A role for lakes in revealing the nature of animal movement using high dimensional

telemetry systems

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Abstract

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44 Movement ecology is increasingly relying on experimental approaches and hypothesis testing to

45 reveal how, when, where, why, and which animals move. Movement of megafauna is inherently

46 interesting but many of the fundamental questions of movement ecology can be efficiently tested

47 in study systems with high degrees of control. Lakes can be seen as microcosms for studying

48 ecological processes and the use of high-resolution positioning systems to triangulate exact

49 coordinates of fish, along with sensors that relay information about depth, temperature,

50 acceleration, predation, and more, can be used to answer some of movement ecology's most

51 pressing questions. We describe how key questions in animal movement have been approached

52 and how experiments can be designed to gather information about movement processes to answer

53 questions about the physiological, genetic, and environmental drivers of movement using lakes.

54 We submit that whole lake telemetry studies have a key role to play not only in movement ecology

55 but more broadly in biology as key scientific arenas for knowledge advancement. New hardware

56 for tracking aquatic animals and statistical tools for understanding the processes underlying

57 detection data will continue to advance the potential for revealing the paradigms that govern

58 movement and biological phenomena not just within lakes but in other realms spanning lands and

59 oceans.

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61 Keywords- telemetry, sensor, biologging, movement ecology, fish ecology

Introduction

Animals are born, they move and reproduce, and then they die. This simple model of life supports all ecological processes and movement has therefore emerged as a frontier for animal research (Nathan et al. 2008; Hussey et al. 2015; Kays et al. 2015). Movement ecology is a multiscale branch of ecology operating from cells to whole animals, populations, and communities across short or long distances for brief intervals or even spanning generations. Where do animals move, when, why, and how? These are foundational ecological questions; the answers to which have significant implications for our understanding of the natural world and the management of resources that we depend upon (Nussbaum 1978; Nathan et al. 2008; Lowerre-Barbieri et al. In Press).

Significant and rapid advances have been made in our understanding of movement ecology coincident with the introduction and proliferation of electronic tags to remotely measure animal behaviour and physiology (Hussey et al. 2015; Kays et al. 2015). The capacity to simultaneously monitor movement and the environment yields great opportunity but also significant responsibility to identify focal systems with which to make inferences (Hays et al. 2016). To this end, Hays et al. (2016) presented a list of research priorities related to megafaunal movement, specific to a system where research is inherently challenging and limited by the vast scale of latitudinal and longitudinal connectivity coupled with profound depths, the marine environment. This daring focus renders many studies, particularly those that concentrate on community scales and consider interactions among species, logistically challenging.

Lakes are ideal study systems for testing ecological paradigms. For over a century they have been acknowledged for providing ample opportunities to investigate ecological, behavioral

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85   and evolutionary questions at manageable scales (Forbes 1887). Lakes are highly important

86   venues for studying ecology because freshwater habitats are among Earth's most valuable, rare,

87   and threatened ecosystems (Dudgeon et al. 2006; Verpooter et al. 2014; Reid et al. 2019). As

88   relatively closed ecosystems with less influence from distant processes (Michalek et al. 2013),

89   animal movement can be linked more directly to local phenomena, including weather patterns

90   and the immediate ecological community. Lakes offer a great diversity of structural and physical

91   processes with great similarity at local scales but substantial variation in fish assemblages and

92   aquatic communities across latitudes and longitudes. Small lakes can effectively be covered by

93   an array of acoustic receivers in a comparable design to a bay or coastal area in the ocean or a

94   great lake but with greater resolution of the processes operating within. Replication of studies in

95   multiple lakes offers the potential for robust inferences from ecological and manipulative

96   experiments (Carpenter 1989; Schindler 1998), including how environmental stressors and

97   ecological interactions modify movement behaviour. For these reasons, lakes have long provided

98   essential venues for ecological inquiry and many paradigms have emerged from the flexibility,

99   observability, and replicability of research in lakes, including ecological regime shifts (Scheffer

100   et al. 2001), predation risk effects (Werner et al. 1983), predator-prey-habitat complexity

101   relationships (Gilinsky 1984), trophic positioning from stable isotopes (Vander Zanden &

102   Rassmussen 1999), habitat degradation (Schindler et al. 1985), and ecological speciation

103   (Schluter 2001, Seehausen & Wagner 2014).

104   We submit that lakes provide perfect venues in which to investigate many of the most

105   fundamental questions of movement ecology with results that are scalable to larger systems. To

106   that end, we turn to the key questions of marine megafaunal movement ecology presented by

107   Hays et al. (2016) and suggest that many of these questions can also be applied to whole lake

108   studies. We interpret these questions as relevant across mobile taxa and not limited to the marine

109   environment or to megafauna specifically. We posit that answering these questions will yield

110   significant advances in our understanding of movement ecology independent of the system. Our

111   approach is to draw on our experiences working in acoustically instrumented lake environments

112   to discuss the vast opportunities these systems have to address 15 movement ecology questions

113   identified by Hays et al. (2016) that we agree will drive the movement ecology field forward in

114   coming years. Each section is divided into three paragraphs in which we first describe key

115   examples and potential connections, followed by questions using lakes as focal systems that

116   could advance understanding, and finally the approaches that could accomplish this. We

117   conclude this essay with a synthesis where we discuss the tools and approaches that we envision

118   researchers applying to better understand the complexities of aquatic life for better habitat

119   management, ecosystem conservation, and fundamental science.

120

121   How Can Movement Data Be Used to Support Conservation and Management?

122

123   Aquatic biodiversity is in steep decline due to a range of anthropogenic factors, including

124   habitat alterations (Reid et al. 2019). There are also increasing examples of overfishing of

125   freshwater stocks (Post et al. 2002) and of other exploitation-induced issues (Lewin et al. 2006,

126   Arlinghaus et al. 2019). Movement data are key, yet underutilized to design effective

127   conservation and management strategies, e.g., in the context of fisheries and conservation of

128   freshwater fish and freshwater habitats (Bajer et al. 2010, Crossin et al. 2017). Lake tracking data

129   can be used to identify seasonal and daily movements, dispersal, connectivity of habitats

130   (Chapman et al. 2012, Hawley et al. 2017, Nakayama et al. 2018), e.g., after stocking (Monk et

131   al. In Press), behavioural diversification and its relation to individual fitness (Kobler et al. 2009),

132   capture probability (Monk & Arlinghaus 2017, 2018), spawning site fidelity (Kobler et al. 2008),

133   stock boundaries among connected ecosystems and within ecosystems (Cooper et al. 2010,

134   Hayden et al. 2014), reactions to human influences, such as boat movement (Jacobsen et al.

135   2014) or catch-and-release (Baktoft et al. 2012), and degree of fishing-induced mortality

136   (Hightower et al. 2001). An obvious further application example from a conservation context is

137   applying telemetry to examine the ability of freshwater protected areas to help heavily exploited

138   fishes recover from heavy fishing pressure (Raabe et al. 2014). In this context, telemetry is useful

139   to identify sites where encounters with fishing gears are rare.

140   Despite the opportunities, there are limited examples of fine-scale, whole-lake tracking

141   studies that have realized the potential of informed management and conservation. The few

142   systems that were or are in place have generated a number of highly relevant results. Baktoft et

143   al. (2012) used whole lake telemetry to assess the reactions of northern pike (*Esox lucius*) to

144   handling, including catch-and-release. Jacobsen et al. (2014) studied the response of different

145   freshwater fish to boating, revealing limited impacts on the behaviour of freshwater fish.

146   O'Connor et al. (2010) showed that a one-time intensive stressor can have carry-over effects

147   many months later during hypoxia in largemouth bass (*Micropterus salmoides*). Work in a small

148   lake in Germany has revealed how angling can directly select on behavioural traits, such as

149   habitat choice in perch (*Perca fluviatilis*) (Monk & Arlinghaus 2018). Similar research has been

150   conducted in "lake-like" coastal systems where small-bodied coastal fish with limited home

151   range were exposed to angling, revealing how angling could be a selective force on home range,

152   activity, and chronotypes (Alos et al. 2016). A ground baiting experiment at a whole lake scale

153   showed how omnivorous fish respond to angler-induced bait and how this novel energy is

154   embedded in certain trophic levels elevating secondary production (Mehner et al. 2018). Fine-

155 scale acoustic telemetry has also been used to study restoration success in Toronto, Canada

156 (Veilleux 2014) and how exposure to pollutants affects the behaviour of Eurasian perch in the

157 wild (Klaminder et al. 2016).

158   Compared to the oceans, spatially finite ecosystems such as ponds or lakes can offer

159 replication and allow whole-ecosystem type experiments to be conducted with appropriate

160 replicates (either in space or time) and with controls (e.g. manipulated vs. unmanipulated; Figure

161 1). Before-after-control-impact studies are a gold-standard in the applied environmental sciences,

162 particularly in freshwater ecology, and are particularly useful to identify how common

163 conservation and management actions work at ecologically realistic scales. Lakes offer excellent

164 experimental arenas for such types of studies. Experiments could, for example, tackle questions

165 of habitat enhancement or degradation, stocking and introductions, selective harvesting and

166 effectiveness of protected areas. Smaller pond ecosystems could also be experimentally warmed

167 to study impacts of climate change. Replicated lakes could be used to study impacts of invasive

168 species, the release of pollutants, light pollution, and exploitation pressures. Stock assessment

169 methods could be calibrated and gear biases and estimation of catchability could be quantified in

170 situ using telemetry. Indeed, whole lake telemetry constitutes an excellent opportunity to

171 estimate the "unmeasurable" (Figure 2), such as size-dependent mortality, predator-prey

172 interactions (e.g. after stocking of piscivores), or ecosystem reactions to changes in fish

173 populations (e.g. invasions). In this context, the success of common restoration measures, such as

174 biomanipulation (Mehner et al. 2004), depends on risk-sensitive foraging (Ahrens et al. 2012),

175 which in the past was indirectly inferred from the capture of fish in gill nets and other gears or

176 was simply inferred from prey responses to introduced predators. Telemetry could be used to

177 directly measure how zooplanktivorous fish respond to stocking of predators, to the removal of

178 fish, to fish-eating birds or otters, or to technological measures (e.g. aeration), or alternatively,

179 how the movements of fish affect turbidity and water quality. Telemetry may also inform

180 eradication of pest species, should this be desired (Bajer et al. 2010).

181

182 <u>Are there Simple Rules Underlying Seemingly Complex Movement Patterns and, hence,</u>

183 <u>Common Drivers for Movement across Species?</u>

184

185   Common rules underlying seemingly complex movement patterns have been identified in

186 a number of aquatic animals, including seabirds, sharks, turtles (Sims et al. 2008; Hays et al.

187 2016), and freshwater fish (Matthews 1998). It has been extensively studied how, where, and

188 when individuals move, from which the following common drivers for movement have been

189 suggested: optimal foraging, site fidelity and revisitation, and temporal patterning. For the first,

190 optimal foraging, Lévy walks (Sims et al. 2008; Viswanathan 2010), Brownian motions

191 (Humphries et al. 2010), or similarly simple random walk-type models have been proposed as a

192 simple evolutionary trait that has been adopted by many species when searching for sparsely

193 distributed prey. In recent years, however, this randomness paradigm (Nathan et al. 2008) was

194 the subject of controversial discussions (cf. Benhamou 2007; Pyke 2015). In fact, conclusive

195 evidence for the Lévy walk and related hypotheses is still lacking, and it is now regarded as

196 overly simplistic. This perspective has catalyzed a shift towards explaining specific movement

197 paths rather than movement behavior in general (Patterson et al. 2017). For site fidelity and

198 revisitation patterns, home range or homing affinities have been identified in various freshwater

199 fishes, for which larger individuals were found to generally have larger home ranges (Matthews

200 1998; Woolnough et al. 2009). Yet, simple random walk-type models such as (truncated) Lévy

201   walks or Brownian motions are generally inadequate to resolve the patterns (Hooten et al. 2017).

202   In addition to an individual's size, the shape of the water body was suggested to affect movement

203   (Woolnough et al. 2009), emphasizing how environmental conditions can be regarded as a

204   common driver for movement. For temporal patterns, diel variation as well as daily and seasonal

205   movement patterns, particularly regarding the times of feeding, breeding, aggregating, and

206   resting behavior, have been found in numerous aquatic species (Helfman 1986). The majority of

207   freshwater fish tend to be predominantly diurnal (Cerri 1983; Clough and Ladle 1997; Baldwin

208   et al. 2002), although marine top predators tend to be more nocturnal (Holland et al. 1993). Time

209   is linked to both temperature and photoperiod, which influence the individual's physiology and

210   motivation for movement. Temperature, for example, has been shown to control activity timing

211   in juvenile salmon (Fraser et al. 1993). Time and photoperiod can be regarded as a common

212   driver for movement, either affecting movement directly or indirectly by affecting the prey's

213   behavior, which is then adopted by its predator.

214   Movement is often assumed to be the result of a single paradigm that neglects the

215   complex nature of movement. An alternative, more comprehensive perspective on movement

216   addresses the animal's internal state ("why does an animal move?"), its motion ("how does it

217   move?"), and navigation ("when and where does it move?") capacities, and external factors all

218   interact to generate movement (Nathan et al. 2008). Lakes provide a nearly ideal environment to

219   collect detailed data that inform complex statistical models and more comprehensive pictures of

220   an animal's behavior. To fully exploit the complex detection data, powerful statistical methods

221   are needed. Popular models for inferring behavioral patterns from high-resolution bio-logging

222   data include discrete-time hidden Markov models (HMMs; Langrock et al. 2012; Patterson et al.

223   2017; McClintock et al. 2020), general state-space models (SSMs; Jonsen et al. 2005; Patterson

224   et al. 2008; Auger-Méthé et al. 2020), and diffusion processes (e.g. Ornstein-Uhlenbeck position

225   models or stochastic differential equations; cf. Patterson et al. 2017 for an overview of the

226   available methods). Fueled by increasingly large and complex telemetry data sets, several

227   methodological extensions towards a more unified picture of movement (cf. Nathan et al. 2008)

228   have recently been proposed. For example, hierarchical HMMs provide a versatile framework for

229   jointly inferring movement patterns at multiple time scales (e.g. fine-scale variation in activity

230   vs. coarse-scale migration patterns; Leos-Barajas et al. 2017; Adam et al. 2019), energy budgets

231   and recharge dynamics have been explicitly incorporated into individual-level movement models

232   (Hooten et al. 2019), and group dynamics have been modeled by relating individuals' movement

233   decisions to herd-level movement patterns (Langrock et al. 2014; Niu et al. 2016).

234   Testing comprehensive models of animal movement in which movement is assumed to be

235   generated by many different factors interacting with each other, against simple null models such

236   as (truncated) Lévy walks, Brownian motions, or related random walk-type models, may provide

237   a promising avenue for confirming (or rejecting) simple rules that have been suggested in the

238   past. This approach can also test the validity of patterns and rules discovered with state-of-art

239   laboratory tracking techniques of aquatic invertebrates (e.g. Cloyed and Dell 2019) for fishes in

240   the wild. In addition, the unprecedented opportunities offered by high-resolution, three-

241   dimensional lake fish telemetry - most notably the possibility to observe an individual's

242   movement throughout an entire ecosystem at fine temporal resolution while being able to control

243   for various variables (Figure 2) that can affect its behavior in replicated designs, may help to

244   identify new common drivers for movement across species.

245

How Do Learning and Memory versus Innate Behaviours Influence Movement Patterns, including Ontogenetic Changes?

Animals moving in their natural environments are typically exposed to a variety of factors and conditions that span from highly beneficial (e.g. food or mates) to highly detrimental (e.g. toxic items or predators). The ability of animals to optimize fitness gain by adjusting their movement in response to complexities depends on both innate and learned skills that enable animals to perceive, respond, learn, and remember the structure and dynamics of such factors in their environment. Studies of animal cognition have yielded numerous insights into the mechanisms affecting spatial learning and memory in various animals (Pearce 2007, Shettleworth 2009) and fish in particular (Dobson 1988, Kieffer and Colgan 1992, Laland et al. 2003, Warburton 2003, Braithwaite 2006; Odling-Smee et al. 2011, Brown et al. 2011, Jonsson and Jonsson 2014, Vila Pouca and Brown 2017). These insights divulged the role of ontogenetic and cognitive processes in shaping movement patterns and their fitness consequences, stressing the critical role of learning from experience during early life. Across species, details were revealed mostly from controlled laboratory experiments on captive animals (Shettleworth 2009; Braithwaite 2006; Odling-Smee et al. 2011), whereas field studies have been much less frequent, and studies based on movement data collected from free-ranging animals in the wild have been scarce and focused on terrestrial systems (e.g. Harel et al. 2016; Sergio et al. 2014; Orgeret et al. 2019a,b, Toledo et al. 2020).

Studies of fish in their natural environment have yielded important insights in the ontogeny of spatial learning and memory. Whereas much of the literature has come from marine species, there is great opportunity to use lakes as a study system to test and advance movement

269   ecology paradigms. Such studies have shown, for example, that the remarkable homing ability of

270   adult salmon depends on long-term olfactory memory of their natal streams learned during early

271   stages of life (Scholz et al. 1976, Hasler and Scholz 1983). Although the basic formulation of

272   this salmon olfactory imprinting hypothesis received further support from later studies and has

273   been broadly accepted, some important details remain controversial (Quinn 2018). For example,

274   does olfactory imprinting occur exclusively in a limited time (the smolt stage) or at specific sites

275   (Scholz et al. 1976), or as a learned sequence of odors acquired during different early-life stages

276   at different times and sites (Havey et al. 2017)? Furthermore, fish might learn other cues and in a

277   more complex manner. For example, juvenile reef fish responded to cues sensed through

278   different mechanisms (olfaction, hearing and vision) at different sites experienced during their

279   early-life movements (Huijbers et al. 2012). Tracking fish movements throughout their life cycle,

280   and especially during early stages of life, offers a unique opportunity to tackle such complexities.

281   Earlier studies of fish movement mechanisms have used boats to follow individual fish marked

282   by a tethered float (Hasler et al. 1958), ultrasonic (Hasler et al. 1969), or radio (Bajer et al. 2010)

283   tags, resulting in relatively limited datasets of few individuals tracked at low frequency and for

284   short durations. Although these studies made some important propositions – that wild white bass

285   (*Morone chrysops*) can swim directly homeward in open water presumably by using a sun

286   compass (Hasler et al. 1958) and other cues (Hasler et al. 1969), and that wild carps can quickly

287   learn and remember the location of new food resources (Bajer et al. 2010) – more conclusive

288   insights and more in-depth investigation of the mechanisms underlying the observed tracks were

289   still rather limited. This powerful research system has just started to be applied to study topics

290   related to ontogeny of spatial learning and memory. Topics strongly related to ontogeny,

291   movement, and spatial learning and memory, such as personality traits (Adriaenssens and

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292   Johnsson 2013), cognitive flexibility, and inter-individual variation in space use (Armstrong et

293   al. 1999, Lucon-Xiccato and Bisazza 2017), time-place associations (Reebs 1996), landmark use

294   (Warburton 2003), and various other orientation and navigation mechanisms (Braithwaite and

295   Burt De Perera 2006), have been predominantly studied in the laboratory, and now can be

296   critically advanced by implementing high-throughput field telemetry approaches.

297   Understanding how early-life processes shape animal movement and behavior through

298   learning and memory is also important for managing populations, for example of fishes in lakes

299   and rivers. Better understanding of these processes can guide the development of infrastructure

300   to facilitate fish migration and survival in light of anthropogenic disturbances such as river dams

301   (Goodwin et al. 2014), or by enriching the relevant early-life environment of captive-reared fish

302   (Jonsson and Jonsson 2014). Studies examining fish response to capture by hooks can also

303   largely benefit from high-resolution fish tracking. For example, movements of both fish and

304   fisher might be tracked rather exhaustively in a closed lake system, to accurately estimate the

305   probability of captures and encounters and to elucidate the factors affecting these probabilities

306   (Alós et al. 2016, Lennox et al. 2017, Monk and Arlinghaus 2017). More generally, high-

307   throughput wildlife tracking systems such as acoustic lake telemetry can unravel some of the

308   most basic relationships between animal cognition/memory and movement (Figure 2). This has

309   recently been shown through the use of ATLAS, a new reverse-GPS tracking system that is

310   principally very similar to acoustic lake telemetry, to reveal the first field evidence for a

311   cognitive map and spatial memory of multiple specific targets by free-ranging animals within

312   their large (100 km^2) natural foraging area (Toledo et al. 2020). Furthermore, such tracking

313   projects can be coupled with methods providing complementary information on behavioral,

314   physiological and environmental changes, as well as experimental manipulations of learning and

315   memory by altering landmarks, fishing habits (e.g. bait type), sensory cues, and the presence of

316   informed vs. naïve fish.

317

318   <u>To what Degree Do Social Interactions Influence Movements?</u>

319

320   The study of animal social behaviour is fundamental to our understanding of behavioural,

321   physiological, and evolutionary ecology. Group living is key for predator-avoidance, foraging,

322   and reproduction in most animal taxa. This directly affects organismal fitness but also modulates

323   the outcome of numerous life-history and evolutionary trade-offs. There is also increasing

324   evidence that sociality plays a key role in the maintenance or erosion of within-species

325   phenotypic variation in behavioural and physiological traits (Jolles et al. 2020). Fish display

326   numerous forms of complex social behaviours including social networks, dominance hierarchies,

327   social learning, and coordinated group movements with leader-follower dynamics (Figure 3) As

328   such, fish are often used as models to study animal social behaviour and form the basis of a large

329   proportion of our knowledge about emergent group behaviours. Notably, however, most of this

330   research with fish has been done in the laboratory, mainly because of the extreme difficulty

331   associated with long-term measurements of individual fish behaviour in the wild (King et al.

332   2018). Our knowledge of how fish social groups function in the wild, and how they are affected

333   by environmental conditions, has therefore been hindered by this basic constraint in our research

334   capabilities (Guttridge et al. 2010).

335   Tools are now available to begin addressing detailed questions of social interactions and

336   animal movement. Lab-based observations of fish social behaviour can be realized with

337   sophisticated software for automatically tracking the trajectories of multiple individuals from

338   recorded video (Pérez-Escudero et al. 2014; Romero-Ferrero et al. 2019). These data are a series

339   of x-y coordinates for each individual within a group that can in turn be used to quantify: 1)

340   group-level metrics, including group cohesion and polarity; 2) the behaviour of individuals

341   within groups such as individual speed, alignment, spatial positioning, distance from group

342   mates, and social network position; and 3) the propagation of changes in movement metrics

343   throughout social groups. The spatial and temporal resolution of telemetry systems in the field

344   can now advance basic forms of these analyses on freely roaming fish in their natural habitats,

345   with the coordinates of individual detections being analogous to the x-y coordinates captured by

346   automated software in laboratory behavioural arenas. Analysis of movement propagation in the

347   lab is used to inform leader-follower dynamics in fish social groups (Jolles et al. 2017; Figure 3),

348   and in the wild could provide information on migrations and other phenomena related to

349   collective movement (Berdahl et al. 2017; Westley et al. 2018). Telemetry data are currently

350   being used to infer differences in individual space use and habitat preferences within species

351   (Nakayama et al. 2016; Fahlman et al. 2020), but it is highly likely that these are also affected by

352   social dynamics in ways that we are yet to understand but that will now be possible. Increased

353   knowledge of fish social systems will also provide knowledge on how group movement and

354   behaviour affect individual vulnerability to different fishing methods (Thambithurai et al. 2018;

355   Hollins et al. 2019). Perhaps most importantly, increased knowledge of fish social systems in the

356   wild will help us understand their responses to natural and human-associated changes in

357   environmental factors such as temperature, oxygen availability, turbidity, and food availability.

358   A promising opportunity also exists to combine telemetry movement data with other forms of

359   logged or transmitted data from individual fish (e.g. heart rate data, temperature) to carefully

360   dissect the interplay among animal movements, their social environment, their physiological

361 state, and the external environment (Cooke et al. 2016). It will also be possible to combine all of

362 this information with established theoretical movement models from lab-based work to more

363 fully understand fish social dynamics, emergent group behaviours, and then predict their

364 responses in the wild and empirically test these predictions.

365 　　　　Despite these exciting opportunities, there remain many challenges that must be

366 addressed before we can fully take advantage of acoustic telemetry in the study of fish social

367 behaviour. In order to fully understand how fish are being influenced by their social

368 environment, we must have data for all or at least the vast majority of fish within a natural

369 system. This is extremely difficult because in most cases it will be impossible to know if all fish

370 within a system have been captured and tagged. A possible solution may be the removal of most

371 fish, followed by stocking with a known number of tagged individuals, or the use of dedicated

372 fishless lakes or artificial ponds. An additional challenge will be the development of a statistical

373 and analytical framework for studying the desired social behaviours and emergent phenomena.

374 To be most useful for social analyses, telemetry data must have a high spatial and temporal

375 resolution and low error. Lab-based work can provide precise positions of individual fish dozens

376 of times per second (Pérez-Escudero et al. 2014; Romero-Ferrero et al. 2019). This is not

377 possible with even the most advanced forms of acoustic telemetry, and so we will need to work

378 back to uncover the minimal adequate spatial and temporal resolutions needed for basic analyses

379 of individual interactions, spatial positioning within groups, and group fission-fusion processes.

380 Enhanced resolution also greatly increases the required computing power and analyses time, and

381 so it might initially only be possible to perform the most sophisticated analyses on subsets of

382 data.

383

384   How Does the Distribution of Prey Impact Movement?

385

386   Prey distribution and availability can highly alter the behaviour and movement of

387   predators (Barbosa and Castellanos 2005). Initially, predation concepts focused on the optimality

388   of foraging behaviour, i.e. maximization of the rate of energy intake, in relation to prey density

389   and distribution (MacArthur and Pianka 1966). Later, predation risk (Werner et al. 1983),

390   competition among conspecifics (Fretwell and Lucas 1970), effects of environmental abiotic

391   factors (Aksnes and Giske 1990), level of individual (Tyler and Rose 1994), or individual state

392   (McNamara and Houston 1996) were introduced into the models explaining the effects of prey

393   on predator distribution. These concepts mostly targeted ultimate causes of predator-prey

394   distribution interactions and their effect on life history traits and fitness of both predators and

395   prey (Giske et al. 1998). Concepts such as optimal foraging, game theory and ideal free

396   distribution further considered that individuals tend to optimize their foraging strategies based on

397   all relevant environmental factors (such as the amount of prey, predation risk, and number of

398   conspecifics) and internal physiological state, and chose the behaviour that maximizes individual

399   fitness and future reproduction (Giske et al. 1998). However, it is now widely recognized that

400   natural organisms are limited by incomplete information and imperfect ability to analyze

401   information and foresee consequences of alternative behavioural options (Andersen et al. 2016).

402   Consequently, recent research has shifted more towards individual level and proximate causes of

403   predator-prey distribution interactions.

404   Much attention has been given to the role of different decision-making processes for

405   involving individual decisions and their regulation into foraging behavior (Nathan et al. 2008,

406   Andersen et al. 2016). Current thinking frames individuals as units determined by various

407 properties (individual genotype, physiological state, age, or size) and moving in space defined by

408 multilevel landscapes of, e.g., fear (Laundré et al. 2001) or energy (Rory et al. 2011). Individual

409 space use then depends on the overlay of these landscape 'bricks' (e.g., low use of locations with

410 rich food and high predation risk) and actual cognitive and physiological state of an individual

411 (Gallagher et al. 2017, Goossens et al. 2020). Both individual state and landscape topography are

412 affected by environmental factors (e.g. temperature and light in aquatic environments) and

413 change dynamically in time (Gallagher et al. 2017). Yet, many important questions are poorly

414 understood in these fields and high-resolution movement data can be a key component in their

415 understanding: e.g. proper matching of the landscapes of fear and energy with resulting

416 movement trajectory (Gallagher et al. 2017); effects of prey availability on predator behaviour

417 under different environmental contexts (Campos-Candela et al. 2019); predator-prey personality

418 interactions in forage/escape behaviour; mismatch in the timing of predator-prey activity peaks

419 (Alós et al.2017); temporal individual variation in the forage/hide behaviour, the role of

420 individual traits in ontogenetic shifts in space and resource use (Muška et al. 2013, Říha et al.

421 2015); and the causes and triggers of diel vertical and horizontal migrations (Mehner 2012; Říha

422 et al. 2015; Sajdlová et al. 2018).

423   Even relatively large water bodies up to several hundreds of hectares can be fully covered

424 by positioning systems (Westrelin et al. 2018; Bašić et al. 2020; Říha et al. in prep) to provide

425 fine-scale positioning of both predator and prey over long periods of time that can be used to

426 answer a variety of questions related to predator-prey interactions. For example, Jacobsen et al.

427 (2015) identified alternative foraging strategies in acoustically tagged Eurasian perch *Perca*

428 *fluviatilis* in mesotrophic and hypereutrophic conditions. In a long-term movement study,

429 Nakayama et al. (2018) found distinct diel horizontal migration of Eurasian perch likely related

430   to foraging opportunities. Baktoft et al. (2016) used tagged Eurasian perch to quantify the links

431   between metabolic rate and activity patterns. Kobler et al. (2009) studied behavioural types of

432   Northern pike *Esox lucius* using radio-telemetry in a lake and found distinct differences in

433   habitat use and activity levels, which they related to an ideal free distribution pattern. Madenjian

434   et al. (2018) demonstrated a positive effect of food availability on consumption rate in walleye

435   *Sander vitreus*. In the same species, Raby et al. (2018) concluded that drivers such as

436   temperature and food availability influence migratory behaviour. All these studies show the high

437   potential of telemetry in studying predator and prey space use and their spatial interactions. We

438   believe that the development of high-resolution telemetry and statistical techniques to identify

439   and analyze patterns in multidimensional big data will help understand predator-prey interactions

440   in great detail. Current technology of high-resolution tracking dramatically expands our abilities

441   to uncover predator-prey spatiotemporal overlay and use it to infer their direct and indirect

442   interactions (Figure 2). Such sampling can be accompanied with measurements of suitable

443   individual traits before or after tracking and use these traits in possible proximate or ultimate

444   explanations of their behavioural strategies and predator-prey interaction strengths (Boukal

445   2014). The main limitation for such studies currently seems to be the need for a carefully

446   planned protocol with a large number of tracked fish to obtain robust patterns.

447

448   What Sensory Information Do Animals Use to Sense Prey, Breeding Partners, and

449   Environmental Conditions?

450

451   The sensory perception of the abiotic and biotic environment is the basic input for fish

452   behaviour. Fish may use a wide array of senses (gustation, olfaction, vision, lateral line, hearing,

453   magnetoreception, and electroreception) for orientation in the environment and one or multiple

454   senses may be used as a basis for their behavioural decisions. To disentangle which sensory

455   system is used for assessing particular situations, experimental designs using sensory blocking,

456   nerve suppression, nerve transection or ablation experiments are frequently used (New et al.

457   2001; Pohlmann et al. 2004; O'Connell et al. 2014). Sensory ecology of aquatic organisms is

458   predominantly studied under controlled laboratory conditions (Munakata & Kobayashi, 2010;

459   Sorensen & Wisenden, 2015). Due to the ability to precisely track animal movement beyond

460   laboratory environments, novel research designs using 3D telemetry technologies have the

461   potential to shed light on many research topics dealing with sensory perception important to

462   predator-prey interactions, communication among conspecifics, and animal orientation within

463   the visually limited space of aquatic environments. This design was implemented to discriminate

464   among visual, magnetic and olfactory navigation to natal stream in sockeye and masu salmons

465   *Oncorhynchus nerka* and *O. masou* (Ueda 2011).

466   The ability to precisely track individual fish opens new opportunities to test hypotheses

467   and validate laboratory findings linking sensory information to individual behaviour (as in, e.g.,

468   Cloyed and Dell 2019) in ponds and lakes. Two approaches can be used for experimental study

469   designs in lakes: manipulation with the environment and manipulation with fish physiology and

470   sensory ability. Using multiple small lakes or ponds (or dividing them with curtains) and

471   manipulating variables (e.g. turbidity, anthropogenic noise, pH or light pollution) may help

472   disentangle the effect of tested variables on the fish behaviour and fitness (Seehausen et al.

473   2008). Study design may alternatively involve manipulation with fish physiology by using slow-

474   release implants and comparing it to non-manipulated individuals (McConnachie et al. 2012;

475   McCallum et al. 2019). Finally, experimental designs using sensory blocking, nerve suppression,

476 nerve transection or ablation experiments may help determine which sense provides critical input

477 for the observed behaviour. Novel approaches using depth, temperature, acceleration, predation,

478 or metabolism-level sensors may be integrated in the study design, thereby enabling a wider

479 interpretation of the data (Algera et al. 2017; Hanssen 2020; Raby et al. 2020).

480   Study designs using 3D telemetry to differentiate among senses used for observed

481 behaviour would require careful study design using one of the above-mentioned options. As an

482 example of such an experiment in semi-wild conditions, disabling a selected sensory input in

483 selected prey individuals and comparing them to controls may help disentangle the role of

484 sensory information in predator avoidance and quantify the role of each sensory input.

485 Manipulation of the sensory ability of predators can be used to discriminate which senses are

486 important in which part of the predator-prey cycle (New et al. 2001; Pohlmann et al. 2004).

487 Uncertainty in the data interpretation may be further minimized by monitoring all potential prey

488 and predator individuals. Given the cost limitations, preference should be given to simple

489 systems with limited predator-prey species interactions to enable thorough interpretation of the

490 results and to minimize the risk of study failure (Lindenmayer & Likens, 2009). While we argue

491 above that purely behavioural studies would benefit from as many tagged fish as possible, we

492 partly take the opposite stance here because experiments targeting sensory information are

493 potentially of an invasive nature. Such experiments should be planned carefully to minimize the

494 number of individuals used for the study and maximize their welfare (Russel & Burch, 1958;

495 Brown, 2015). Therefore, the questions should be addressed primarily using non-invasive

496 methods such as environmental manipulation or temporary sensory suppression by chemical

497 treatment (New et al. 2001). Joint efforts of physiologists and behavioral ecologists respecting

498   these limitations can still provide novel insights in the use of sensory information in fish

499   behaviour in lakes.

500

501   <u>Can Movement Data Provide Information on the Ecosystem Role of Megafauna?</u>

502

503   Ecosystems are built upon matter and energy, the movement of which generates

504   ecosystem services (Costanza et al. 1997). In lakes, matter and energy cycle among riparian,

505   benthic, littoral, and pelagic zones; gravity and flow create connections but organismal

506   movement is critical to creating linkages and generating ecosystem services. Rates at which these

507   processes occur vary as a function of a variety of factors operating at broad spatial scales such as

508   those driven by temperature as well as shorter scales such as depth and nutrient loads (Seekell et

509   al. 2015). Organisms carry out ecosystem services by cycling matter and energy through their

510   bodies, as such, they develop functional roles in the ecosystem as producers, consumers,

511   decomposers, etc. (Holmlund and Hammer 1999; Bauer and Hoye 2014). Valuable research has

512   been carried out in lakes to reveal relationships among lake morphology, productivity, and fish

513   biomass (e.g. Carpenter et al. 2011; Seekell et al. 2018) and with telemetry tools we have the

514   capacity to expand this knowledge with finer-scale details of the functional roles that fish have in

515   these systems and the feedbacks between consumers and producers in the ecosystem.

516   Throughout the field of ecology there is broad interest in understanding how roles are partitioned

517   among species in an ecosystem, and how the system responds under stress such as when

518   challenged by invasive species, climate change, or pollution. Understanding roles and identifying

519   pathways through which ecosystem services are generated is therefore a key question to ecology,

520   albeit one that has been afforded less consideration in the context of movement ecology (Hays et

23

521   al. 2016). In lakes, productivity scales with the perimeter/area ratio, suggesting that small lakes,

522   rather than great lakes or seas, would be ideal venues for investigating habitat coupling and

523   ecological roles with replicated whole lake experiments including manipulations of the fish

524   assemblage and experimental alterations of lake productivity (Wetzel 1990; Schindler and

525   Scheuerell 2002).

526   Whole-lake studies have contributed in substantial ways to our understanding of energy

527   landscapes and ecosystem services. Predation and competition are the key biotic processes that

528   structure lake fish communities and manipulative experiments in lakes have illuminated how

529   these processes operate (Jackson et al. 2001). Replicated whole-lake experiments have been

530   conducted by modifying the fish community and observing changes in abundance and growth to

531   reveal mechanisms that structure assemblages (e.g. Byström et al. 1998; Carpenter et al. 2011).

532   However, existing studies have lacked the resolution to observe competition and predation in

533   situ. Manipulative experiments in whole lakes provide ideal templates for research on ecosystem

534   roles when coupled with tools that allow direct inference of material and energy cycling, such as

535   stable isotopes (Vander Zanden et al. 1997) or chlorophyll measurements in situ (Carpenter et al.

536   2011). Stable isotopes have revealed transmission of carbon and nitrogen within lakes and the

537   terrestrial-aquatic interface (Pace et al. 2004) as well as shifts in the trophic network as a

538   consequence of species invasions (Vander Zanden et al. 1999). Measurement of stable isotopes

539   linked with movement data can illustrate how matter is transferred within the lake and what

540   functional movement classes exist within species and whether movement syndromes (i.e.

541   consistent individual differences) exist. Movement syndromes may be key to determining how

542   intraspecific differences in behaviour drive ecosystem roles. Acoustic telemetry in replicated

543   whole-lake experiments will reveal how individuals, populations, and communities shift their

24

544   patterns of space use across days, seasons, and years to incorporate and deposit matter and

545   energy within their confined landscape. Layering this information with abiotic data will reveal

546   drivers of migration and dispersal within habitats across time scales (Brönmark et al. 2013;

547   Bauer and Hoye 2014). We can then link where and when animals move with the consequences

548   of that movement for the ecosystem established from site-specific sampling of lake productivity

549   and contrasts among species under investigation. Multispecies studies in whole lakes can also

550   reveal dynamic niche partitioning and species interactions including predation, competition, and

551   parasitism when multiple species are tagged (Figure 2). Critical to this is considering scale by

552   contrasting results from lakes of different size: we will likely find increased sympatry and

553   decreased connectivity with increasing habitat size, a factor that can easily be investigated in

554   these closed systems (Jackson et al. 2001).

555   We envision replicated whole-lake experiments that specifically investigate multi-species

556   dynamics in habitat use and the nature of connectivity within lake ecosystems. Instrumented

557   individuals moving within an array of acoustic receivers will reveal patterns and drivers of

558   movement across spatial, temporal, and ontogenic scales. Spatial overlap of individuals and

559   species can be calculated using kernel density or convex hulls from two- or three-dimensional

560   positions within arrays (e.g. Guzzo et al. 2016; Figure 2). Detection data from acoustic receivers

561   can be investigated using network analysis (Figure 3) to determine which species are central to

562   connecting the ecosystem across space and time (Jacoby and Freeman 2016) and functional

563   movement classes can be identified within and across systems from cluster analysis (Brodie et al.

564   2018). Contextual data can be derived from biologging sensors including accelerometers that

565   measure fine-scale behaviours that can be interpreted as foraging or reproduction to reveal the

566   frequency and spatiotemporal distribution of these exchanges of matter and energy (e.g. Tsuda et

567 al. 2006; Brownscombe et al. 2014). Novel tag sensors and analytical models can also be used to

568 remotely reveal predation in lakes with smaller risk of a predator evading detection than in

569 marine systems but the tag size still limits the size of fish that can be studied (Gibson et al. 2015;

570 Hanssen 2020). Telemetry data can predominantly be derived from fish but interactions with

571 other species such as ducks (Nummi et al. 2016), crayfishes (Whitledge and Rabeni 1997), semi-

572 aquatic mustelids, turtles, frogs, or alligators are also certain to be important and some of these

573 species could be tagged as part of a broad community study. Investigating movement responses

574 of fish to experimental manipulations such as nutrient subsidy (e.g. Pace et al. 2004),

575 introduction of novel species (Byström et al. 1998), change in water quality (e.g. temperature,

576 clarity, pH) can then be used to establish mechanisms explaining movements observed in

577 telemetry data. Replicated experimental designs will be critical to establish causality and

578 determine whether movement phenotypes drive ecosystem services or whether characteristics of

579 the ecosystem shape the movements of animals that reside within.

580

581 How Much Does the Physical Environment Influence Movement?

582

583   Ecologists are continually searching for fundamental patterns of movement that are

584 predictable across organisms and scales (Sims et al. 2008). One encompassing pattern deals with

585 how much an environment influences movement patterns, and whether collected trajectories are

586 representative of an animal's full potential for movement (Austin et al. 2004; Bastille-Rousseau

587 et al. 2018; Brodie et al. 2018). Movement data for such comparative problems are typically

588 collected from a wide range of environments that are often assumed comparable rather than

589 explicitly tested. These limitations are an artefact of early movement tracking technologies and

590   their relatively small sample sizes, while contemporary technology allows for greater scalability

591   and replication. Many of the largest lakes on the planet have previously or currently contained

592   extensive tracking networks, suggesting that the gap between technology and scale-appropriate

593   studies closes by the day. But there is ample room to investigate ecological phenomena at

594   smaller scales that encompass a greater diversity of lake types and ages and thus physical

595   environments (Jackson et al. 2001). Such a broad variety of smaller and usually self-contained

596   ecosystems gives researchers the ability to perform either observational or experimental studies.

597   The field of limnology consistently takes full advantage of small lake attributes to investigate

598   fundamental patterns of abiotic interactions (e.g., biological, chemical, and physical). The

599   morphometry of smaller lakes can range from simple gradual depressions with circular

600   boundaries to complex depth profiles with asymmetrical boundaries. Depending on where a lake

601   is located will affect how its morphometry limits utilization of light and thus thermal input and

602   stratification. There are many other physical environment modifiers (e.g., wind, geothermal,

603   underwater springs) that can also be influenced by location and have the potential to affect fish

604   movement. Uncovering how the physical environment influences organismal movement across

605   and within gradients of change (e.g., aging, disturbances) is another avenue to consider that is

606   also understudied. In summary, lakes can provide the necessary scalability to investigate the

607   relations between physical environment and movement, through both observational and

608   experimental means in stable or dynamic contexts.

609   There are relatively few lake studies that specifically examine the physical environment

610   using telemetry and even fewer that study multiple lakes simultaneously. Often, studies will

611   characterize an entire lake's physical environment (e.g., temperature, light) with relatively coarse

612   sampling resolution, either spatially or temporally. Yet, lakes are perfect arenas for detailed fine-

613   scale sampling of processes that cannot easily be detected in the vast marine environment.

614   Gerking (1959) described the variability of individual fish movement behaviour as an association

615   between an individual and its surroundings that is informed by sensory stimuli and driven by

616   recognition of familiar areas. A more modern perspective also suggests that physical

617   environments often contain recognizable landmarks so fish can learn and generate spatial maps

618   (Braithwaite and De Perera 2006). What is not clear is what drives shifts in fish home ranges,

619   which stimuli inform movements more than others, and how to respond to changes – all as a

620   function of their physical environment. At a coarse scale, studies have shown that fish can

621   consistently find the same food patches, discriminate among habitats using multiple cues, and

622   optimize foraging strategies in heterogeneous physical environments (Braithwaite 2006; Huijbers

623   et al. 2012; Nyboer and Chapman 2013). Interestingly, when multiple connected lakes are

624   considered, fish dispersal seems to be more affected by spatial distribution of lakes, number of

625   connections, and suitability of corridors as opposed to local environmental factors (Olden et al.

626   2001; Beisner et al. 2006). At a finer scale, studies have shown that lake morphology (simple

627   basin vs. complex) can influence habitat use, spatial distribution, and activity (Radabaugh et al.

628   2010). Furthermore, lakes with stratification can influence vertical movement patterns (Nowak

629   and Quinn 2002; Gorman et al. 2019). As understanding of individual lakes and their physical

630   characteristics continues to grow so will the opportunities to link such phenomena with fish

631   movement ecology.

632   Lakes are ideal for revealing relationships between the physical environment and animal

633   movement particularly when considering using multiple lakes simultaneously. There are

634   unlimited ways to design movement studies using lakes but to disentangle the physical

635   environment from organismal movement we suggest the following possibilities. Our

636 recommendations consist of four different types of studies 1) before and after, 2) gradients

637 (longitudinal or latitudinal), 3) replicated, and 4) stable vs. dynamic comparison. Before and

638 after style studies can take a lake or multiple lakes monitored before and after some ecological

639 phenomenon, alteration in lake morphology or physical change occurs but the sample unit is the

640 lake (e.g., some lakes are controlled while others represent treatments). The second is the same

641 but the sample unit is the lake in a nested design (e.g., the lake is subdivided with an

642 impermeable barrier). Often, these studies emphasize on using lakes with similar physical

643 characteristics and are in close proximity of one another. Longitudinal and latitudinal gradients

644 are simply studies where lake choice is spread along a coordinate axis (e.g., north-south, east-

645 west) so variations of light and thermal regimes can be incorporated. These studies are

646 characterized by long distances between study areas where each lake is arranged at the furthest

647 and opposite edges of the study organism's species distribution. For example, one lake in this

648 study may be affected by ice coverage in winter while another lake in the study has year-round

649 open water. Additionally, gradients along elevations are also possible. The third recommendation

650 is focused on lakes where anthropogenic activity manipulates the physical environment

651 intermittently or frequently to introduce altered physical environments. Examples of alterations

652 include but are not limited to different forms of pollution (e.g light, sound), boating traffic and

653 shipping, habitat modification (e.g., aeration, weed removal, shoreline development, heat

654 affluent). Comparing the differences between altered and unaltered environments is particularly

655 suitable for urban environments. Alternative disturbances could be drought and severe water

656 level decrease, prolonged ice coverage and increased ice thickness, hypoxic events driven by

657 algal blooms, and introduction of an invasive species that specifically modifies the physical

658 environment. Overall, all the recommendations here only scratch the surface of possibilities but

29

659 provide a template for an unexplored research area that can be enhanced with other experimental

660 design techniques such as transplanting fish and manipulating physical environments.

661

662 <u>How Will Climate Change Impact Animal Movements?</u>

663

664 Climate change is a ubiquitous process affecting all ecosystems and one of the major

665 drivers of species extinctions (IPBES 2019; Urban 2015). In response to climatic change,

666 geographic range and distribution shifts have been observed in a number of species (Sunday et

667 al. 2012; Last et al. 2011). Ectotherms are particularly sensitive to environmental temperature

668 extremes (Porter and Gates 1969), explaining the conformity found between their latitudinal

669 ranges and thermal tolerance (Sunday et al. 2012). In freshwater teleosts, moving away and

670 dispersing to find a more suitable environment, matching with their own biological constraints, is

671 indeed commonly observed in response to climatic change (Comte et al. 2013), with a general

672 tendency of range contractions at warm range edges and shifts to higher altitudes or latitudes

673 (Sunday et al. 2012). However, animals are constrained by system boundaries with limited

674 opportunities to disperse and relying upon alternative strategies to cope with climate change

675 (Comte and Olden 2017). This is especially true for lake teleosts, for which climate-induced

676 changes of lake properties and phenology, such as catchment hydrology, lake ice phenology,

677 thermal characteristics, nutrient supply and cycling, primary production, and bacterial blooms

678 (George 2010) can create challenging conditions for their development and survival.

679 Additionally, climatic effects often coincide with other anthropogenic stressors affecting lake

680 ecosystems such as eutrophication, pollution, biological invasions, habitat degradation, and

681 direct exploitation of organisms (Carpenter et al. 2011; Harrod 2015).

682   Beyond distribution shifts, teleosts strongly rely on their phenotypic plasticity, i.e. ability

683   to adjust their behavior and physiology, to cope with new climatic regimes and associated

684   ecosystem changes (for a general review see Beever et al. 2017), in particular under a rapid

685   climate change that is limiting the capacity for evolutionary adaptation (Van Buskirk 2012).

686   Changes in the abiotic environment can directly affect the metabolic processes of fish, more

687   specifically, increasing water temperatures increases metabolic rates leading to an overall

688   increase in the demand for energy (Fry 1969). Fishes can acclimate to warming conditions by

689   metabolic thermal compensation of resting cardiorespiratory functions (Sandblom et al. 2016).

690   Metabolic plasticity and thermal compensation to extreme temperatures carries implications on

691   performance and fitness-related traits, such as cognition (Závorka et al. 2020) or predation rates

692   (Sentis et al. 2015), although the extent to which thermal plasticity affects animals in the wild is

693   largely unknown. In addition to physiological adjustments, fish can adjust their habitat use and

694   activity patterns to avoid additional energetic costs of sub-optimal environments. To escape from

695   warming waters in summer, fish exhibit behavioural thermoregulation (Snucins and Gunn 1995).

696   Alternatively, fish may also reduce energetically costly behaviours and overall activity when

697   environmental temperatures exceed their thermal optimum. Water temperature also drives

698   spawning migrations, with inter-annual variations of water temperature affecting their timing

699   (Tao et al. 2017; Krabbenhoft et al. 2014) but also the propensity of migrations among partial

700   migrants (Brönmark et al. 2010; Brodersen et al. 2011). Finally, climate change is not restricted

701   to changes in temperature, and alterations of other physico-chemical water properties can be

702   expected to challenge the survival and persistence of lake teleost fish, such as levels of dissolved

703   oxygen, pH, and load of dissolved and particulate organic matter (Lennox et al. 2020). Further,

704   changes in general energy fluxes, habitat use and phenology in fish will also impact interactions

705 within and among species, such as prey-predator interactions and the spread of invasive species,

706 possibly inducing feedback effects on ecosystem functioning by affecting lower trophic levels

707 and nutrient cycling (see section on the Ecosystem Role of Marine Megafauna) and ultimately

708 causing regime shifts (Carpenter 2003, Brönmark et al. 2010). Research shows for instance that

709 changes in hydrology and temperature will favour the spread of warm-affinity and temperature

710 tolerant species (Rooke et al. 2017, Bae et al. 2018).

711   Under the strong influence of terrestrial and atmospheric inputs, freshwater ecosystems

712 are sensitive to climatic changes (Dudgeon et al. 2006) and considered the sentinels of global

713 climate change (Woodward et al. 2010). Small lake systems could therefore serve as sentinels of

714 the risk associated with climate change and provide unique information on the capacities of

715 ectotherms to adjust and adapt to changing environments. Plastic changes of labile phenotypic

716 traits being the first line of action to changing environmental conditions (Beever et al. 2017),

717 fine-scale animal tracking in small whole-lake systems can provide a window into plastic

718 responses of animals and their capacity for adaptation, but also an alert system predicting the

719 effects of climate change on natural populations and ecosystems. We therefore suggest multi-

720 species tracking in replicated whole-lake systems along a latitudinal gradient covering the

721 geographic range of sentinel teleost species. The study of animal movements in whole-lake

722 systems in combination with the bio-logging of key physiological functions (*e.g.* accelerometer

723 and heart-rate loggers – see section on Physiology) will inform us on the behavioural and

724 physiological adjustments to changing environments before the effects on lifetime fitness and

725 patterns of natural selection and evolutionary change become evident. Given the difficulty to

726 measure effects of climate change over relatively brief timescales inherent to single-lake

727 telemetry studies, such studies could be replicated and carried out along climate gradients

728 following a Space-for-Time Substitution SFTS approach that can provide novel insights on the

729 effects of climate change on wildlife (Meerhoff et al. 2012). Such an approach could also be

730 complemented by manipulative studies in relatively small mesocosm or pond systems to test

731 specific climatic scenarios (Stewart et al. 2013), which would further contribute to our

732 understanding of the plastic and adaptive responses of teleosts to climate change.

733

734 How Can Risks, Consequences and Benefits of Biologging at the Level of Individuals and

735 Populations Be Evaluated?

736

737   Fish are widely used animal models in research and are a frequent subject of telemetry

738 research; consequently, increasing attention is paid to the tagging protocols (Zahl et al. 2012;

739 Cooke et al. 2016; Breine et al. 2017; Gerber et al. 2019). Evaluations and testing address all

740 stages from capture to release (Thiem et al. 2011) and even post-tagging evaluation (Gerber et al.

741 2017; Vollset et al. 2020). Evidence of pain perception by fish suggests that caution must be

742 devoted to these tagging procedures (Brown 2015) that can impair their welfare and introduce

743 bias in experiments when data reflect distressed, injured, or otherwise inauthentic movements. It

744 is therefore of utmost importance to ensure that best surgical practices are being used (Brown et

745 al. 2011). As such, numerous studies on the effects of analgesics, substances dedicated to reduce

746 or suppress the pain sensation, have been conducted on fish (e.g. Mettam et al. 2011; Zahl et al.

747 2012; Chatigny et al. 2017; Rozynski et al. 2018) and recently reviewed by Chatigny et al.

748 (2018). Previously, the impact of the tag size and weight relative to fish weight had also been

749 debated (Winter, 1983; Brown et al. 1999; Jepsen et al. 2005; Snobl et al. 2015). To determine

750 the limits and avoid negative effects on the behaviour, the 2% limit (tag weight over fish weight

751   in the air) from Winter (1983) was adopted as a general rule for a long time. The handling of fish

752   and implantation of transmitters on or into fish inevitably raises the question of tagging effects

753   (Cooke et al. 2013). It is especially challenging to study this for aquatic animals in the wild

754   because visual observations are often impractical and complex (Rub et al. 2014) and it is almost

755   impossible to gather data on fish behaviour without handling and/or biologging. Most studies

756   have been conducted in laboratories but these can underestimate tagging effects as fish do not

757   have to cope with natural stressors (Rub et al. 2014). Jepsen et al. (2015) reviewed the effects of

758   external electronic tags on fish and listed the following that have been addressed in the literature:

759   retention/expulsion, survival, infections/wounds/tissue reactions/healing, general

760   behaviour/activity, swimming performance, feeding, growth, migration, equilibrium,

761   physiological effects, buoyancy, predation, catchability, social interactions, reproduction, and

762   responses to transmitter output.

763   There are a growing number of laboratory-based studies that evaluate various aspects of

764   the surgical implantation of electronic tags (reviewed in Cooke et al. 2011). For example, Brown

765   et al. (1999) tested the impact of tag weight on swimming performance of juvenile rainbow trout

766   implanted with radio transmitters in a Blazka type chamber (Smith & Newcomb, 1970): the

767   swimming performance was not altered up to tags representing 6-12% of the body weight, but

768   changes in behaviour have not been evaluated. Wagner & Stevens (2000) tested the effect of

769   intra-peritoneal transmitters and sutures on swimming behaviour (number of C-turns and sprints,

770   total distance travelled) of rainbow trout three weeks after surgery. Control fish were also

771   anaesthetized and handled but did not undergo surgery, which apparently had no effects on

772   behaviour. Newby et al. (2007) showed in chambers that PIT tagging had no short-term effects

773   on the feeding behavior of juvenile rainbow trout. They also tested their swimming performance

34

774   (time to fatigue) by comparing a pool of individuals tagged 40 days before the experiment, for

775   which the wound had healed, with another group tagged on the day of the experiment; they

776   found no significant differences. Harms et al. (2005) tested the effects of analgesics on koi

777   (*Cyprinus rubrofuscus*), both on behaviour in tanks and on clinical changes. Except for one of

778   the applied analgesics, all fish that had surgery showed reduced activity, deeper position in the

779   water column, and decreased feeding activity; they also exhibited clinical pathology changes. In

780   the field, Wilson et al. (2017) compared downstream spawning movement of walleye tagged in a

781   given season to individuals tagged in previous years in lakes. Fish tagged in a given season

782   travelled slower downstream from the river spawning sites. Jepsen (2003) provided evidence that

783   growth and survival of radio-tagged pikeperch was not altered over the long-term. Handling is

784   also part of the tagging process. Baktoft et al. (2013) concluded that pike handling had only a

785   transitory effect on the activity level and this effect was not detectable 48h post-release.

786   In the future, we expect that technological advances in transmitter miniaturization (e.g. Li

787   et al. 2015; Lu et al. 2016; Nishiumi et al. 2018) and injectability (Li et al. 2015) will diminish

788   both risks and impacts associated with tagging. Addressing issues with tag expulsion will also be

789   important to improve resolution of fates. Nevertheless, the greatest care must be devoted to

790   tagging protocols and fish welfare in order to reduce to the largest extent possible the tagging

791   effects and ensure reliable results from experiments. Moreover, attention should be paid to short-

792   term impacts of tagging, by comparing behaviours in the days following the release to later

793   periods when the wound has healed; longer-term effects can also be tackled by comparing fish

794   tagged over longer periods. This is not a perfect solution because it assumes that the control

795   tagged fish are not impacted by tagging, but it may still be a good compromise where untagged

796   fish cannot be tracked reliably. Ultimately, the benefits of telemetry studies must be weighed

797   against the potential costs, emphasizing the importance of fish welfare by mitigating negative

798   effects and refining handling protocols for optimal research validity.

799

800   <u>How Do We Integrate Physiological Context into Tagging Studies to Gain a More Synoptic</u>

801   <u>P</u>icture of Movement and Behaviour?

802

803   Effective species management requires detailed knowledge of focal species' movements

804   and patterns of habitat use (Cooke 2008; Crossin et al. 2017). Biotelemetry and biologging are

805   powerful tools in this regard, permitting the construction of models assessing population and

806   community-level processes from information gleaned from individual animals (Cooke et al.

807   2016b; Costa et al. 2012). However, accurately predicting the response of animal populations to

808   environmental change (Last et al. 2011) requires mechanistic links between the environment and

809   population-level processes (Jørgensen et al. 2012; Peck et al. 2018; Seebacher and Franklin

810   2012; Teal et al. 2018). Individual-level processes are governed by physiological responses to

811   environmental conditions determining individual fitness and performance (Cooke et al. 2014;

812   Horodysky et al. 2015). In fish, much of the work deriving physiological links between the

813   environment and population-level processes applies the frameworks of metabolic/aerobic scope

814   (AS), or dynamic energy budgets (DEB; Cucco et al. 2012; Mangano et al. 2019; Teal et al.

815   2018). AS and DEB approaches rely on compartmentalising different physiological processes

816   within budgets determined by the capacity of an organism to supply the required oxygen and/or

817   energy, to fuel those processes. In both cases, elevated metabolic costs associated with persisting

818   in energetically demanding (McElroy et al. 2012) or otherwise suboptimal environmental

819   conditions can reduce resources available for other processes, reducing fitness. Environmental

820   modulation of basal metabolic costs could therefore drive patterns of movement and habitat

821   selection in fish as individuals select habitats where metabolic scope and scope for activity are

822   maximised (Holt and Jørgensen 2015), or otherwise avoid engaging in energetically costly

823   behaviours in conditions where metabolic budgets are reduced (Sims et al. 2006; Whitlock et al.

824   2015). Both AS and DEB approaches linking physiology with population level processes often

825   rely on the results of laboratory experiments, and so suffer from the difficulty of transferring

826   these findings to wild animals in natural environments. There is a paucity of information

827   regarding the ecological consequences of intraspecific variation in physiological traits, how

828   changes in the physiological status of fish influence the relative importance of environmental

829   conditions in determining fitness, and how behavioural responses to environmental stress may

830   modulate their impact. While many physiological measurements and biomarkers are currently

831   restricted to quantification under lab conditions, advances in biologging and biotelemetry allow

832   us to better understand the ecological relevance of these biomarkers, and even measure them in

833   free swimming fish (Cooke et al. 2016a; Metcalfe et al. 2016; Treberg et al. 2016).

834   Complete coverage of lakes by high-resolution acoustic telemetry arrays allows

835   continuous monitoring of fish at the fine spatiotemporal scales (Baktoft et al. 2016) required to

836   identify rapid or infrequent behaviours which contribute significantly to metabolic demand

837   (Brownscombe et al. 2014; Jørgensen et al. 2012). Lakes also restrict the dispersal of fish,

838   maximising opportunities for retrieval of biologgers (Cooke et al. 2016a) and facilitating

839   repeated measures of physiological traits in recaptured wild fish (Norin et al. 2011). Multi-sensor

840   approaches for monitoring the environment, physiological state, and movement of fish provide

841   direct indications of the role of physiological processes in determining patterns of movement and

842   behaviour. Lucas et al. (1991) recorded heart rate and fish position alongside environmental

843　temperatures to estimate metabolic rates in free swimming pike (*Esox lucius*), and partition the

844　metabolic costs incurred by activity, digestion, and water temperature. The majority of work

845　incorporating physiology into fish movement studies has been conducted in non-lake

846　environments, but used approaches readily applicable to lake systems. Brownscombe et al.

847　(2017, 2019) calibrated accelerometer-derived measures of activity with metabolic demand in

848　bonefish (*Albula vulpes*) using swim-tunnel respirometry, and subsequently monitored fish

849　energy expenditure across habitat types and environmental gradients, whereas Slavik et al.

850　(2014) were able to assess the energetic costs associated with specific patterns of space use in

851　catfish (*Silurus glanis*) using a combination of positional and electro-myocardiogram (EMG)

852　telemetry. Data loggers concurrently recording heart rate, temperature and acceleration (e.g. DST

853　centi-HRT ACT logger, Star-Oddi) implanted in fish alongside an acoustic transmitter would

854　allow simultaneous estimates of fish position, activity, heart rate, and ambient temperature

855　within a telemetry array. Multisensor approaches such as this have been successfully employed

856　to record physiological and behavioural stress responses in response to seismic air gun noise in

857　Atlantic cod (Davidsen et al. 2019). Laboratory calibration of sensor outputs with measures of

858　energetic demand would strengthen these approaches further. Comparing patterns of movement

859　in the wild to lab-derived physiological traits measured in focal fish is an alternative way to

860　incorporate a physiological context in fish telemetry studies. Baktoft et al. (2016) implemented a

861　combination of lab-based respirometry and high-resolution acoustic telemetry to investigate links

862　among phenotypic variation in metabolic rate and swimming activity in wild perch (*Perca*

863　*fluviatilis*). No relationships between traits were found, providing evidence that links among

864　physiology and patterns of movement may not manifest as predictively as some theoretical

865   frameworks proclaim (e.g. Pörtner, 2010), and this work remains one of the few attempts to test

866   the relevance of such concepts in the wild.

867   Whereas metabolic traits are relevant to the study of animal movement, and standardised

868   approaches to their measurement improve comparability among systems (Chabot et al. 2016),

869   there are alternative physiological traits that can be measured. For example, testing the resilience

870   of individual fish to environmental extremes in laboratory conditions (Morgan et al. 2018), and

871   subsequently monitoring their movements and behaviour across environmental gradients in the

872   wild could contextualise the role of physiological performance constraints in shaping habitat use.

873   Relevant physiological biomarkers may also be provided by tissue and blood sampling but have

874   yet to be incorporated into animal movement studies. For example, enzyme activities (e.g. citrate

875   synthase, lactate dehydrogenase) in metabolically important tissues such as the heart or liver can

876   provide indications of fish's aerobic and anaerobic metabolic capacities (Norin and Malte 2012),

877   and so may be relevant for determining how fish utilise habitats with differing oxygen

878   availability. Similarly, traits related to stress-responsiveness (e.g. circulating levels of

879   catecholamines and corticosteroids after a stress event) have been found to correlate with levels

880   of activity in free swimming fish (Koeck et al. 2018), and so may also be involved in shaping

881   patterns of movement in the wild. Recent developments in stable isotope analysis now also

882   permit the back-calculation of metabolic rates experienced by free swimming fish using otoliths

883   (Chung et al. 2019), which could also provide a physiological perspective on fish movement

884   when combined with telemetry data. Fish telemetry and biologging can also be used to

885   empirically test assumptions and predictions of physiological frameworks of animal movement.

886   For example, Gannon et al. (2014) tested predictions of performance limited biogeography of

887   dusky flathead (*Platycephalus fuscus*) by recording patterns of fish activity alongside

888   environmental temperature via acoustic accelerometry. Flathead activity data approximated a

889   thermal performance curve, and extrapolated estimates of zero activity were found to correspond

890   to minimal and maximal water temperatures experienced by flathead at their latitudinal extremes.

891   Examining fish tracking data in the context of physiological mechanisms in this way can

892   therefore be a powerful approach to incorporating physiological context into telemetry studies

893   where practical constraints prevent collection of physiological data on focal fish species.

894

895   <u>What Are the Major Drivers of Long-Distance Movements?</u>

896

897   Potadromous fishes migrate between natal and feeding areas entirely within freshwater

898   and, although relatively shorter, these movements may be just as important for survival, growth,

899   and reproduction as the migrations of oceanadromous or diadromous species (Tamario et al.

900   2019). Regardless of the type and size of the waterbody, there are several known internal (sex,

901   life stage, size, condition, species) and external factors (water level, flow, temperature, salinity,

902   dissolved oxygen) known to drive the long-distance movements in fish (Nathan et al. 2008;

903   Tamario et al. 2019). The internal drivers are measurable in fish across all systems, however, the

904   environmental factors are much more difficult to measure in a large open-water system. For

905   example, water temperature is repeatedly identified as a driver of movement, often to exploit

906   some form of patchy food resource or to obtain a bioenergetic advantage (Sims et al. 2001;

907   Edwards and Richardson, 2004; Perry et al. 2005). For oceanic migrations, sea surface

908   temperature obtained from satellites and in-situ buoys are often correlated with animal

909   movement (Neumann 2001), however, this provides very little information about the subsurface

910   temperatures that the fish are experiencing.

911   Telemetry studies on these lentic inland systems are common. Given their scale (relative

912   to open ocean systems), scientists are often able to track large numbers of fish from one end of

913   the waterbody to the other. Moreover, because water flows downstream, most lakes have various

914   tributaries or are otherwise interconnected, providing opportunities to study migrations of

915   various forms that are not unlike the types of migrations observed in open ocean systems or

916   between oceans, estuaries and inland systems. Because inland systems are smaller, it is often

917   possible to obtain much more information on environmental drivers of movements. In some

918   cases, it may even be possible to recapture fish several times, which allows one to assess how

919   aspects of organismal physiology relate to space use and movement. Several common themes

920   have emerged from studies of freshwater long-distance movements that have relevance to

921   understanding similar phenomena at ocean scales. For example, Raby et al. (2018) used whole-

922   lake telemetry in the Lake Erie to identify that while movements were directly related to

923   behavioural thermoregulation, walleye that travelled ~100km further east experienced similar

924   temperatures and therefore, potential foraging opportunities could have driven the longer

925   migration distances. Some movements, especially those related to reproduction or overwintering

926   are often triggered by a very specific water temperature. For example, a study of maturing adult

927   sockeye salmon revealed specific temperatures when fish moved onto spawning grounds (Newell

928   and Quinn 2005). Yet, the cues can be much more diverse. Given dramatic seasonal influence in

929   freshwater systems, changes in daylight with changing season can influence fish movements

930   (Baldwin et al. 2002). In more fluvial systems, flows can trigger movements and are often

931   responsible for enticing fish to move upstream from lakes into tributaries to reproduce (e.g.,

932   Hayden et al. 2014). Tides are not relevant in freshwater systems but it is not uncommon to study

933   water drawdowns on fish movement in lakes/reservoirs (e.g., Bergersen et al. 1993) or fish

934 responses to seiche events (Jill Brooks, Unpublished Data) which could both be relevant to

935 understanding fish movements in marine systems. In some cases, fish in freshwater lakes have

936 been observed to undertake diel bank migrations (e.g., Cott et al. 2015) not unlike what would be

937 observed in marine systems during intense tides. Endocrine and other physiological triggers for

938 migration have been studied in a number of freshwater systems. For example, Shaw et al. (2013)

939 tagged lake sturgeon with telemetry transmitters and collected blood samples to assess

940 reproductive status. That analysis enabled the researchers to establish the endocrine

941 characteristics associated with different levels of movement.

942   Environmental conditions that may drive long-distance movements of aquatic animals are

943 difficult to measure at fine spatial resolution. Aquatic loggers are often placed in grids or lines,

944 ideally in three dimensions to sample profiles of temperature, salinity, oxygen, light penetration,

945 water density, current, and other hydrological parameters that fluctuate spatially and temporally

946 in a system. Habitat mapping may be efficient to understand how substrate, depth, and flow in an

947 area dictate the presence/absence of animals. However, the temporal extent of these

948 measurements will dictate their efficiency. Macrophyte cover will vary seasonally and changes

949 in water chemistry can change on short time scales, especially where point-source pollutants are

950 present. Investigators using telemetry should be aware of how changes in water temperature,

951 density, salinity, gas saturation, plant biomass, and other factors will affect the detection

952 probability and the ability to confidently resolve presence or absence of animals at a given

953 location at a specific time. Biological properties such as plankton or fish larvae can be sampled

954 by hydroacoustic monitors, which can provide context about prey biomass in an area to be linked

955 to the arrival/departure of fish based on detections on acoustic arrays. For long-distance

956 migrations of freshwater fish, it has been shown that grid arrays are more efficient and

957   statistically robust than line arrays for tracking seasonal movements and yielding data that are

958   useful for testing hypotheses about long-distance movements (Kraus et al. 2018).

959

960   <u>How Does Predation Risk Influence Movement Strategies?</u>

961

962   From an evolutionary perspective, individual fish should strive to maximize their fitness.

963   This implies acquiring resources (energy, material) needed for growth, maturation, and

964   reproduction, but also surviving until successful reproduction (or in some cases helping kin

965   survive reproduction; e.g. killer whale, *Orcinus orca*). The optimal foraging theory (OFT)

966   predicts that animals should maximize their energy intake rate (Pyke 1984). OFT may help

967   explain prey choice, when to leave a foraging patch, etc., but it does not account for risk effects.

968   Typically, there is a positive correlation between foraging modes and predation risk. Aiming for

969   foraging success often involves a lower survival probability, whereas aiming for a high survival

970   probability (in terms of avoiding predation) is associated with a reduction in foraging potential.

971   Animals tend to behave according to certain strategies, where foraging gain to a smaller or larger

972   degree is traded off for reduced predation risk. Because predation risk and characters influencing

973   foraging potentials change with body size for a growing individual, the optimal strategy may be

974   stage-dependent and change with ontogenetic development or during periods of starvation (Lima

975   & Bednekoff 1999). Understanding these strategies is key to understanding ecology, life-history

976   tactics, and evolution. In broad terms, fish can manage predation risk in multiple ways, including

977   1) reducing activity or visits to risky habitats, 2) seeking shelter among conspecifics (i.e.,

978   shoaling, schooling), 3) seeking shelter among structures (macrophytes, stones etc.), and 4)

979   seeking shelter in the darkness of the deeper waters. Minimizing the ratio between predation risk

980   and foraging gain (μ/g) is one well-known example of such strategies, first described for the

981   optimal habitat choice of bluegill sunfish (*Lepomis macrochirus*) and for optimal size for

982   metamorphosis in tadpoles (Werner & Gilliam 1983, 1984). Later, minimizing μ/g was used to

983   explain diel vertical migration in sockeye salmon (*Oncorhynchus nerka*; the antipredator window

984   hypothesis; Clark & Levy 1988, Scheuerell & Schindler 2003) as well as other planktivorous fish

985   and zooplankton (e.g. Gjelland et al. 2009), where planktivorous fish feed in the plankton-rich

986   epilimnion from dusk till dawn when predation risk from visual predators is low.

987   Synchronization among individuals can provide protection through predator swamping, i.e.

988   predation risk is reduced because the predator(s) is full, and/or the predator gets confused by the

989   synchronised behaviour of schooling individuals (e.g. Barber et al. 2000). Moreover, parasite

990   infection may have profound effects on the behaviour of an individual, altering its susceptibility

991   to predation (Barber et al. 2000).

992   Altered predation pressure, either through changes in native predator densities, or through

993   introductions of novel predators, may have direct population effects on prey fish through

994   consumption, but the non-consumptive effects mediated through altered behaviour of prey may

995   be as strong (Lima 1998, Dill et al. 2003, Kohl et al. 2018) and may also lead to trait-mediated

996   effects on other species (Peacor & Werner 2001). Understanding these interactions is important

997   from a management point of view. As an example, fish density in lakes is typically sampled as

998   catch per unit of effort in fishing nets, but is a reduction in catches caused by truly reduced

999   densities, by different activity or habitat use related to temperature, or by reduced activity levels

1000   or changed habitat use as a response to increased predation risk? Moreover, predator-induced

1001   changes in behaviour may also change life history tactics, and ultimately lead to evolutionary

1002   changes such as speciation or hybridization.

1003   Lakes are ideal ecosystems to study the arms race driving predator and prey movement

1004   strategies. Regardless of size, lakes are defined by physical boundaries and especially smaller

1005   lakes can be considered as relatively closed systems. Small and moderate-sized lakes (up to a

1006   few km^2 area) may be fully covered by acoustic tracking systems and, if instrumented with

1007   acoustic hydrophone arrays, act as upscaled field versions of video surveyed laboratory

1008   aquariums (Figure 2). Small to medium-sized experimental ponds may also be controlled and

1009   manipulated, and much easier replicated than lakes. By tracking both predator and prey species

1010   in such systems, experimental ponds can facilitate experimentally designed single or multi-

1011   species fish communities (including multiple trophic levels) in a replicate manner, preferably

1012   with a before-after control-impact (BACI) design when possible. Examples include introduction

1013   of predators (native, neonative or invasive) to otherwise predator-void systems, removal of

1014   predators, effects of chemical and visual cues of predators, effect of habitat complexity. Through

1015   such designed experiments, underlying mechanisms of the intricate interactions between predator

1016   and prey behaviour can be studied, tested, and established. Furthermore, combining such

1017   experiments with other manipulations such as contamination by anthropogenic compounds or

1018   inoculation with pathogens should make it possible to reveal interactions. This is an important

1019   field of research, considering that there is little knowledge for aquatic animals, whereas the

1020   pressure from local, regional and global environmental contaminants and pathogens is to a large

1021   extent ever increasing.

1022

1023   What Areas Can Be Considered Hotspots for Multiple Species on a Global Scale?

1024

1025   Freshwater ecosystems represent biodiversity and conservation hotspots (Strayer and

1026   Dudgeon 2010). Biodiversity hotspots represent assemblages of multiple species and therefore

1027   require investigation of representatives of multiple trophic scales. Fishes in lake ecosystems

1028   represent suitable study objects in this respect, because they span the whole trophic scale, from

1029   primary consumers to top predators. Studies focused on freshwater fish diversity, community

1030   structure, and distribution rely mostly on lethal or harmful sampling methods, such as fishing

1031   nets, traps and electrofishing (Kubečka et al. 2012, Oliveira et al. 2012). However, these methods

1032   are inadequate to investigate whole fish community dynamics at a finer scale. While this led to

1033   proposals for the use of combined multiple sampling methods to better describe the fish

1034   community in lakes and reservoirs (Kubečka et al. 2009), such approaches are costly and still not

1035   able to capture the dynamics of fish populations at a high spatio-temporal resolution. The

1036   integration of novel tools with traditional methods seems to be the best approach to understand

1037   the fish community dynamics (Cooke et al. 2016) and the hotspots for lake biodiversity on a

1038   global level. While the global pattern of biodiversity hotspots is that the most diverse

1039   communities are found at lower latitudes, lakes are unevenly distributed, with higher lake density

1040   at higher latitudes (Verpoorter et al. 2014). Consequently, lakes do not necessarily follow the

1041   same biodiversity richness patterns as other aquatic environments. As a result, distribution

1042   patterns of fishes in lakes provides a unique perspective to understand the relationship between

1043   animal distribution patterns and latitudinal patterns in global biodiversity distribution.

1044   Acoustic telemetry can provide insight in fish community distribution by identifying the

1045   most frequently used areas of the lake through time by different fish species (Figure 2). One of

1046   the advantages of telemetry over traditional sampling methods is the possibility to operate well in

1047   less accessible terrains, such as shallow zones and deep or highly structured areas of lakes.

46

1048 Telemetry combined with environmental monitoring can provide detailed information on habitat

1049 preferences of different fish species, especially on critical habitats such as spawning, feeding,

1050 and nursery grounds, which tend to be species-specific and temporally dynamic (e.g. Bégout

1051 Anras et al. 1999, Ehresmann et al. 2018, Hahn et al. 2019). Such data allows the development of

1052 detailed maps of critical habitats for multiple species through time in a given lake (Stehlik et al.

1053 2017), generating tools to improve the environmental management, such as the selection of areas

1054 within lakes that have specific characteristics that favor only target species, while inhibiting the

1055 proliferation of invasive species (McGowan et al. 2017, Rous et al. 2017). Due to the bounded

1056 nature of lakes, understanding the habitat preference, dynamics, and activity of different fish

1057 species is easier to accomplish than in open ecosystems such as the marine environment where

1058 animals are able to move beyond monitoring areas. Therefore, the knowledge gained in lakes can

1059 contribute to better understanding of species distribution and critical areas, which can be

1060 transposed to other types of ecosystems.

1061   One challenge when applying acoustic telemetry to assess distribution and habitat use of

1062 the whole fish community in an ecosystem is that it requires simultaneous tracking of all, or at

1063 least most, of the community members. Tracking multiple species is, however, costly, whereas

1064 the use of telemetry for some species is not possible due to overly small body size for transmitter

1065 implantation. In this respect, the advantage of lake ecosystems is that they can have a relatively

1066 small number of species than marine habitats, which makes it more affordable to conduct such

1067 studies in lakes. Furthermore, one potential way to resolve these obstacles would be to apply

1068 surrogate species concepts to fish telemetry, especially indicator and umbrella species concepts

1069 (Caro and Doherty 1999). Indicator species represent organisms whose characteristics can be

1070 used as an indication of particular ecosystem aspects that are too difficult to measure for other

1071 species, or by other methods (Caro and Doherty 1999; Hunter et al. 2016). The two most relevant

1072 types of indicator species in this respect are indicators of environmental health and biodiversity

1073 richness (Pearson 1994; Caro and Doherty 1999). Umbrella species are characterized by similar

1074 resource and habitat requirements as sympatric species, which makes management and

1075 protection measures directed at such species at the same time effective and supportive for other

1076 species (Caro 2010). Umbrella species concept has been applied in practice with mixed success,

1077 which mainly depends on the criteria used for umbrella species selection (Seddon and Leech

1078 2008; Branton and Richarson 2014). In this respect, whole-lake acoustic telemetry represents a

1079 suitable approach to test and develop this concept further. If applied properly, indicator and

1080 umbrella species concepts provide an opportunity to obtain valuable information by tracking

1081 movement of just a selected set of species. Due to considerably smaller diversity of fish

1082 assemblages in lakes than in fluvial and marine systems, the surrogate species concept is likely to

1083 be comparatively more efficient in lakes, being thus a feasible alternative to gather information

1084 on the community at substantially lower costs than in other aquatic environments.

1085

1086 How Do Anthropogenic Activities (e.g., Shipping, Fishing, and Water Management) Affect

1087 Movements?

1088

1089 　　　　The impact of human activities such as fishing, stocking, shipping, construction,

1090 extraction processes and pollution on fish is a major topic addressed by a wide range of scientific

1091 disciplines, including ecology, eco-toxicology and conservation. Population-level parameters

1092 such as recruitment, abundance and size-structure have often been regarded as ultimate endpoints

1093 in many impact studies (Allen & Hightower 2010), however attention has increasingly also been

1094   directed toward individual-level sub-lethal parameters such as behavior and movement (Crossin

1095   et al. 2017). Behavioural alterations following anthropogenic activities may potentially have

1096   severe long-term ecological effects, and lead to population decline and even extinction

1097   (Tuomainen & Candolin 2011). Until recently, studies evaluating impacts on behavior and

1098   movement have relied on traditional tag-recapture methods or low-resolution telemetry to collect

1099   data (Cooke et al. 2016). These methods often generate very sparse data, with large temporal

1100   gaps between observations, which limits the ability to evaluate impact at any detail. Moreover,

1101   technical challenges with tracking fish behavior across large spatial scales in the field have made

1102   laboratory studies the preferred method in many disciplines, e.g ecotoxicology. Here,

1103   behavioural effects seen in the lab are extrapolated to the field, often with little or no validation

1104   of the transferability of such effects between the one-dimensional laboratory environment and

1105   the often vastly complex natural systems (Hellström et al. 2016).

1106   The ability of acoustic telemetry to track fish with high spatial and temporal resolution

1107   across large areas promise exciting new opportunities to study the impact of anthropogenic

1108   activities on fish behavior. Lakes provide the perfect platform for such studies, because they

1109   have natural boundaries that contain the fish within the receiver/tracking array, in contrast to

1110   open systems such as oceans or rivers. Dense receiver networks can be used to fine-scale

1111   position fish over the entire lake for many months or years (Figure 2). This effectively closes the

1112   spatiotemporal gaps limiting earlier impact studies, and allows for very detailed investigations of

1113   behavioral effects at an unprecedented scale. Although still in its infancy, fine-scale tracking

1114   studies in lakes have already contributed significantly to our understanding of the behavioural

1115   impact of anthropogenic activities, such as recreational fishery, habitat degradation and damming

1116   (e.g Baktoft et al. 2013, Jellyman & Unwin 2019; Brooks et al. 2017)

1117   A clear example of how lake-studies in combination with fine-scale acoustic telemetry

1118   have advanced the way anthropogenic effects are evaluated is its use in field ecotoxicology.

1119   Chemical pollution has long been recognized as a major threat to aquatic ecosystems worldwide

1120   (Gilbert 2011, Depledge 2011). Many chemicals enter waterways via treated wastewater effluent

1121   (Kolpin et al. 2002, Brooks et al. 2005), or from production industries (Sanchez et al. 2011, Fick

1122   et al. 2009), and remain bioactive after they reach aquatic systems (Dietrich et al. 2002,

1123   Glassmeyer et al. 2005). Whereas much of the work on contaminants has focused on lethal

1124   effects associated with high chemical concentrations, lower concentrations can alter a diverse

1125   array of behaviors, including predator–prey interactions, mating and social behaviors (Clotfelter

1126   et al. 2004, Leduc et al. 2004, Zala 2004, Rohr et al. 2004, Fisher et al. 2006). Until now,

1127   studying behavioral effects of chemicals have been restricted to laboratory environments, and to

1128   what extent results generated by standardized lab experiments with low complexity can be

1129   translated to the real world has been debated (Klaminder et al. 2016; Saaristo et al. 2018).

1130   However, due to technological advances of acoustic telemetry we now have the tools to test and

1131   validate lab-based ecological risk assessment of chemical pollution in full lake studies

1132   (Hellström et al. 2016). The implementation of acoustic telemetry in risk-assessment using lakes

1133   as study units would have multiple benefits. First, it allows for testing if chemicals identified to

1134   invoke behavioral effects in the lab also do so in the real world (e.g. Klaminder et al. 2016).

1135   Second, it allows for the introduction of ecological endpoints that we are unable to study in the

1136   lab, e.g. home-range size and habitat choice. Third, large-scale studies also allow for realistic

1137   assessments of effects on interspecific interactions such as predation and competition, and how

1138   these effects affect life-history characters like growth, development and ultimately mortality. The

1139   monitoring of anthropogenic effects on behavioral traits using acoustic telemetry in lakes is a

1140   much needed innovation that will increase the ecological relevance, reliability and precision of

1141   ecological risk-assessment of different types of aquatic pollution (e.g. chemical, light, sound).

1142

1143   **Synthesis**

1144

1145   Hays et al. (2016) outlined questions specifically focused on marine megafaunal

1146   movement. We have interpreted them as canonical questions in movement ecology, where

1147   significant gains can be made by understanding processes and mechanisms that provide natural

1148   microcosms for biotic interactions. Although we propose study designs that could advance our

1149   understanding of fundamental principles of aquatic animal movement, these will of course be

1150   enhanced by having broad-scale studies of wide-ranging marine and terrestrial species as well.

1151   For example, studying major drivers of long-distance movements is an incredibly important

1152   frontier in improving our understanding of animal movement principles, and although partial

1153   answers can be ascertained from lakes, this question is inherently best suited to be studied in

1154   vast, unconstrained environments such as seas. Animals in lakes are range restricted and

1155   therefore it is possible to instrument entire basins. This has been demonstrated even across large

1156   areas such as Lake Erie, where a whole-lake telemetry array has been established to track fish

1157   movements basin-wide.

1158   Logging tags can be recovered by recapturing the tagged animal or by having a pop-off

1159   mechanism on the tag package that makes it recoverable. Raby et al. (2019) used such a pop-off

1160   package with depth and temperature sensors on Great Lakes salmonids to compare the niche of

1161   native lake trout (*Salvelinus namaycush*) and introduced chinook salmon (*Oncorhynchus*

1162   *tschychawa*). Lack of two-dimensional (latitude-longitude) data from this method, however, was

1163   identified as a limitation by the authors. Positioning of aquatic animals can be accomplished by

1164   Fastloc GPS tags that connect to satellites and relay information when animals break the surface

1165   (Dujon et al. 2014), by calculating Doppler shift from Argos satellites, or by light-based

1166   geolocators (see Harcourt et al. 2019). However, positioning of tags in space across small areas

1167   can be accomplished by acoustic telemetry. Transmitters fitted with pressure sensors can then be

1168   used to model three-dimensional space use using kernel smoothing methods, hidden Markov

1169   models, or network analysis to investigate the spatial distribution of the animals within

1170   environments such as lakes where there is sufficient spatial coverage of receivers to generate

1171   reliable animal presence data.

1172   Whole-lake studies are challenged by factors affecting detection distance and the

1173   probability that a tagged animal will be reliably detected. Environmental conditions can alter the

1174   detection radius of a receiver and synchronization tags or reliable range testing are necessary to

1175   accurately position animals. Marine environments are characterized by similar challenges in the

1176   form of boat noise, tidal streams and maelstroms, as well as biological noise from species such as

1177   shrimp. The largest lakes can encounter substantial boat noise but smaller lakes will be exposed

1178   to smaller crafts and slower motors. Hydropower facilities, however, can greatly influence the

1179   noise routine in a lake, and affect the detection distance of receivers, which may in turn influence

1180   position estimation. Phenomena such as gas supersaturation may also affect acoustic receiver

1181   detection radius.

1182   Many ecological phenomena are manifested at particular scales, which have to be

1183   matched by an appropriate study system scale to properly address a movement ecology question

1184   (Figure 1). Ponds and small lakes, where individuals can easily access the entire habitat and

1185   differentiated niches exist for only a small number of species, can easily be replicated and used

1186   as experimental units in studies requiring better control. Investigating mechanisms of fish

1187   movement may be optimal in relatively small natural systems where many individuals can be

1188   tracked at higher spatiotemporal resolution (Figure 2) than at larger systems, with fewer

1189   confounding factors, higher capacity to quantify the dynamics of relevant environmental factors,

1190   and greater potential for replications in a more experimental design. For example, this can

1191   include studies of responses to anthropogenic activities and predation risk, sensory information

1192   used for navigation, and the role of social interactions. Larger systems with more habitat

1193   heterogeneity and biodiversity are ideal systems for addressing questions requiring ecological

1194   realism. For example, questions about how climate change could impact fish movements, what

1195   habitat features create ecological hotspots, and drivers of complex long-distance movements

1196   require large, heterogeneous habitats to investigate fish movement. Larger systems may be more

1197   challenging to replicate because of the smaller degree of control that can be exerted on these

1198   systems and the greater expense associated with such large-scale monitoring. Ultimately the

1199   scale of the study will dictate the results; larger, replicated, controlled studies will reveal more

1200   than observational studies in smaller, unreplicated, and uncontrolled ones, but only if they are

1201   conducted robustly with good coverage and consideration of potential pitfalls (e.g. fish

1202   emigration, unreliable receiver detections, poor characterization of environmental dynamics, or

1203   cryptic predation). Recent progress in terrestrial wildlife tracking has pushed forward the spatial

1204   and temporal trade-offs that have long limited movement ecology research, enabling high-

1205   resolution data on wild animals and their natural environment across much larger areas, longer

1206   durations and many more interacting individuals/species compared to traditional tracking

1207   systems (Toledo et al. 2020). Acoustic telemetry provides the means to push forward such limits

1208   in aquatic and coastal ecosystems as well.

1209   Lakes are seminal habitats for studying ecological theory and research in these habitats

1210   has been a catalyst for revealing important paradigms relevant to trophic ecology (e.g. Williams

1211   et al. 2002; Romo et al. 2004) and relationships between animals and their habitat (Randall et al.

1212   1996). We have submitted here ways in which aquatic telemetry systems deployed in lakes now

1213   have the potential to play a key role in unravelling many of the remaining questions in movement

1214   ecology, in particular when combined with environmental data with high spatiotemporal

1215   resolution (Hays et al. 2016). Necessarily these systems will predominantly use fish as model

1216   species, but there are exciting opportunities for other species. Although aquatic invertebrates are

1217   more abundant and diverse than fish, fish are more readily tagged than insect larvae given their

1218   size and use more of the water column. Moreover, many insects are aquatic only as nymphs and

1219   their adult phases emerge to become terrestrial. Larger invertebrates such as crayfish and

1220   *Bellostomata* spp. can carry tags and may be integrated into some whole-lake studies and there is

1221   a promising future for tracking aquatic insects with miniaturization of tags (Daniel Kissling et al.

1222   2014). Predatory birds, particularly cormorants, herons, kingfishers, and ducks, along with

1223   mammals, such as mink and otter, turtles, and crocodilians, can spend significant time in the

1224   water and could also be tagged to study predator landscapes. Ichthyofauna will nevertheless be

1225   the preferred study system for fundamental ecological questions, either studying a single sentinel

1226   species, a pair of interacting species, or several members of a fish community. These studies will

1227   benefit from understanding the abundance of the tagged species and the proportion of the

1228   population carrying tags, and therefore also the demographic rates of the tagged species to

1229   ascertain how quickly this proportion will decline as tagged and untagged fish die, and untagged

1230   fish are born into the population. Individual studies may investigate questions in single lakes and

1231   later become integrated within meta-studies to answer new questions as part of post-hoc

1232   replicated experiments. For applied research, there is a growing need to forecast movement

1233   behaviour, e.g. to understand vulnerability to angling (Monk & Arlinghaus 2018) or responses to

1234   potential mitigation measures, and simulation studies parameterized by tracking studies of wild

1235   fish have a great potential to this end (Szabo-Meszaros et al. 2019).

1236   Mining the benefits of whole lake telemetry for conservation and management depends

1237   on a number of challenges. Besides the obvious challenges of resources to equip entire lakes with

1238   hydrophones and manage the big data stream, key issues revolve around the difficulty of

1239   obtaining random fish samples as all gears suffer from gear biases in terms of which behavioural

1240   types are captured for tagging (Brownscombe et al. 2019). Moreover, tag life can limit the

1241   observation time window and may not allow us to arrive at assessments of whole life-cycles and

1242   ecosystem responses to experimental perturbations. Tagging effects can affect growth and

1243   fecundity and thereby limit how well the tagged fish represent the fish population. As pointed out

1244   earlier in this paper, there is a particular need for more research on small fish, and development

1245   of smaller acoustic tags with pressure sensors and potentially other sensors is highly warranted.

1246   Clearly, some of the experiments proposed above may also be ethically problematic, in particular

1247   when destructive experiments (e.g., release of pollutants) are conducted. Nonetheless, there are a

1248   growing number of experimental lake facilities where such work can be conducted (e.g.,

1249   Experimental Lakes Area in northwestern Ontario), and new environmentally safe methods for

1250   exposing fish to chemicals in the field using implants is currently being developed (McCallum et

1251   al. 2019).

1252   Work on threatened species might also be limited as tagging demands invasive

1253   procedures that may not be welcomed by authorities and the public at large. On the flip side,

1254   when pairing telemetry with other novel ecological methods (e.g., eDNA, stable isotopes, genetic

1255 tagging, genomics, ecoacoustics) possibly entire lakes can be transformed into large, real-life

1256 laboratories to tackle pertinent questions of management, assessment and conservation at the

1257 right ecological and managerial scales. Clearly, lakes could offer test arenas to tackle questions

1258 that will not be possible to address in more open systems such as the ocean. While marine

1259 fisheries has a tendency to be largely based on modelling, freshwater ecology tends to emphasize

1260 ecological questions in fish ecology. By combining modelling techniques for population

1261 dynamics developed in the marine realm with the beauty of being able to measure detailed

1262 ecological processes (e.g., exchange dynamics among refuge and open habitat, Matthias et al.

1263 2014) in the freshwater ecosystem, a revolution in fish and fisheries sciences with relevance to

1264 management can be expected from whole-lake studies involving telemetry.

1265   Networks for archiving animal movement data can facilitate these studies so that data are

1266 available to contemporary researchers and future generations (Nguyen et al. 2017). The Ocean

1267 Tracking Network and European Telemetry Network can act as hubs for connecting researchers

1268 with relevant data, and ensuring that these data are accessible for meta-studies that can integrate

1269 research from multiple lakes to ask new questions. In order for this to be possible researchers

1270 must be committed to collecting and archiving metadata about their study system, including

1271 technical details such as receiver detection radius and especially environmental parameters such

1272 as temperature, lake stratification, and species assemblage.

1273

1274 **Declarations**

1275

1276 Ethics approval and consent to participate

1277

1278 No human or animal subjects were used and no consent for use was sought. All authors have

1279 read and approved the content of this submission. Contributors not meeting the threshold for

1280 authorship have been acknowledged.

1281

1282 <u>Consent for publication</u>

1283

1284 Not applicable

1285

1286 <u>Availability of data and materials</u>

1287

1288 No data were generated for this manuscript and none are available for further use.

1289

1290 <u>Competing interests</u>

1291

1292 The authors wish to bring to attention of readers no interests in competition with the content of

1293 the manuscript.

1294

1299

1300   <u>Authors' contributions</u>

1301

1302   Lennox, Arlinghaus, and Jarić conceived and outlined the manuscript. Lennox, Arlinghaus, and

1303   Jarić wrote the introduction, Lennox, Arlinghaus, Jarić, and Cooke wrote the synthesis. Lennox,

1304   Westrelin, Souza, Šmejkal, Říha, Prchalová, Nathan, Monk, Koeck, Killen, Jarić, Gjelland,

1305   Hollins, Hellstrom, Hansen, Cooke, Boukal, Brooks, Brodin, Baktoft, Adam, and Arlinghaus

1306   drafted subsections and edited the full manuscript. Lennox, Arlinghaus, and Jarić sketched the

1307   conceptual figure with input from all other authors.

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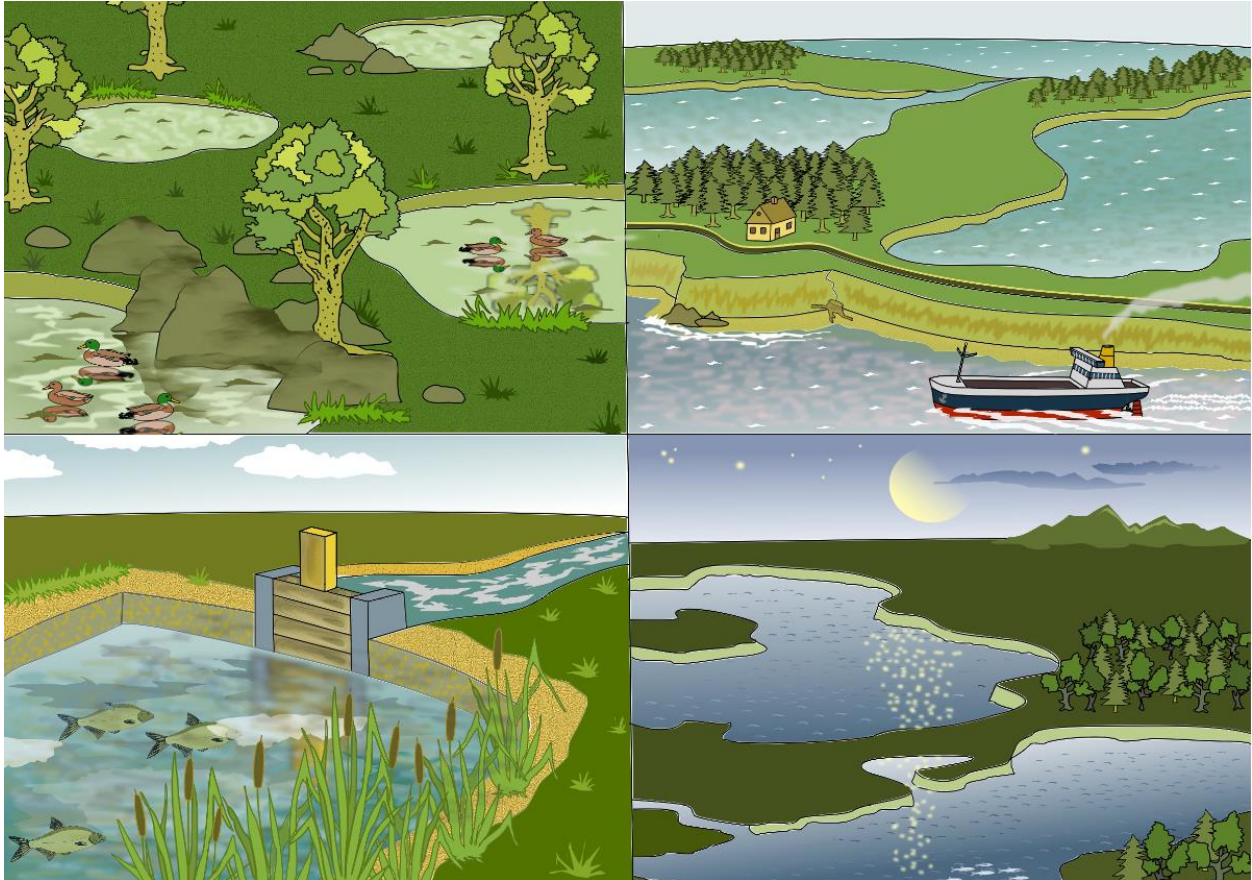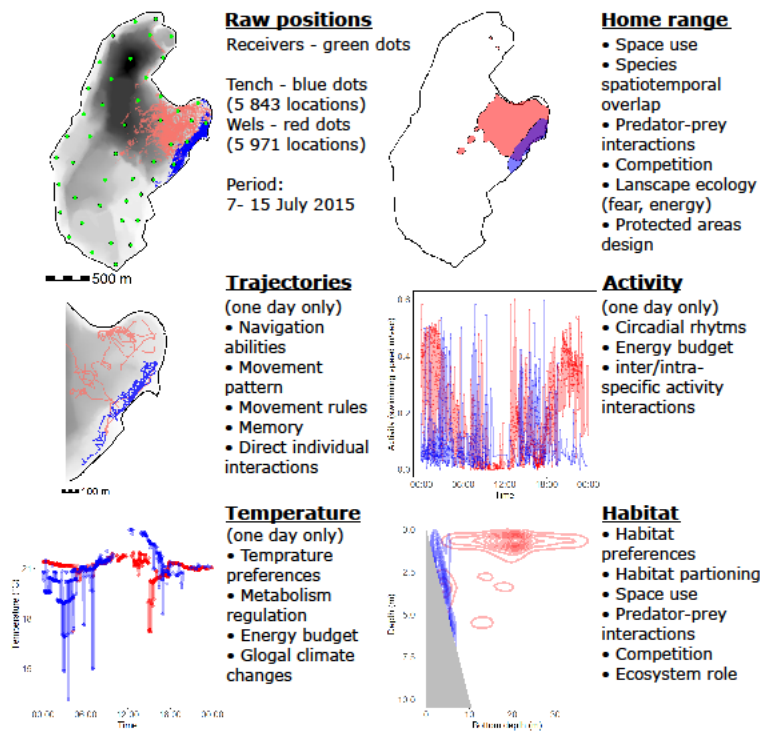
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Figures

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2066   Figure 1. Lakes come in many shapes and sizes, all of which have the potential to be monitored

2067   using environmental sensors and telemetry to reveal the nature of animal movement. In this grid

2068   we show lake size scales between small (left half) and large (right half) and experiments can be

2069   conducted in isolation (a single lake, lower half) or in a replicated design (upper half). Finding

2070   matching lakes to replicate experiments allows a degree of control that is difficult or impossible to

2071   achieve in other systems. Moreover, scaling lakes from small to large allows a degree of

2072	environmental realism desired for the experiments, with animals in small lakes using all habitats

2073	but in large lakes habitat segregation and different competitive mechanisms emerging.
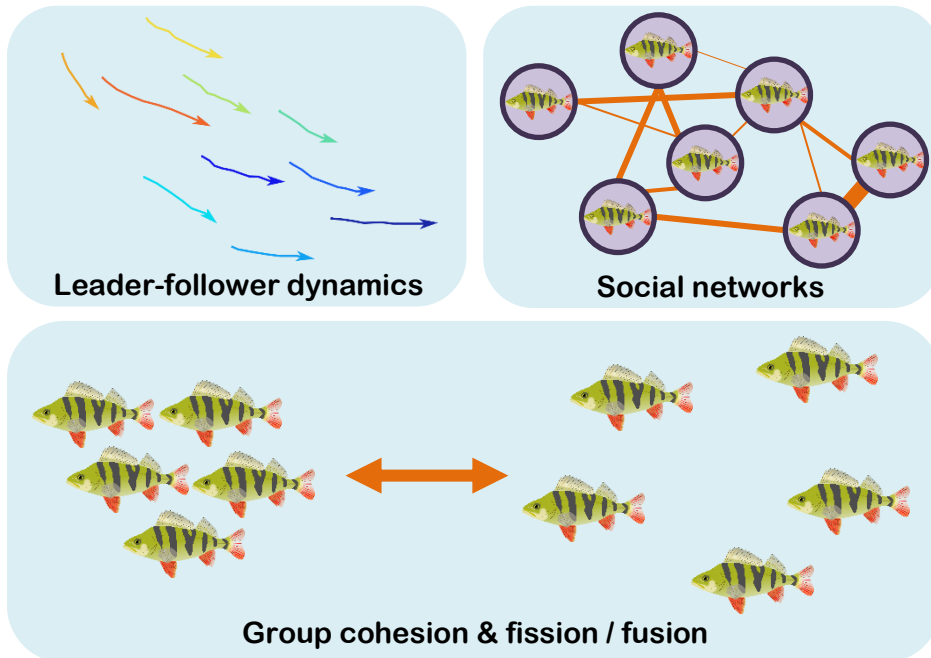
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Raw positions
Receivers - green dots

Tench - blue dots
(5 843 locations)
Wels - red dots
(5 971 locations)

Period:
7- 15 July 2015

500 m

Home range
• Space use
• Species spatiotemporal overlap
• Predator-prey interactions
• Competition
• Lanscape ecology (fear, energy)
• Protected areas design

Trajectories
(one day only)
• Navigation abilities
• Movement pattern
• Movement rules
• Memory
• Direct individual interactions

100 m

Activity
(one day only)
• Circadial rhytms
• Energy budget
• inter/intra-specific activity interactions

Temperature
(one day only)
• Temprature preferences
• Metabolism regulation
• Energy budget
• Glogal climate changes

Habitat
• Habitat preferences
• Habitat partitioning
• Space use
• Predator-prey interactions
• Competition
• Ecosystem role

Figure 2. Acoustic telemetry yield data on the instrumented animal's positions, path, space use, activity levels, temperature use, and habitat selection in up to four dimensions. Here, we illustrate how detections on a grid of acoustic receivers can be used to investigate patterns in the behaviour and physiology of free living fish to describe where, when, how, and why animals are moving. Together, lake telemetry studies are powerful tools for inquiry about processes and patterns in ecology.
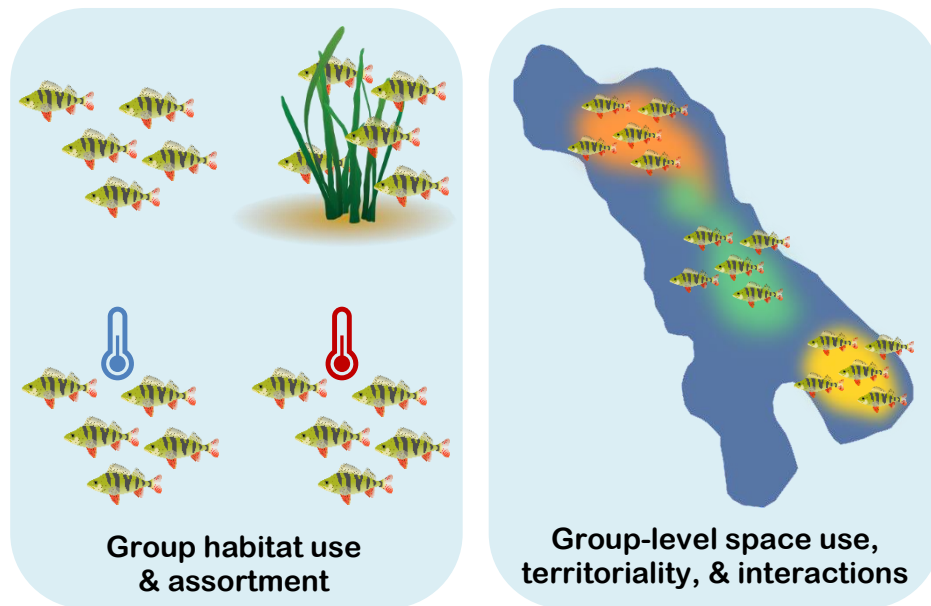
Figure 3. Data from acoustic telemetry will greatly enhance our analysis of social and collective behaviour in fish, as well as allow new forms of analysis that have previously been impossible in the wild. The analysis of leader-follower dynamics, social networks, and group cohesion can now be performed at much greater temporal and spatial scales using telemetry data. This will allow

2108   study of how these social factors affect ecological phenomena including group foraging,

2109   migrations, and predator avoidance, and how changing environments further modulate these

2110   effects. Telemetry data will revolutionize the study of the interactions between habitat use (e.g. in

2111   response to physical structure or factors such as temperature of oxygen availability) and passive

2112   and active assortment of phenotypes among and within groups. In addition, an opportunity now

2113   exists to examine among-group variation in space use, territoriality, and changes in social group

2114   membership, with possible effects on individual fitness.

2115