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1 **A moving target – incorporating knowledge of the spatial ecology of fish into the**
2 **assessment and management of freshwater fish populations**

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20 **Abstract**

21 Freshwater fish move vertically and horizontally through the aquatic landscape for a variety of
22 reasons, such as, to find and exploit patchy resources or to locate essential habitats (e.g., for
23 spawning). Inherent challenges exist with the assessment of fish populations because they are
24 moving targets. We submit that quantifying and describing the spatial ecology of fish and their
25 habitat is an important component of freshwater fishery assessment and management. With a
26 growing number of tools available for studying the spatial ecology of fishes (e.g., telemetry,
27 population genetics, hydroacoustics, otolith microchemistry, stable isotope analysis), new
28 knowledge can now be generated and incorporated into biological assessment and fishery
29 management. For example, knowing when, where and how to deploy assessment gears is
30 essential to inform, refine, or calibrate assessment protocols. Such information is also useful for
31 quantifying or avoiding bycatch of imperiled species. Knowledge of habitat connectivity and
32 usage can identify critically important migration corridors and habitats, and can be used to
33 improve our understanding of variables that influence spatial structuring of fish populations.
34 Similarly, demographic processes are partly driven by the behaviour of fish and mediated by
35 environmental drivers. Information on these processes is critical to the development and
36 application of realistic population dynamics models. Collectively, biological assessment, when
37 informed by knowledge of spatial ecology, can provide managers with the ability to understand
38 how and when fish and their habitats may be exposed to different threats. Naturally, this
39 knowledge helps to better evaluate or develop strategies to protect the long-term viability of
40 fisheries production. Failure to understand the spatial ecology of fishes and to incorporate
41 spatiotemporal data can bias population assessments and forecasts, and potentially lead to
42 ineffective or counterproductive management actions.

43

44 Key words: habitat use, movement ecology, behaviour, fisheries, telemetry, hydroacoustics,
45 sampling strategy, trophic ecology

46

47 **Introduction**

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

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

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

86 At times, consideration of the spatial ecology of fish appears to be an afterthought in
87 assessment and monitoring programs. We know of few examples where knowledge of spatial
88 ecology is fully integrated into biological assessment programs in freshwater (noting that some
89 exceptions exist in the marine realm; Cooke et al. 2014), perhaps because the recent maturity of
90 advanced technologies has not been widely recognized and to integrate new methods and
91 information into standard assessment protocols takes time. In past decades, a number of

92 important technological innovations have enabled scientists and resource managers to effectively
93 study the spatial ecology of fish (Lucas and Baras 2000, Cooke et al. 2013). Indeed, spatial
94 ecology can now be studied at a variety of spatial (e.g., from micro-habitats to macro-habitats)
95 and temporal (e.g., from seconds to millennia) scales. This expanding toolbox provides
96 opportunities for unprecedented understanding and has great potential to improve fishery
97 assessment and management.

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

114 **A primer on the toolbox for studying fish spatial ecology**

115 Historically fishery assessment and management often did not include key elements of
116 the spatial ecology of fish. Although mark-recapture (Gerking 1950, 1953) and visual census
117 (Allen 1966) methods have been employed for many decades, the resolution of the information
118 they can yield was not well-matched to the resolution required for many ecological processes
119 (see Gowan et al. 1994). The development of electronic tags (especially radio telemetry, acoustic
120 telemetry, and passive integrated transponders) has provided scientists with a much improved
121 capacity to collect fine-scale spatiotemporal information on fish, thus, revolutionizing our
122 understanding of freshwater fish ecology (Lucas and Baras 2000, Cooke et al. 2012, 2013,
123 Hussey et al. 2015). In response to the availability, hundreds of studies have used electronic tags
124 to study fish ecology (see Cooke and Thorstad 2012). Fish can now be tagged across a variety of
125 sizes (including as small as several grams) and life-stages in habitats as diverse as headwater
126 streams to the largest lakes in the world, with monitoring covering all seasons (including under
127 ice; Cooke et al. 2013). Tagged fish can be coarsely-positioned as they swim past receivers or
128 can yield high-resolution positions through manual tracking or the use of algorithms that position
129 the fish in 2-dimensional receiver networks (Donaldson et al. 2014). Pressure sensors in
130 electronic tags enable the positioning of fish in the water column and in 3 dimensions when
131 combined with positional telemetry and high resolution bathymetry (Martins et al. 2014).
132 Satellite tags are being explored for use on a variety of large freshwater fish but we are unaware
133 of any published studies that have reported such data. New modeling techniques have also been
134 developed to identify behaviours and environmental correlates of behaviours and habitat use
135 (Goodwin et al. 2014; Gurarie et al. 2015).

136 Hydroacoustics (including traditional split-beam approaches and Dual-Frequency
137 Identification Sonar (DIDSON) acoustic cameras) can provide detailed information on fish

138 distribution, abundance, and behaviour on a fine time-scale in discrete locations (Arrhenius et al.
139 2000, Belcher et al. 2002, Melegari 2015). Various videography and camera techniques
140 (especially novel digital action cameras) can be used to observe fish behavior, including timing
141 and extent of movements in relation to environmental conditions with high temporal and spatial
142 resolution (Struthers et al. 2015). Use of these technologies is expanding with miniaturization of
143 cameras and availability of autonomous and remotely-operated sampling platforms (e.g., gliders,
144 AUVs, ROVs, fish wheels), but large, complex datasets necessitate concurrent development of
145 algorithms and software to efficiently extract useful information from those data.

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

160 thorough understanding of the processes that ultimately drive the movements and distributions of
161 fishes (see also Crook et al. 2015).

162

163 **Spatial Ecology in the Assessment and Management Cycle**

164 Fishery assessment and management (especially adaptive management [Walters and Holling
165 1990] or an ecosystem approach framework [Garcia and Cochrane 2005, Beard et al. 2011]) are
166 best described as an interconnected cycle of various feedbacks (See Figure 1; Cowx 1996,
167 Krueger and Decker 1999, King 2013). Spatial ecology is fundamental to being able to design,
168 implement, and interpret biological assessment, to develop models (e.g., habitat and
169 environmental models) to inform management, and to evaluate various fishery management and
170 conservation strategies. We have organized material under a thematic structure that fits within
171 the assessment and management cycle.

172

173 **DEVELOPMENT OF ASSESSMENT PROTOCOLS**

174 To develop an effective assessment protocol, information on the spatial ecology of fish across
175 the life history is needed to determine when (e.g., season, time of day), where (e.g., habitat types,
176 movement corridors), and how (e.g., gear types, replication) sampling should be undertaken.
177 Because inland fisheries typically involve multiple species - often at different life stages - and
178 multiple gears, one cannot adopt a “one size fits all” approach to sampling (Jackson and Harvey
179 1997, Welcomme et al. 2010). Timing and location of assessments and gear types must be
180 tailored to the specific species or life stage of interest to accurately represent the underlying
181 population. In the Laurentian Great Lakes, assessments of walleye (*Sander vitreus*) year-class

182 recruitment are often performed for early life history stages (i.e., prior to becoming vulnerable to
183 a fishery). For larval walleye, assessments require unique gears (e.g., ichthyoplankton trawls,
184 light traps), knowledge of habitat requirements (Roseman et al. 2005), the timing of large-scale
185 water movements that influence the distribution of larval walleye (Höök et al. 2006), and
186 necessitate a completely different sampling strategy to that for the population segment vulnerable
187 to fishing. Given the complexity of fish movements in inland fisheries, assessments protocols
188 should be accompanied by a deep understanding of several key components of fishery
189 management including population structure, spatial distribution, and spawning habitat.

190 Populations (i.e., also termed “stocks” but for the purposes of this paper we use the word
191 “populations” for consistency) are best assessed separately because vital rates (e.g., growth and
192 survival), vulnerability to fishing mortality, and resilience to environmental change may vary
193 considerably (Begg et al. 1999). Abundance, growth, survival, and catch estimates based on data
194 from mixed-population assessments can lead to over fishing of less productive populations and
195 sub-optimal harvest strategies (Larkin 1977; Begg et al. 1999). Life history attributes, such as
196 reproductive timing and success, can also vary substantially among wild populations and
197 between wild- and hatchery-origin fish (Perkins et al. 1995, Wang et al. 2007, Hoffnagle et al.
198 2008). Incorporation of information on the reproductive timing and spatial distribution of
199 different populations can yield effective temporal and spatial assessment strategies to avoid these
200 problems.

201 In mixed-population systems, understanding how different populations are segregated,
202 when they are mixed, and how to sample them is necessary for biological assessments.
203 Biological assessments require stock-specific knowledge about vital rates, spatial distribution of
204 various life stages, and reproductive timing to generate reliable population estimates for

205 vulnerable segments of fish populations and fisheries. Sampling bias is often an issue in
206 assessment programs, where possible bias associated with variation in growth rate and
207 personality traits (e.g., boldness, catchability) among populations (or strains) can have potential
208 long-term consequences on the resulting assessments of the growth potential of a particular
209 population (Biro and Post 2008). In many circumstances, multiple gears should be deployed
210 concurrently to eliminate over- or under-estimation of population size and generate estimates
211 from the broadest possible range of phenotypes. For example, the simultaneous use of
212 hydroacoustics and gill nets has been used to assess population dynamics, abundance, and
213 biomass of vendace (*Coregonus albula*) across a range of age classes (Mehner and Schulz 2002)
214 emphasizing that different tools, some of which are spatially-explicit, are needed.

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

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

238

239 **EVALUATION OF SAMPLING PROTOCOLS AND GEAR EFFECTIVENESS**

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

247 Temporal variations in the behaviour of fish can strongly influence their distributions and
248 susceptibility to sampling, with important implications for biological assessment. For example,
249 many species of fish in lentic systems undertake diel vertical migrations that must be accounted

250 for if biased or erroneous conclusions regarding their abundance are to be avoided. In a
251 hydroacoustic survey of Arctic charr (*Salvelinus alpinus*), Winfield et al. (2007) noted that
252 nearest-neighbour distance increased when fish moved off bottom at dusk, enabling more precise
253 estimates of population abundance and size structure to be gathered at night than during day via
254 hydroacoustics. Similarly, fish in some systems tend to be more active, and thus more
255 “available” for detection via hydroacoustics, during night than day (Duncan and Kubecka 1996).
256 Similar issues apply for many fishery assessment gear types, in particular passive gears, such as
257 nets and traps, which rely on specific fish behaviour (e.g., active foraging) within the sampling
258 area to be effective. Environmental conditions not only influence the rate at which fish encounter
259 the gear (Bravener and McLaughlin 2013) but also influence if, and how, fish sense and respond
260 to the gear (e.g., avoidance).

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

273

274 **AVOIDING AND ASSESSING COLLATERAL DAMAGE**

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

287 Evaluating the consequences of fishery interactions on non-target species is important
288 where instances of bycatch cannot be avoided. Biotelemetry tools have been embraced as one of
289 the most effective means of evaluating post-release behavioural impairments and mortality
290 (Donaldson et al. 2008). For example, Raby et al. (2014) used radio telemetry to quantify the
291 effects of incidental capture of endangered coho salmon (*Oncorhynchus kisutch*) in an aboriginal
292 beach seine fishery in the lower Fraser River, Canada. The authors were able to identify fall-back
293 and delayed migration among fish that were in poor condition at time of release and generated
294 the first post-release estimate of mortality (i.e., 17%) for the fishery. Similar studies using

295 telemetry to track post-release behaviour and survival of bycatch have been conducted on sub-
296 legal sized American paddlefish (*Polyodon spathula*) in a reservoir in Tennessee (Kerns et al.
297 2009) and on northern pike (*Esox Lucius*) captured in a coarse-fish fyke net fishery in small lakes
298 in Ontario (Colotelo et al. 2013). The same approaches have also been used in the context of
299 recreational fisheries to evaluate post-release behaviour and survival (e.g., largemouth bass,
300 northern pike, and common carp tracked with radio tags in lakes [Thompson et al. 2008,
301 Arlinghaus et al. 2009, Rapp et al. 2014]) often in the context of comparing different angler
302 handling methods.

303

304 **DEFINING HABITAT CONNECTIVITY**

305 Fish seek habitat conditions that optimize survival, growth, and reproductive success. Suitable
306 fish habitat, however, is generally distributed in patches across the aquatic landscape relative to
307 seasons and ontogeny. Functional connectivity between habitat patches may be necessary to
308 reach a successive life stage (Ferguson et al. 2011, Hall et al. 2012), maintain genetic diversity
309 (Policansky and Magnuson 1998), or maintain stable population size among sources and sinks
310 (Crowder et al. 2000, Figueira et al. 2009). Many native fish species have declined in population
311 size or growth rates when connectivity has been compromised (Ferguson et al. 2011, Hall et al.
312 2012). Firstly, landscape aspects of physical connectivity that are principally hydrological are
313 drivers for geomorphic, biogeochemical, and ecological processes of aquatic environments. The
314 interaction between connectivity and these important processes is particularly apparent
315 longitudinally in rivers (Ward 1989, Nestler et al. 2012), laterally in floodplains (e.g. Junk et al.
316 1989), and with vertical and horizontal dimensions in lakes. Secondly, connectivity reflects

317 patterns of residency, dispersal, and migration across temporal and spatial scales, which is
318 necessary for the management and conservation of fish and fisheries (Fausch et al. 2002).

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

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

340 Measuring passage past partial barriers is vital for biological assessment of migratory
341 fisheries in regulated rivers and telemetry provides the most valuable and detailed method of
342 providing information on aspects such as timing, attempt rates, passage success, survival, and
343 energetic cost (Cooke et al. 2013). Fish passes are the most common measure to support
344 functional longitudinal connectivity for fish. Determining the effectiveness of fish pass systems
345 and the conditions required for fish passage are important to maintain ecologically sustainable
346 populations of migratory fishes (Lucas and Baras 2001, Godinho and Kynard 2009, Cooke et al.
347 2013). Landscape-scale ecological information and models can be crucial in the optimal
348 deployment of barriers (see Rahel 2013) for conserving native fish populations (e.g., cutthroat
349 trout (*Salmo clarkii*), from downstream invasive competitor species (Fausch et al. 2009).

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

363

364 **IMPROVING HABITAT SCIENCE, MODELS, AND MANAGEMENT**

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

376 From a fishery management perspective, maintenance of the specific habitat conditions
377 required for successful spawning of target species is the most emphasised aspect of habitat
378 functionality in most restoration actions. Facilitating successful spawning is critical to
379 maintaining self-sustaining and productive fisheries, however, it is essential to also consider
380 critical habitat functions at all stages of life history. Spawning habitats may not be limiting and
381 density dependent mechanisms or environmental influences within the suitable habitat can affect
382 later life stages. For example, the larval stages of many riverine fishes use near-shore
383 “slackwater” habitats that provide low flow velocities, abundant food, warm water and shelter
384 from predators (King 2004). Similarly, the juvenile and adult stages of many lacustrine fishes
385 move into seasonally inundated floodplains to access food resources (Winemiller and Jepsen

386 1988) and preferred habitats at different time scales. Loss of connectivity between rivers or lakes
387 and their floodplains due to levees and flow regulation reduces this movement and is a
388 significant cause of fishery declines in many regions of the world (Cowx and Welcome 1998).

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

406

407 **MEASURING DEMOGRAPHIC PROCESSES**

408 Management actions such as stocking, habitat protection and restoration, and limiting harvest
409 (including predators and prey), are often justified on the basis of how those actions affect the
410 survival of individuals in a population. Therefore, effective management requires accurate
411 estimates of survival and sources of mortality. Demographic processes (e.g., survival,
412 immigration, emigration) are often measured by capture-recapture methods from marked
413 individuals. Although the fates of individuals are determined by processes that can change
414 quickly and vary widely across time and space, logistical constraints often limit capture-
415 recapture approaches to estimates of mortality and migration at resolutions of a year or more, and
416 at a geographic scale of an entire and connected watershed. In contrast, telemetry methods often
417 using autonomous receivers that sample continuously can provide high-resolution (e.g., hours,
418 meters) information about demographic processes over broad scales (e.g., years, kilometers).
419 Minimally, telemetry receivers can be arranged in open systems to detect movement among
420 discrete regions so that the fates of fish presumed dead can be attributed to activities or structures
421 in the region of loss, such as harvest (Hightower et al. 2001), hydroelectric dams (Skalski et al.
422 2001), water withdrawals (Svendsen et al. 2011), or predators (Fayram and Sibley 2000). Not
423 surprisingly, telemetry data are increasingly being used in addition to, or in place of, data from
424 more traditional sampling (e.g., nets, traps) in capture-recapture models.

425 Specific sources of mortality have been identified by fine-scale positional telemetry and
426 by integrating telemetry with other approaches and technologies, including mark-recapture
427 modeling. For example, tag-recovery data can be useful for estimating fishing mortality
428 (Bacheler et al. 2009) and fine-scale tracking has been used to attribute mortality to specific
429 predators (Romine et al. 2014) and structures at dams (Skalski et al. 2002). Telemetry has also
430 revealed how natural processes (e.g., predation, thermal stress, river entry, pathways) can be

431 altered by anthropogenic structures and activities. For example, Gauld et al. (2013) showed the
432 synergistic impacts of small-scale weirs and river discharge on mortality of emigrating brown
433 trout (*Salmo trutta*) smolts, apparently mediated through loss to predators. English et al. (2005)
434 showed that survival of adult Sockeye Salmon in the Fraser River was strongly dependent on
435 timing of river entry. Hayden et al. (2014) showed that Walleye from a Lake Huron tributary
436 seasonally migrated along coastlines, potentially exposing them to harvest far from their
437 spawning river.

438 **UNDERSTANDING ENVIRONMENTAL DRIVERS**

439 The environment is one of the fundamental drivers of animal movements and their distribution
440 across a landscape (Nathan et al. 2008). For example, variation in temperature, light, and
441 nutrients determine the spatio-temporal availability of food resources for aquatic organisms and
442 will then influence the spatial distribution of freshwater fishes (Allan and Castillo 2007).
443 Temperature, often regarded as the master environmental driver for fish (Fry 1971), also sets
444 physiological limits to the movement and distribution of fish via its direct effects on their
445 metabolism and cardiorespiratory physiology (Pörtner and Farrell 2008, Isaak et al. 2010, Eddy
446 and Handy 2012).

447 River flow is another major driver of the movement and distribution of freshwater fishes.
448 Spatio-temporal variation in flow generates a highly dynamic energy landscape in freshwater,
449 with the energetic costs associated with maintaining position at or moving to/from any given
450 location changing over timescales ranging from seconds to months (Shephard et al. 2013),
451 sometimes predictably and sometimes stochastically. Increases in water level under high flow
452 also connect rivers with their floodplains (Allan and Castillo 2007), which are often sought out

453 by fish due to its high food availability compared with river channels (Goulding 1980, Junk et al.
454 1997).

455 Knowledge of the influence of environmental drivers on the spatial ecology of freshwater
456 fishes is critical for predicting their spatio-temporal occurrence and abundance, and informing
457 the design of biological assessments. Capture-dependent (e.g., mark-recapture, telemetry) and
458 capture-independent (e.g. hydroacoustics, visual observations) techniques exist that are available
459 to collect data on the movement and distribution of fish – their appropriateness/effectiveness
460 varying according to the spatio-temporal resolution required (Lucas and Baras 2000).
461 Concomitantly, data on environmental drivers can be collected using data loggers (e.g.,
462 temperature, light, oxygen) attached to the fish or deployed in strategic locations throughout the
463 sampling area. Alternatively, data on environmental drivers can be acquired locally or regionally
464 (e.g., weather and hydrological monitoring stations) and from databases of remote sensing data
465 (e.g., ENV-Data system at Movebank; Dodge et al. 2013). The analysis of the relationship
466 between movement or distribution of fish and environmental drivers can be accomplished using
467 a number of statistical approaches including, but not limited to, generalized linear models and
468 their mixed-effects counterparts (Zuur et al. 2009), Bayesian approaches with diffuse or
469 informative priors (Punt and Hilborn 1997), step selection functions (Thurfjell et al. 2014),
470 occupancy models (Dextrase et al. 2014), and various spatial statistics methods (Fortin and Dale
471 2005).

472

473 **UNDERSTANDING TROPHIC ECOLOGY**

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

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

496 et al. 2005). Similarly, spawning migrations of iteroparous fish can enrich inland freshwater
497 systems (Childress et al. 2014).

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

512 Movement has implications for predator-prey interactions, with the feeding range of an
513 individual considered to be critical for food-web dynamics because it determines the spatial scale
514 of predator-prey interactions (DeAngelis and Petersen 2001). For example, the spatial feeding
515 range of organisms in lower-quality feeding habitats is likely to be larger than in higher-quality
516 feeding habitats where the density and/or quality of prey are high (Kramer and Chapman 1999).
517 Furthermore, the impact of predators on prey will be related to their own patterns of movement
518 and the relative locality of their movement patterns as compared to those of the prey.

519 Accordingly, movement will influence the strength of predator-prey interactions and has
520 consequences for top-down, predatory regulation of food webs. Fish vulnerability to fishers is
521 largely driven by trophic ecology, thus understanding how fish move within and between
522 habitats and their relative contribution along the food chain is paramount to conservation and
523 management.

524

525 **EVALUATING FISHERY ENHANCEMENT STRATEGIES**

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

535 Fishery managers and scientists are often concerned about the interactions between wild
536 and stocked individuals in the natural aquatic environment (Mackey et al. 2001). A variety of
537 examples exist where research programs have focused on these interactions, particularly with
538 Atlantic salmon on the Eastern seaboard and with Pacific salmon on the western seaboard of
539 North America. However, for inland fisheries, these interactions between propagated and native
540 conspecific are less evident in the literature. Time-resolved tools for investigating the spatial

541 ecology can provide information with regard to interactions between cultured individuals and
542 native populations. Understanding the spatial-temporal patterns of stocked and wild fish is
543 important for evaluating and improving restoration and enhancement programs. For example,
544 Bolland et al. (2009) used PIT-telemetry to compare the distribution, survival, and movements of
545 hatchery-reared and wild cyprinid fish upon liberation and found that in the short term (< 1 year)
546 the stocked fish were able to cope with the stochastic environmental conditions in the natural
547 riverine environment in which they were liberated, but behaved differently to wild fish.

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

559

560 **MONITORING OR ADDRESSING HUMAN IMPACTS**

561 Fish are an effective indicator for aquatic habitat assessments because they are sensitive to
562 anthropogenic disturbances (both facilitated and direct) and can be used over small and large

563 temporal and spatial scales (Harris 1995). Fish spatial ecology can provide a long-term indicator
564 of the health of an aquatic system. While challenging and not always an option, collecting
565 baseline information on the spatial ecology of fish prior to human-induced changes allows for
566 pre- and post-monitoring comparisons for directing management actions and priorities (e.g.,
567 before-after-control-impact studies; Palmer et al. 2005). Large numbers of restoration projects in
568 the past have not addressed the short- and long-term spatial ecology of fishes through the
569 progression of the projects, and indeed, only a small number have used or been able to
570 incorporate a BACI experimental design to monitor fish responses to environmental change
571 (Lapointe et al. 2013).

572 Applying tools to address movement and habitat use of fish can also allow for insight into
573 the spread and impacts of invasive species, disease, and parasitism (e.g., Pratt et al. 2009).
574 Studies have used ecological tools for tracking the movements of invasive sea lamprey to address
575 the capture efficiency of traps positioned below hydropower stations with manipulation of the
576 discharge rate (Rous 2014; Holbrook et al. In Press). Researchers have also investigated the
577 spatial ecology of invasive aquatic fish species to determine aggregation sites to improve
578 eradication efforts. Common carp (*Cyprinus carpio*) have been tracked in midwestern lakes in
579 North America (Bajer et al. 2011), while others have investigated the spatial ecology of invasive
580 lake trout (*Salvelinus namaycush*) in Yellowstone National Park to determine high-density areas
581 of use to focus eradication efforts (Dux et al. 2011, Gresswell et al. 2012). In several locations
582 within the Laurentian Great lakes, protections are extended to vulnerable life stages by excluding
583 destructive common carp from the spawning habitat of native species (Casselman and Lewis
584 1996, Chow-Fraser 2005). Similar approaches have also been employed in the Murray-Darling

585 Basin in Australia to control carp by installing screens to prevent access to preferred spawning
586 habitat in floodplain wetlands (Hillyard et al. 2010).

587

588 **SYNTHESIS AND CONCLUSIONS**

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

601 In this paper, we have demonstrated how spatial ecology is fundamental to being able to
602 design, implement, and interpret biological assessment, to develop models (e.g., habitat and
603 environmental models) to inform management, and to evaluate various fishery management and
604 conservation strategies. In fact, we believe that our examples are sufficiently compelling that
605 designing or implementing fishery assessment programs without information on the spatial
606 ecology of fish populations is unwise. The “excuse” that not doing so is impossible due to

607 technical challenges or expense is no longer valid in most instances. Clearly, application is not
608 easy, but the tools and knowledge exist for a wide range of species and systems (e.g., from
609 under-ice to the largest of rivers and lakes). As these tools have become more widely embraced,
610 the cost has decreased substantially (e.g., radio tags now cost around \$100 each, PIT tags cost \$4
611 each, isotope analyses are generally cheaply and widely available). Indeed, the ecological costs
612 of not studying the spatial ecology of a population may be much greater – both in terms of
613 economics and conservation. Nonetheless, challenges remain related to trying to better
614 characterize the spatial ecology of larval life-stages as well as working in some conditions (e.g.,
615 large rivers, winter in temperate regions, monsoon/flood season in the tropics). Moving forward,
616 our expectation is that inland fishery assessment will be enhanced by the inclusion of knowledge
617 on the spatial ecology of fish, which will lead to improved management and conservation
618 outcomes.

619

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621

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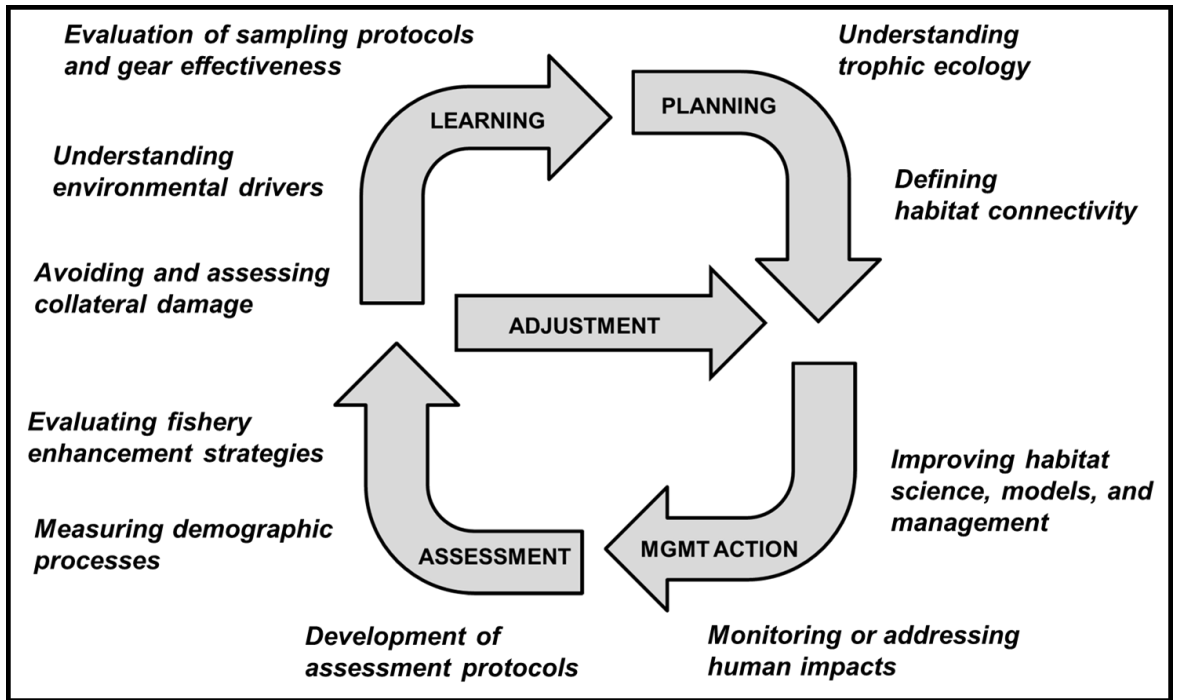
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1038 **Figures**

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1042 Figure 1- A conceptual diagram of the fisheries management cycle with relevant aspects of
1043 spatial ecology (and components of this paper – in italics) mapped onto the cycle. We recognize
1044 that the components of the paper fit in various places on the management cycle such that this
1045 visualization is not the only way in which individuals components relate to phases of the
1046 management cycle. Assessment and adjustment are key components to the management cycle in
1047 contemporary fisheries management.

1048