. We recognize that the components of the paper fit in various places on the management cycle such that this visualization is not the only way in which individuals components relate to phases of the management cycle. Assessment and adjustment are key components to the management cycle in contemporary fisheries management

fisheries, assessment protocols should be accompanied by a deep understanding of several key components of fishery management including population structure, spatial distribution, and spawning habitat.

Populations (i.e., also termed "stocks" but for the purposes of this paper we use the word "populations" for consistency) are best assessed separately because vital rates (e.g., growth and survival), vulnerability to fishing mortality, and resilience to environmental change may vary considerably (Begg et al. 1999). Abundance, growth, survival, and catch estimates based on data from mixed-population assessments can lead to over fishing of less productive populations and sub-optimal harvest strategies (Larkin 1977: Begg et al. 1999). Life history attributes, such as reproductive timing and success, can also vary substantially among wild populations and between wild- and hatchery-origin fish (Perkins et al. 1995; Wang et al. 2007; Hoffnagle et al. 2008). Incorporation of information on the reproductive timing and spatial distribution of different populations can yield effective temporal and spatial assessment strategies to avoid these problems.

In mixed-population systems, understanding how different populations are segregated, when they are mixed, and how to sample them is necessary for biological assessments. Biological assessments require stock-specific knowledge about vital rates, spatial distribution of various life stages, and reproductive timing to generate reliable population estimates for vulnerable segments of fish populations and fisheries. Sampling bias is often an issue in assessment programs, where possible bias associated with variation in growth rate and personality traits (e.g., boldness, catchability) among populations (or strains) can have potential long-term consequences on the resulting assessments of the growth potential of a particular population (Biro and Post 2008). In many circumstances, multiple gears should be deployed concurrently to eliminate over- or under-estimation of population size and generate estimates from the broadest possible range of phenotypes. For example, the simultaneous use of hydroacoustics and gill nets has been used to assess population dynamics, abundance, and biomass of vendace (*Coregonus albula*) across a range of age classes (Mehner and Schulz 2002) emphasizing that different tools, some of which are spatially explicit, are needed.

Although contemporary fishery managers generally consider spatial distribution to be a critically important source of information for the design of assessment programs, generating this information can be challenging and requires the use of multiple assessment tools across different sampling periods. Indeed, assessment estimates can be deceiving if based on a single sampling technique, over a short-time frame, or within a localized area. For instance, Mason et al. (2005) found striking differences between lake cisco (*Coregonus artedi*) and rainbow smelt (*Osmerus mordax*) biomass estimates collected from hydroacoustics compared with those taken from bottom trawl surveys in the spring. A given species, stock, or population segment can also be spatially segregated by age (Morita et al. 2010). Thus, assessments during the non-reproductive period must employ a sampling strategy that considers the specific spatial distributions for species, population, and life stages. By considering spatial distribution, managers can decide when to perform assessments and which gears are appropriate, thereby generating the most accurate estimates of population parameters.

For many species, population estimates of sexually mature individuals and future recruits can be generated during the reproductive period. Knowing the timing of spawning migrations, migration routes, and the locations of suitable spawning habitat is highly valuable for biological assessment (Lucas and Baras 2001). Spawning habitat is often protected during certain periods of the year, thereby affording sanctuary for spawning adults. Along migration routes, fishers may enjoy an exploitation window of limited harvest which contributes to the local economy (Masters et al. 2006). However, the high proportion of fishery infractions (e.g., prosecutions for overharvest) that tend to occur along migratory routes and within designated spawning habitat further underscores the importance of developing spatially and temporally appropriate assessment protocols, for example to estimate exploitation rates, during this critical period.

Evaluation of sampling protocols and gear effectiveness

Once a biological assessment program (as described above) is implemented, knowledge of the spatial ecology of fish is required to evaluate the effectiveness of different sampling protocols and gears to understand biases and refine protocols/gears to address them. Understanding the effectiveness of various assessment gear types for different species, sexes, and life stages and ensuring that they are used in a manner (when, where, how) to optimally intercept fish of the desired target and avoid bias (or use bias to one's advantage) is key to fishery assessment (Christie et al. 1987).

Temporal variations in the behavior of fish can strongly influence their distributions and susceptibility to sampling, with important implications for biological assessment. For example, many species of fish in lentic systems undertake diel vertical migrations that must be accounted for if biased or erroneous conclusions regarding their abundance are to be avoided. In a hydroacoustic survey of Arctic charr (*Salvelinus alpinus*), Winfield et al. (2007) noted that nearest-neighbor distance increased when fish moved off bottom at dusk, enabling more precise estimates of population abundance and size structure to be gathered at night than during day via hydroacoustics. Similarly, fish in some systems tend to be more active, and thus more "available" for detection via hydroacoustics, during night than day (Duncan and Kubecka 1996). Similar issues apply for many fishery assessment gear types, in particular passive gears, such as nets and traps, which rely on specific fish behavior (e.g., active foraging) within the sampling area to be effective. Environmental conditions not only influence the rate at which fish encounter the gear (Bravener and McLaughlin 2013) but also influence if, and how, fish sense and respond to the gear (e.g., avoidance).

Some efforts have been devoted to developing "corrections" for capture probabilities of sampling gears such as gill nets (e.g., Rudstam et al. 1984; Henderson and Wong 1991), especially in the context of size selection (Millar and Fryer 1999). To date, the approach that has typically been employed incorporates general knowledge of fish movements based on published telemetry studies (often in other systems by other research teams). However, a recent study of fish assemblages in the Murray River, Australia (Lyon et al. 2014) used surveys of river reaches containing known numbers of radio-tagged fish to estimate electrofishing sampling efficiency under varying environmental conditions (river discharge, turbidity, conductivity). Information from this study and additional telemetry data was then incorporated into population estimates for the same river reach to reduce bias related to variation in sampling efficiency and immigration/emigration (Bird et al. 2014). Such studies provide excellent examples of how spatial information can be incorporated into biological assessment of fish populations.

Avoiding and assessing collateral damage

Just as knowledge of fish spatial ecology can inform interception of species or life stages of interest with assessment gears, the same knowledge can be used to avoid certain species (or life stages) during harvesting periods or when sampling with potentially lethal assessment gears. Although not as prominent as in the marine realm, bycatch does occur in inland systems (Raby et al. 2011). Bycatch tends to occur when target and non-target species overlap in space and time (Hall 1996); such that identifying times or locations when overlap is minimized can theoretically reduce bycatch. Indeed, telemetry has been used in marine systems to identify spatiotemporal overlap between target species (reviewed in McClellan et al. 2009). Such information can be used to predict fishery bycatch given different fishing scenarios (Žydelis et al. 2011) and to plan harvest strategies to minimize bycatch (Sims et al. 2008). The same approach has been less common in freshwater (see Drake and Mandrak 2014) but has much promise.

Evaluating the consequences of fishery interactions on non-target species is important where instances of bycatch cannot be avoided. Biotelemetry tools have been embraced as one of the most effective means of evaluating post-release behavioral impairments and mortality (Donaldson et al. 2008). For example, Raby et al. (2014) used radiotelemetry to quantify the effects of incidental capture of endangered coho salmon (*Oncorhynchus kisutch*) in an aboriginal beach seine fishery in the lower Fraser River, Canada. The authors were able to identify fall-back and delayed migration among fish that were in poor condition at time of release and generated the first post-release estimate of mortality (i.e., 17 %) for the fishery. Similar studies using telemetry to track post-release behavior and survival of bycatch have been conducted on sub-legal sized American paddlefish (*Polyodon spathula*) in a reservoir in Tennessee (Kerns et al. 2009) and on northern pike (*Esox lucius*) captured in a coarse-fish fyke net fishery in small lakes in Ontario (Colotelo et al. 2013). The same approaches have also been used in the context of recreational fisheries to evaluate post-release behavior and survival (e.g., largemouth bass, northern pike, and common carp tracked with radio tags in lakes [Thompson et al. 2008; Arlinghaus et al. 2009; Rapp et al. 2014]) often in the context of comparing different angler handling methods.

Defining habitat connectivity

Fish seek habitat conditions that optimize survival, growth, and reproductive success. Suitable fish habitat, however, is generally distributed in patches across the aquatic landscape relative to seasons and ontogeny. Functional connectivity between habitat patches may be necessary to reach a successive life stage (Ferguson et al. 2011; Hall et al. 2012), maintain genetic diversity (Policansky and Magnuson 1998), or maintain stable population size among sources and sinks (Crowder et al. 2000; Figueira 2009). Many native fish species have declined in population size or growth rates when connectivity has been compromised (Ferguson et al. 2011; Hall et al. 2012). Firstly, landscape aspects of physical connectivity that are principally hydrological are drivers for geomorphic, biogeochemical, and ecological processes of aquatic environments. The interaction between connectivity and these important processes is particularly apparent longitudinally in rivers (Ward 1989; Nestler et al. 2012), laterally in floodplains (e.g., Junk et al. 1989), and with vertical and horizontal dimensions in lakes. Secondly, connectivity reflects patterns of residency, dispersal, and migration across temporal and spatial scales, which is necessary for the management and conservation of fish and fisheries (Fausch et al. 2002).

Rivers provide migration corridors for fishes moving between river habitat patches or to/from lentic or marine habitats. Fish migration routes are often bottlenecked, from coast, lake, or seasonally inundated floodplain rearing areas to the river channel and so are highly susceptible to exploitation (Welcomme 1979). Disruption of migration routes by dams and weirs along rivers can increase exploitation rates (Lucas and Baras 2001) but, universally, breakage in the river's hydrological connectivity has more pervasive effects. Disruption of connectivity alters habitat, reduces access to critical habitat (upstream, downstream, or laterally) relative to barriers (Lucas and Frear 1997; Bolland et al. 2012), impairs completion of one or more (e.g., downstream dispersal and upstream migration) key life stages (Gauld et al. 2013), and reduces gene flow (Melgaard et al. 2003). Thus, identifying and quantifying these effects is fundamental to the choice of management actions to implement.

Floodplain river systems with major fisheries are inherently dependent on inundation cycles (Welcomme 1979; Baigún et al. 2013) but also to the well-defined repeatable patterns of fish migration (Fernandes 1997). Knowledge of the movements, habitat use, and fate of different life stages is crucial to the sensitive management of these systems (both the fish and wider ecosystems through the subsidies that they provide), especially in the face of increasing river regulation (Louca et al. 2009; Ziv et al. 2012; Finer and Jenkins 2012) and in trying to improve ecologically sensitive management of rivers already impacted (Lucas and Baras 2000; Bolland et al. 2012). Pre-spawning migrations, especially of abundant semelparous species such as Pacific salmons, can also drive trophic subsidies to freshwater systems (Naiman et al. 2002) and management needs to consider those processes.

Measuring passage past partial barriers is vital for biological assessment of migratory fisheries in regulated rivers, and telemetry provides the most valuable and detailed method of providing information on aspects such as timing, attempt rates, passage success, survival, and energetic cost (Cooke et al. 2013). Fish passes are the most common measure to support functional longitudinal connectivity for fish. Determining the effectiveness of fish pass systems and the conditions required for fish passage are important to maintain ecologically sustainable populations of migratory fishes (Lucas and Baras 2001; Godinho and Kynard 2009; Cooke et al. 2013). Landscape-scale ecological information and models can be crucial in the optimal deployment of barriers (see Rahel 2013) for conserving native fish populations (e.g., cutthroat trout (*Salmo clarkii*), from downstream invasive competitor species (Fausch et al. 2009).

Much debate surrounds the degree that fish passes can fulfill habitat connectivity requirements by many fish species, especially in Asia, South America, and Africa. The normal repeat longitudinal migrations of adult, iteroparous fishes may be prevented by dams or if facilitated by fish passes then strongly inhibited in the downstream direction by large reservoirs and other obstructions (O'Connor et al. 2006; Pelicice et al. 2016). Fish passes promoting upstream migration to areas with or without spawning habitat and providing no return downstream migration combined with deposition of eggs into unsuitable habitat generate "ecological trap" conditions (Pelicice and Agostinho 2008; Da Silva et al. 2014; Pelicice et al. 2016). In such large-river conditions, biological assessment of inland fisheries cannot robustly be carried out at a small scale; the integrity of the migratory populations can be reliant upon large-scale habitats and processes (Da Silva et al. 2014) and these may not be effectively mitigated by local actions alone. This emphasizes the importance of the combined riverscape and life history ecological approach both in population assessment and management of fisheries.

Improving habitat science, models, and management

The relationship between habitat quality and fishery productivity in inland waters is well established (Roni 2005), but underlying mechanisms are sometimes elusive. To appreciate how human activities can "degrade" habitat from a fish perspective, we need an understanding of habitat functionality—that is, how do fish use specific types of habitat, and what habitat functions serve in terms of individual fitness and population processes? From this understanding, we can begin to predict baseline productivity of different habitats, the likely consequences of human activities that reduce or remove habitat functionality, and thus limit their inherent but naturally variable fishery productivity. Relatedly, streamlining habitat assessment and management is afforded, if one knows which species are present, how they move through and use different habitat types, and how the supply of that habitat may affect a population's production in an ecosystem context.

From a fishery management perspective, maintenance of the specific habitat conditions required for successful spawning of target species is the most emphasized aspect of habitat functionality in most restoration actions. Facilitating successful spawning is critical to maintaining self-sustaining and productive fisheries; however, it is essential to also consider critical habitat functions at all stages of life history. Spawning habitats may not be limiting and density-dependent mechanisms or environmental influences within the suitable habitat can affect later life stages. For example, the larval stages of many riverine fishes use near-shore "slackwater" habitats that provide low flow velocities, abundant food, warm water, and shelter from predators (King 2004). Similarly, the juvenile and adult stages of many lacustrine fishes move into seasonally inundated floodplains to access food resources (Winemiller and Jepsen 1998) and preferred habitats at different time scales. Loss of connectivity between rivers or lakes and their floodplains due to levees and flow regulation reduces this movement and is a significant cause of fishery declines in many regions of the world (Cowx and Welcomme 1998).

Habitat models used in fishery assessment and management often assume we have understanding of where fish go and what resources they need. However, fish life histories vary and many stages are cryptic, so our knowledge is imperfect and modeling approaches need to account for uncertainty and variability. Data derived from studies of spatial ecology (e.g., with telemetry, hydro acoustics, or stratified sampling design) can be used to build a conceptual framework of what a species or population does, why it does it, where it spends its time, and when movements among habitat patches occur (Mouton et al. 2012). By using such empirical and inferential approaches (i.e., various methods including habitat-based models) to develop and test our understanding of the mechanisms by which human alterations to aquatic habitat limit fish populations and fisheries, we will improve our capacity to identify critical habitats and mitigate the effects of habitat degradation (Vélez-Espino and Koops 2009). Using stage-structured population models that take habitat supply into account is one method of including important environmental drivers (Hayes et al. 1996). Simpler approaches also occur that infer the importance of different habitat types from knowledge of fish usage (Minns 2001) and statistically determine niches based on distribution patterns (McCusker et al. 2014). The former has been used in offset and restoration calculations and the latter in species at risk conservation planning.

Measuring demographic processes

Management actions, such as stocking, habitat protection and restoration, and limiting harvest (including predators and prey), are often justified on the basis of how those actions affect the survival of individuals in a population. Therefore, effective management requires accurate estimates of survival and sources of mortality. Demographic processes (e.g., survival, immigration, emigration) are often measured by capture-recapture methods from marked individuals. Although the fates of individuals are determined by processes that can change quickly and vary widely across time and space, logistical constraints often limit capture-recapture approaches to estimates of mortality and migration at resolutions of a year or more and at a geographic scale of an entire and connected watershed. In contrast, telemetry methods often using autonomous receivers that sample continuously can provide high-resolution (e.g., hours, meters) information about demographic processes over broad scales (e.g., years, kilometers). Minimally, telemetry receivers can be arranged in open systems to detect movement among discrete regions so that the fates of fish presumed dead can be attributed to activities or structures in the region of loss, such as harvest (Hightower et al. 2001), hydroelectric dams (Skalski et al. 2001), water withdrawals (Svendsen et al. 2011), or predators (Fayram and Sibley 2000). Not surprisingly, telemetry data are increasingly being used in addition to, or in place of, data from more traditional sampling (e.g., nets, traps) in capture-recapture models.

Specific sources of mortality have been identified by fine-scale positional telemetry and by integrating telemetry with other approaches and technologies, including mark-recapture modeling. For example, tag recovery data can be useful for estimating fishing mortality (Bacheler et al. 2009) and fine-scale tracking has been used to attribute mortality to specific predators (Romine et al. 2014) and structures at dams (Skalski et al. 2002). Telemetry has also revealed how natural processes (e.g., predation, thermal stress, river entry, pathways) can be altered by anthropogenic structures and activities. For example, Gauld et al. (2013) showed the synergistic impacts of small-scale weirs and river discharge on mortality of emigrating brown trout (*Salmo trutta*) smolts, apparently mediated through loss to predators. English et al. (2005) showed that survival of adult sockeye salmon in the Fraser River was strongly dependent on timing of river entry. Hayden et al. (2014) showed that walleye from a Lake Huron tributary seasonally migrated along coastlines, potentially exposing them to harvest far from their spawning river.

Understanding environmental drivers

The environment is one of the fundamental drivers of animal movements and their distribution across a landscape (Nathan et al. 2008). For example, variation in temperature, light, and nutrients determines the spatiotemporal availability of food resources for aquatic organisms and will then influence the spatial distribution of freshwater fishes (Allan and Castillo 2007). Temperature, often regarded as the master environmental driver for fish (Fry 1971), also sets physiological limits to the movement and distribution of fish via its direct effects on their metabolism and cardiorespiratory physiology (Pörtner and Farrell 2008; Isaak et al. 2010).

River flow is another major driver of the movement and distribution of freshwater fishes. Spatiotemporal variation in flow generates a highly dynamic energy landscape in freshwater, with the energetic costs associated with maintaining position at or moving to/from any given location changing over time scales ranging from seconds to months (Shepard et al. 2013), sometimes predictably and sometimes stochastically. Increases in water level under high flow also connect rivers with their floodplains (Allan and Castillo 2007), which are often sought out by fish due to its high food availability compared with river channels (Goulding 1980; Junk et al. 1997).

Knowledge of the influence of environmental drivers on the spatial ecology of freshwater fishes is critical for predicting their spatiotemporal occurrence and abundance and informing the design of biological assessments. Capture-dependent (e.g., mark-recapture, telemetry) and capture-independent (e.g., hydroacoustics, visual observations) techniques exist that are available to collect data on the movement and distribution of fish—their appropriateness/effectiveness varying according to the spatiotemporal resolution required (Lucas and Baras 2000). Concomitantly, data on environmental drivers can be collected using data loggers (e.g., temperature, light, oxygen) attached to the fish or deployed in strategic locations throughout the sampling area. Alternatively, data on environmental drivers can be acquired locally or regionally (e.g., weather and hydrological monitoring stations) and from databases of remote sensing data (e.g., ENV-Data system at Movebank; Dodge et al. 2013). The analysis of the relationship between movement or distribution of fish and environmental drivers can be accomplished using a number of statistical approaches including, but not limited to, generalized linear models and their mixed-effects counterparts (Zuur et al. 2009), Bayesian approaches with diffuse or informative priors (Punt and Hilborn 1997), step selection functions (Thurfjell et al. 2014), occupancy models (Dextrase et al. 2014), and various spatial statistics methods (Fortin and Dale 2005).

Understanding trophic ecology

Understanding the feeding ecology of fishes is critical to understanding the success of individuals and populations as it influences survival, growth, and reproductive potential (Wootton 1998). As a result, fish will move within and between habitats to improve feeding opportunities. For example, diel vertical migration is a behavioral strategy observed in many fish (Brett 1971; Gjelland et al. 2009; Hrabik et al. 2006), with diel shifts often linked to changes in diet and habitat use (Nunn et al. 2010). Similarly, anadromy is typically considered to be driven by differences in marine and freshwater productivity linked to differences in feeding opportunity (Gross et al. 1988) that permit higher growth rates, larger size-at-age, and greater energy stores (Hendry et al. 2004), biological characteristics that have all been associated with ultimately determining patterns of population dynamics (Power 2007). Lateral movements between river channels and floodplain habitats in tropical environments enhance feeding and growth opportunities (Castello 2007), with seasonal growth in many species correlated with the flood-pulse period (Perez and Fabre 2009).

Movement may further serve to link disparate ecosystems, with the importance of migrating fishes for connecting spatially isolated ecosystems having been increasingly seen as important for overall ecosystem structure and function (Polis et al. 1997). In that regard, Pacific salmon provide one of the most widely documented examples of migratory fishes that link ecosystems (in terms of trophic ecology) at large spatial scales as result of their combined semelparous and anadromous life history characteristics. As 95 % of growth is accumulated during the marine phase of the life cycle, the nutrients and energy derived from post-spawning adult mortalities flow directly from marine ecosystems and produce a significant nutrient subsidy to the freshwater spawning and nursery habitats of salmon and other resident species (Schindler et al. 2005). Similarly, spawning migrations of iteroparous fish can enrich inland freshwater systems (Childress et al. 2014).

While less dramatic, such cross-system subsidies occur at other spatial scales as a result of fish movement. Daily vertical movements by fish facilitate nutrient translocation across depth boundaries in freshwater (Polis and Winemiller 1996), whereas horizontal movements facilitate the operation of "nutrient pumps" (Vanni 1996) that provide cross-habitat energy subsidies and make fish important integrators of benthic and pelagic food webs in lakes (Vander Zanden and Vadeboncoeur 2002). In tropical ecosystems, the transfer of production between rivers by migratory fishes appears to be a general phenomenon that facilitates high abundance of large piscivores in the otherwise oligotrophic river ecosystems that exist throughout the region (Hoeinghaus et al. 2006; Jardine et al. 2011). Movement may also allow fish to exploit temporally limited habitats that promote growth and survival (Jeffres et al. 2008). Thus, at multiple spatial scales, fish movement is an important determinant of aquatic food web structure and function, with migration serving to link food webs across landscapes via the transport of production among otherwise separated ecosystems that provide important resource subsidies to resident consumers (Polis et al. 1997, 2004).

Movement has implications for predator–prey interactions, with the feeding range of an individual considered to be critical for food web dynamics because it determines the spatial scale of predator–prey interactions (DeAngelis and Petersen 2001). For example, the spatial feeding range of organisms in lower-quality feeding habitats is likely to be larger than in higher-quality feeding habitats where the density and/or quality of prey are high (Kramer and Chapman 1999). Furthermore, the impact of predators on prey will be related to their own patterns of movement and the relative locality of their movement patterns as compared to those of the prey. Accordingly, movement will influence the strength of predator–prey interactions and has consequences for top-down, predatory regulation of food webs. Fish vulnerability to fishers is largely driven by trophic ecology, thus understanding how fish move within and between habitats and their relative contribution along the food chain is paramount to conservation and management.

Evaluating fishery enhancement strategies

Fish stocking or supplementation is a common strategy for enhancing wild populations and commercial and recreational fisheries. Assessing the spatial ecology of stocked fish can provide insight into their behavior and interactions that provide managers with information to make informed decisions for fishery enhancement. Knowledge on spatiotemporal patterns of habitat use, residency, site fidelity, and home range sizes of cultured and wild fish in a natural environment is used to make informed comparisons between population origins. Understanding the spatial ecology of propagated fish can inform management decisions by determining the effectiveness of stocked fish for restoring and augmenting wild populations and recreational fisheries (Krueger et al. 1986; Bronte et al. 2007; Brown and Day 2002; Ebner and Thiem 2009).

Fishery managers and scientists are often concerned about the interactions between wild and stocked individuals in the natural aquatic environment (Mackey et al. 2001). A variety of examples exist where research programs have focused on these interactions, particularly with Atlantic salmon on the eastern seaboard and with Pacific salmon on the western seaboard of North America. However, for inland fisheries, these interactions between propagated and native conspecific are less evident in the literature. Time-resolved tools for investigating the spatial ecology can provide information with regard to interactions between cultured individuals and native populations. Understanding the spatial-temporal patterns of stocked and wild fish is important for evaluating and improving restoration and enhancement programs. For example, Bolland et al. (2009) used PIT-telemetry to compare the distribution, survival, and movements of hatchery-reared and wild cyprinid fish upon liberation and found that in the short term (<1 year), the stocked fish were able to cope with the stochastic environmental conditions in the natural riverine environment in which they were liberated but behaved differently to wild fish.

From a management perspective, addressing spatial ecology questions such as dispersal, migration, activity patterns, and survival is important for evaluating goals and actions of stocking projects. For example, time-resolved tools such as telemetry have shown that cultured rainbow trout (*Oncorhynchus mykiss*) were more active and dispersed more readily than wild fish which led to increased mortality in cultured fish than wild resident trout (Bettinger and Bettoli 2002). Similarly, radiotelemetry showed that survival of hatchery-reared sub-adult trout cod (*Maccullochella macquariensis*) was lower than wild fish and that hatchery fish had limited downstream dispersal and occupied limited home ranges within a 13-km extent of the river (Ebner and Thiem 2009). The success and mitigation of failing stocking programs can be addressed by using readily available tools that provide researchers with a combination of biological, physical, and temporal information.

Monitoring or addressing human impacts

Fish are an effective indicator for aquatic habitat assessments because they are sensitive to anthropogenic disturbances (both facilitated and direct) and can be used over small and large temporal and spatial scales (Harris 1995). Fish spatial ecology can provide a long-term indicator of the health of an aquatic system. While challenging and not always an option, collecting baseline information on the spatial ecology of fish prior to human-induced changes allows for pre- and post-monitoring comparisons for directing management actions and priorities (e.g., before-after-control-impact studies; Palmer et al. 2005). Large numbers of restoration projects in the past have not addressed the short- and long-term spatial ecology of fishes through the progression of the projects, and indeed, only a small number have used or been able to incorporate a BACI experimental design to monitor fish responses to environmental change (Lapointe et al. 2013).

Applying tools to address movement and habitat use of fish can also allow for insight into the spread and impacts of invasive species, disease, and parasitism (e.g., Pratt et al. 2009). Studies have used ecological tools for tracking the movements of invasive sea lamprey to address the capture efficiency of traps positioned below hydropower stations with manipulation of the discharge rate (Rous 2014; Holbrook et al. 2016). Researchers have also investigated the spatial ecology of invasive aquatic fish species to determine aggregation sites to improve eradication efforts. Common carp (*Cyprinus carpio*) have been tracked in midwestern lakes in North America (Bajer et al. 2011), while others have investigated the spatial ecology of invasive lake trout (*Salvelinus namaycush*) in Yellowstone National Park to determine high-density areas of use to focus eradication efforts (Dux et al. 2011; Gresswell et al. 2012). In several locations within the Laurentian Great Lakes, protections are extended to vulnerable life stages by excluding destructive common carp from the spawning habitat of native species (Casselman and Lewis 1996; Chow-Fraser 2005). Similar approaches have also been employed in the Murray-Darling Basin in Australia to control carp by installing screens to prevent access to preferred spawning habitat in floodplain wetlands (Hillyard et al. 2010).

Synthesis and conclusions

Our assertion is that knowledge of the spatial ecology of freshwater fish can directly inform fishery assessment and, in doing so, improve management outcomes. On the surface, this assertion may seem obvious; however, in reality, information on spatial ecology is often lacking for many fish populations/fisheries. Several decades ago, one could have simply attributed the lack of understanding of the spatial ecology of fish to a rather restricted toolbox (e.g., mark and recapture). With the advent of novel research tools and technologies (e.g., biotelemetry, molecular genetics, stable isotope analyses, otolith chemistry, hydroacoustics), we are learning much more about how fish are distributed in space and time. Of particular benefit have been those tools that enable one to resolve fine-scale aspects of geo-spatial positioning over short time periods. Beyond tackling research questions, these tools now are being adopted as part of routine fishery monitoring and assessment and thus are being incorporated into the fishery assessment and management cycle.

In this paper, we have demonstrated how spatial ecology is fundamental to being able to design, implement, and interpret biological assessment, to develop models (e.g., habitat and environmental models) to inform management, and to evaluate various fishery management and conservation strategies. In fact, we believe that our examples are sufficiently compelling that designing or implementing fishery assessment programs without information on the spatial ecology of fish populations is unwise. The "excuse" that not doing so is impossible due to technical challenges or expense is no longer valid in most instances. Clearly, application is not easy, but the tools and knowledge exist for a wide range of species and systems (e.g., from under ice to the largest of rivers and lakes). As these tools have become more widely embraced, the cost has decreased substantially (e.g., radio tags now cost around $100 each, PIT tags cost $4 each, isotope analyses are generally cheaply and widely available). Indeed, the ecological costs of not studying the spatial ecology of a population may be much greater—both in terms of economics and conservation. Nonetheless, challenges remain related to trying to better characterize the spatial ecology of larval life stages as well as working in some conditions (e.g., large rivers, winter in temperate regions, monsoon/flood season in the tropics). Moving forward, our expectation is that inland fishery assessment will be enhanced by the inclusion of knowledge on the spatial ecology of fish, which will lead to improved management and conservation outcomes.

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