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**What acoustic telemetry can and can't tell us about fish biology**

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17 **Abstract**

18 Acoustic telemetry (AT) has become ubiquitous in aquatic monitoring and fish biology,  
19 conservation and management. Since the early use of active ultrasonic tracking that  
20 required researchers to follow at a distance their species of interest, the field has diversified  
21 considerably with exciting advances in both hydrophone and transmitter technology. Once a  
22 highly specialised methodology however, AT is fast becoming a generalist tool for those  
23 wishing to study or conserve fishes, leading to diversifying application by non-specialists.  
24 With this transition in mind, we evaluate exactly what AT has become useful for, discussing  
25 how the technological and analytical advances around AT can address important questions  
26 within fish biology. In doing so, we highlight the key ecological and applied research areas  
27 where AT continues to reveal crucial new insights, and in particular, when combined with  
28 complimentary research approaches. We provide a comprehensive breakdown of the state  
29 of the art for applications of AT, discussing the ongoing challenges, where its strengths lie,  
30 and how future developments may revolutionise fisheries management, behavioural  
31 ecology and species protection. Through selected papers we illustrate specific applications  
32 across the broad spectrum of fish biology. By bringing together the recent and future  
33 developments in this field under categories designed to broadly capture many aspects of  
34 fish biology, we hope to offer a useful guide for the non-specialist practitioner as they  
35 attempt to navigate the dizzying array of considerations and ongoing developments within  
36 this diverse toolkit.

37 *Keywords: Biotelemetry; Conservation; Movement Ecology; Fisheries; Fish behaviour;*  
38 *Tracking*

39	<b>Table of Contents</b>	
40	<b>Abstract</b> .....	<b>2</b>
41	<b>Introduction</b> .....	<b>4</b>
42	<b>1) Fundamental Ecological Research</b> .....	<b>8</b>
43	<i>Migration patterns</i> .....	<b>8</b>
44	<i>Space use and fine-scale movement strategies</i> .....	<b>11</b>
45	<i>Habitat connectivity and energy landscapes</i> .....	<b>13</b>
46	<i>Segregation</i> .....	<b>15</b>
47	<i>Fish interactions</i> .....	<b>17</b>
48	<i>Aggregation and social structure inference</i> .....	<b>17</b>
49	<i>Fine-scale social associations and trophic interactions</i> .....	<b>19</b>
50	<i>Depth preferences and temperature regulation</i> .....	<b>22</b>
51	<i>Invasion biology</i> .....	<b>24</b>
52	<b>2) Applied Research</b> .....	<b>25</b>
53	<i>Species conservation and management</i> .....	<b>25</b>
54	<i>Evaluating extinction risk and threat assessments</i> .....	<b>25</b>
55	<i>Fisheries management</i> .....	<b>28</b>
56	<i>Evaluating spatial protection</i> .....	<b>31</b>
57	<i>Human-wildlife conflict</i> .....	<b>33</b>
58	<i>Kinematics, energetics and physiological impacts of human modified systems</i> .....	<b>35</b>
59	<b>3) Future directions and considerations</b> .....	<b>37</b>
60	<i>Tracking small species and life-stages</i> .....	<b>38</b>
61	<i>Multi-sensor transmitters, combined technologies and surrogates</i> .....	<b>40</b>
62	<i>Live data for near real-time management</i> .....	<b>42</b>
63	<i>Accuracy, precision and validation</i> .....	<b>43</b>
64	<b>Conclusions</b> .....	<b>45</b>
65	<b>Acknowledgements</b> .....	<b>46</b>
66	<b>Data Availability Statement</b> .....	<b>47</b>
67	<b>References</b> .....	<b>47</b>
68	<b>Figure Legends</b> .....	<i>Error! Bookmark not defined.</i>
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## 71 **Introduction**

72 Sound propagates four times faster, attenuates slower and travels considerably further in  
73 water than it does in air. On this premise, acoustic telemetry (AT) technologies have, over  
74 the last 70 years or so, developed and diversified into a vast and lucrative industry enabling  
75 researchers to track numerous aquatic species over substantial spatial and temporal scales  
76 (Cooke, Hinch, et al., 2004; Hockersmith & Beeman, 2012; Hussey et al., 2015). Once a  
77 highly specialised methodology, typically adopted to understand the movement and space  
78 use of relatively large animals, it has since become embedded into a variety of ecological  
79 and applied research areas, co-evolving alongside a suite of complimentary aquatic research  
80 approaches. Nowhere has this transition been more pronounced than within the fish  
81 biology community. AT has now become very much a generalist tool and one being adopted  
82 by an increasing diversity of practitioners from early career researchers to conservationists  
83 within the charity sector, to those managing recreational and commercial fisheries (Curtis et  
84 al., 2015; Hussey et al., 2017), aquaculture (Hassan et al., 2019) and commercial water  
85 facilities (Klimley et al., 2017). In light of this broadening market, and in the context of the  
86 rapid and ongoing technological developments within the AT field, there is a necessity to  
87 critically evaluate which aspects of fish biology this technology can now be useful in  
88 addressing.

89 In essence, animal borne, acoustic telemetry transmitters (hereafter 'transmitters')  
90 that generate coded acoustic signals at a specific frequency, can be logged by a researcher  
91 directly with a hydrophone from a boat (active tracking) or by stationary, *in situ* 'receivers'  
92 with hydrophones attached, recording the presence of an individual within a particular, and  
93 highly variable range. Since the early days of active, continuous ultrasonic tracking in the

94 1950s, the field of AT has undergone a number of significant phase transitions; perhaps  
95 most significantly, the implementation of passive tracking using arrays of fixed receivers,  
96 which revolutionised the scope and scale of research question that could be tackled (Cote et  
97 al., 1998; Heupel & Hueter, 2001). This development put the onus firmly on study design,  
98 dramatically increasing the number of individuals that could contribute to a given study by  
99 reducing the effort required to collect data for each. Today, depending on the spatial  
100 arrangement and type of receivers installed within an array, data can take two forms; it can  
101 be returned either as presence only, recording the identification, time and date of a fish  
102 anywhere within an ellipsoid that represents the detection range of a particular receiver; or  
103 alternatively, by closely-spacing receivers to produce detection ranges that overlap, high-  
104 resolution tracking can be conducted generating sub-metre positional estimates of fish  
105 movement (Brownscombe *et al.*, 2019a). Nuances in the placement of acoustic receiver  
106 arrays are often dictated by the geography or environmental conditions of specific study  
107 sites. Arrays therefore can be highly variable leading to placements of receiver gates within  
108 bottlenecks, grided arrays within enclosed lakes or embayments or receiver 'chains' that  
109 track the shape of a coastline, island or river bed (Heupel et al., 2006). With recent advances  
110 in both transmitter and receiver technologies comes the opportunity to track fishes for  
111 longer, with higher precision or greater spatial coverage, follow them in deeper habitat or in  
112 near real-time, while also gathering physiological data on the individuals that carry tags  
113 (Lennox *et al.*, 2017). This increasing data richness and quantity per transmitter also  
114 provides opportunity to address ethical considerations by reducing the number of  
115 individuals required to undergo procedures. Perhaps then, it is unsurprising that this toolkit  
116 has become more attractive in recent years, to the diversity of people that work directly and  
117 indirectly with fish.

118           Whether using the simplest or the most advanced set up, the challenges and trade-  
119 offs facing practitioners can be similar. These may include weighing up tag size against  
120 battery life (longevity) and the ethical implications associated with this (Brownscombe *et al.*,  
121 2019a) or balancing acoustic coverage against research costs and questions (Heupel *et al.*,  
122 2006). Alternatively, it might be quantity versus quality of data and how best to analyse  
123 them (Guzzo *et al.*, 2018; Whoriskey *et al.*, 2019), the biases associated with the spatial  
124 configuration of an array (Kraus *et al.*, 2018) or how detection range can vary through time  
125 impacting the accuracy and precision of the data, with significant implications for  
126 interpretation (Brownscombe, Griffin, *et al.*, 2019; Kessel *et al.*, 2014; Payne, Gillanders,  
127 Webber, & Semmens, 2010). These challenges (and more), have led to a wealth of  
128 developments in the visualisation and statistical analyses of acoustic telemetry data  
129 (Campbell, Watts, Dwyer, & Franklin, 2012; Jacoby, Brooks, Croft, & Sims, 2012; Niella *et al.*,  
130 2020; Whoriskey *et al.*, 2019) which continue to improve our understanding of fish biology  
131 across a diverse array of aquatic environments.

132           Recent developments within AT offer new and more diverse opportunities to explore  
133 different aspects of fish biology. The increasing miniaturisation, reduced cost and improved  
134 battery life of current acoustic transmitters for instance, has ensured that AT has become a  
135 vital part of the toolkit for those seeking to influence the conservation of imperilled aquatic  
136 species (Cooke, 2008) or inform management practices to mitigate pressures on their  
137 ecosystems (Matley *et al.*, 2021). Alongside hardware developments, data management  
138 strategies, once rare and often unstandardized (Heupel, Semmens, & Hobday, 2006), now  
139 offer broad scale, even global collaboration between researchers operating different  
140 project-specific AT arrays (Abecasis *et al.*, 2018; Cooke *et al.*, 2011). Such innovation,

141 however, is reliant on open methods and compatibility between manufacturer tag protocols  
142 (a set of unique tag IDs) and code maps (a list defining the particular tag IDs a receiver can  
143 listen for). Users new to AT therefore, need to carefully consider the availability of sensor  
144 combinations and receiver-transmitter, two-way compatibility, offered by the different AT  
145 manufacturers, if collaborative research is desirable (Reubens *et al.*, 2021). Where analyses  
146 used to be largely descriptive, they have started to become considerably more hypothesis-  
147 driven and quantitative (Donaldson *et al.*, 2014). Even the very description of the field now  
148 goes beyond referring simply to tags that transmit a unique ID code to passive monitoring  
149 stations, to incorporate multifunctional temperature, pressure, acceleration and even heart-  
150 rate sensors (e.g. Kadar, Ladds, Mourier, Day, & Brown, 2019; Payne *et al.*, 2015), with the  
151 option to retrieve real-time updates on detections via satellite (e.g. Forget *et al.*, 2015). For  
152 those relatively new to the field, this diversification and continuing development can offer  
153 up a daunting array of challenges and decisions (summarised in Fig. 1), and as a growing  
154 number of excellent reviews will attest, the applications of these technologies are broad  
155 (Brownscombe *et al.*, 2019a; Donaldson *et al.*, 2014; Heupel *et al.*, 2006; Hussey *et al.*, 2015;  
156 Matley *et al.*, 2023, 2021).

157         In light of the transition of AT from a very specialised methodology to more of a  
158 generalist toolkit, our intention for this paper is to take stock of where the field is at in its  
159 capacity to reveal crucial information about fishes occupying an increasingly unpredictable  
160 and impacted world – our marine and freshwater ecosystems. As increasingly diverse  
161 practitioners enter the field, we wish to address the impact that AT can have on both  
162 fundamental ecological and applied research themes. We discuss these themes in turn  
163 breaking them down into more specific areas, utilising key papers that exemplify progress in

164 each of these research areas (we also summarise this information in Table 1). At the same  
165 time, we aim to discuss some of the current limitations and future advances of AT, as well as  
166 celebrate the progress the field has and continues to make within fish biology.

167

## 168 1) Fundamental Ecological Research

169 In this section we focus on areas where AT has revealed significant ecological insight within  
170 fish biology. The aim is to summarise the developments in several key fields, using studies  
171 that exemplify notable progress in these particular research areas.

172

### 173 *Migration patterns*

174 As a behaviour, migration is both ecologically important but also significantly threatened  
175 worldwide, yet understanding migration in fishes is often complicated by variation within  
176 species and between populations (Lennox *et al.*, 2019). An appreciation of where, when and  
177 what proportion of fish populations migrate, however, is of critical importance for the  
178 management of threatened and/or commercially important fish stocks, the conservation of  
179 threatened species and our fundamental understanding of species distributions. Deriving  
180 this information for many species however is challenging, not least because fish movements  
181 do not abide by human imposed political boundaries and species rarely range in areas under  
182 a single jurisdiction. Furthermore, depending on the species, migration can occur across  
183 different orders of spatial magnitude from tens to thousands of kilometres (Chapman *et al.*,  
184 2012; Lédée *et al.*, 2021; Lowerre-Barbieri *et al.*, 2021).

185 For fishes that migrate either entirely in freshwater (potadromy) or between  
186 freshwater and marine environments (diadromy), the use of AT has proven critical for

187 revealing the scale and variability associated with migration, particularly in the freshwater  
188 component of this behaviour. Strategic use of receiver 'lines' or check points that span  
189 waterways and reliably capture both upstream and downstream movements of tagged  
190 individuals, enable estimates of migration distance, timing and relative survivorship  
191 (Clements *et al.*, 2005; Melnychuk *et al.*, 2007). Indeed, the mechanics of moving between  
192 salinity gradients for diadromous species have only really been fully understood by  
193 combining AT with otolith microchemistry. Telemetry defined migratory behaviour, in  
194 combination with otolith analyses, has been used to validate or disregard chemical  
195 signatures associated with transitions in pinkey mullet *Trachystoma petardi* (Castelneau  
196 1875) (Miles *et al.*, 2018) but also to determine partial anadromy in non-native rainbow  
197 trout *Oncorhynchus mykiss* (Walbaum 1792) (Roloson *et al.*, 2020).

198         These combined, interdisciplinary approaches provide new levels of ecological  
199 understanding, particularly for complex migratory species, helping to better link the  
200 influence of flexibility in migration strategy to threats that may impact individuals/groups  
201 within populations disproportionately (Tamarío *et al.*, 2019). A closer look from a recent  
202 study however, suggests that 50% of published articles that use AT to understand fish  
203 movement or ecology, fail to incorporate or consider mortality within their study, while  
204 those that did estimate an ~11% loss on average of tagged individuals from the system  
205 (Klinard & Matley, 2020). This is pertinent as transmitters will continue to be detected even  
206 after depredation, leading to movement patterns that reflect the predator rather than the  
207 prey species (Bohaboy *et al.*, 2020). Even those that survive but leave the array, and thus  
208 exhibit different behaviour to individuals typically included in analyses, remain rarely  
209 discussed in studies on movement. Yet despite these important caveats, AT continues to

210 prove invaluable for understanding fish migration. Hayden et al. (2014) for example, used  
211 receiver lines situated in the nearshore waters of Lake Huron and a multi-state mark-  
212 recapture model to describe three migratory pathways for walleye *Sander vitreus* (Mitchill  
213 1818), demonstrating that males spent significantly longer in the rivers before migrating out  
214 into a bay than females, despite no sex preferences for specific pathways. Acoustic tracking  
215 of lake sturgeon *Acipenser fulvescens* (Rafineque 1817) in the same region (Huron-Erie  
216 Corridor, HEC) has also proven instrumental in highlighting intraspecific variability in  
217 freshwater migrants, known as divergent migration (Kessel et al., 2018). As anthropogenic  
218 barriers continue to pose one of the biggest threats to riverine migration, the identification  
219 of consistent migratory behavioural states, including partial migration where only some  
220 individuals from a population migrate and non-migratory residency within populations,  
221 illuminates the need for separate management strategies as well as the potential for species  
222 to respond to continued change to their habitat (Kessel et al., 2018).

223         As indicated, moving from a freshwater environment to marine imposes considerable  
224 physiological demands on fishes but also our ability to utilise AT to monitor migration,  
225 without the natural 'bottleneck' that rivers provide. Array design between habitats can vary  
226 substantially (Fig. 2) highlighting the need to carefully consider species ecology. For  
227 diadromous species like freshwater eels (*Anguilla spp.*) that mature in rivers and estuaries  
228 before undertaking their only spawning migration to the open ocean, understanding the  
229 timing, drivers and threats to migration is vital for conserving these imperilled species  
230 (Jacoby et al., 2015). Béguer-Pon et al. (2014) successfully deployed acoustic receivers  
231 covering a distance of 420 km to monitor the 'silver eel' escapement of mature America eels  
232 *Anguilla rostrata* (Lesueur 1821) as they headed out towards the Sargasso Sea to spawn

233 from the St Lawrence River. The acoustic data revealed substantial individual variation in the  
234 timing and speed of migration, but for the first time a strong reliance on nocturnal, ebb tide  
235 transport by silver eels to escape the estuary (Béguer-Pon *et al.*, 2014). When tracking  
236 species in the marine environment, horizontal migration is typically detected on departure  
237 and arrival by strategically-deployed receiver arrays, as documented for example in bull  
238 sharks *Carcharhinus leucas* (Müller & Henle 1839) (Daly, Smale, Cowley, & Froneman, 2014;  
239 Heupel *et al.*, 2015). Alternatively, with depth-temperature sensor tags, active acoustic  
240 tracking can provide a window into the short-term vertical migrations (e.g. diel vertical  
241 migration) of highly-mobile species of pelagic fishes (Block, Booth, & Carey, 1992; Nakano,  
242 Matsunaga, Okamoto, & Okazaki, 2003). Finally, long-distance movements in the marine  
243 environment, normally outside the capabilities of passive AT, are beginning to be captured  
244 via coordinated networks of acoustic arrays operating data sharing agreements to track  
245 cross-jurisdictional migration of wide ranging, commercially important or threatened  
246 species (Lédée *et al.*, 2021; Young *et al.*, 2020).

247

#### 248 *Space use and fine-scale movement strategies*

249 Across most aquatic environments, AT has been used to great effect to estimate fish activity  
250 space, home range, core areas or 'central places' and residency patterns, in addition to how  
251 these parameters vary by species, sex or time of day, month or year (Garcia, Mourier, &  
252 Lenfant, 2015; Heupel, Simpfendorfer, & Hueter, 2004; Heupel, Lédée, & Simpfendorfer,  
253 2018; Kirby, Johnson, & Ringler, 2017; Nakayama *et al.*, 2018; Papastamatiou *et al.*, 2018;  
254 Simpfendorfer, Heupel, & Hueter, 2002; Watson *et al.*, 2019). The accuracy of space use  
255 estimates derived from passive telemetry data are very much dependent on the metric used

256 (Dwyer *et al.*, 2015). Some of the most widely used are now built into bespoke packages,  
257 such as those in the R statistical environment (R Core Team, 2022) for example *VTrack*,  
258 offering standardised tools for deriving and comparing these metrics between locations  
259 (Udyawer *et al.*, 2018). It is important to stress however, that there remain a number of  
260 challenges associated with estimating space use from AT data, not least that estimates are  
261 constrained by the size of the array, limiting reliability to species that use smaller areas than  
262 are being monitored. Accurate estimation of space use and home range of fishes is first  
263 contingent on precise estimation of location (Hostetter & Royle, 2020), and must consider  
264 biases that include autocorrelation, small numbers of tagged individuals (sample size) and  
265 irregular data collection. The pros and cons of home range estimator methods have been  
266 discussed in detail by Silva *et al.*, (2022) and (Kraft *et al.*, 2023) offering accessible guides to  
267 choosing between the different options, in addition to R code for applying autocorrelated  
268 kernel density estimators (AKDEs) for home range analyses. With these caveats in mind, and  
269 for species that show some form of site-attachment or fidelity, AT has remained invaluable  
270 for understanding space use at multiple spatial scales, particularly in recent years with the  
271 advent of open source data platforms enabling the coordination of data streams from  
272 multiple acoustic arrays to cover significantly broader spatial ranges for more mobile species  
273 (Brownscombe, Lédée, et al., 2019; Campbell et al., 2012; Harcourt et al., 2019; Heupel,  
274 Kessel, Matley & Simpfendorfer, 2018; Udyawer et al., 2018).

275         Aggregated by species or sex, movement metrics (including range and dispersal)  
276 provide an important overview of space use at the population level. However, metrics from  
277 individual animals inform another important area of research; the role of individual  
278 variability or personalities (consistent individual behaviours) and behavioural syndromes (a

279 correlated suite of behaviours) on population stability and adaptive resilience (Villegas-Ríos  
280 *et al.*, 2017). Using Atlantic cod *Gadus morhua* L. as a model species, Villegas-Ríos, Réale,  
281 Freitas, Moland, & Olsen (2018) exposed individuals to repeated and standardised  
282 behavioural laboratory assays prior to releasing them with acoustic tags into a high-  
283 resolution, acoustic tracking array (Innovasea Positioning System, VPS) to monitor their  
284 movements in response to changes in sea surface temperature. From hyperbolic positioning  
285 within the VPS array and depth-sensing tags, fine-scale reconstructions of three-dimensional  
286 (3D) movements were modelled against individual home range across the proactive (bold)  
287 to reactive (shy) behavioural spectrum. In short, one of the key results to come from this  
288 novel work was that personality was found to be a significant predictor of changes in home  
289 range size (Villegas-Ríos *et al.*, 2018).

290

### 291 *Habitat connectivity and energy landscapes*

292 The design of a passive acoustic array and the equipment used, can vary significantly (Fig. 2).  
293 As such, data can be generated as discrete, presence-only packages associated with  
294 important monitoring locations or as discussed, near-continuous, high-resolution 3D  
295 individual tracks reliant on receiver overlap and considerable post-processing of the data to  
296 determine fine-scale position. Particularly when tracking species in the marine environment  
297 or in very large water bodies, positional accuracy is regularly sacrificed for spatial coverage.  
298 Arrays can be designed around habitats of interest such as reefs, islands or atolls (Espinoza,  
299 Heupel, Tobin, & Simpfendorfer, 2015; Papastamatiou, Meyer, Kosaki, Wallsgrove, & Popp,  
300 2015), or as gridded arrays and receiver lines, which are sometimes adopted where the  
301 physical geography of the study location and the research question permits, such as

302 bottlenecks or enclosed embayments (Block et al., 2019; Braccini, Rensing, Langlois, &  
303 McAuley, 2017; Farmer & Ault, 2011; Hussey et al., 2017) (Fig. 2).

304       When covering broad geographic areas or different habitat types, discrete spatial data  
305 lend themselves well to spatial network analyses of movements between receiver locations  
306 (Jacoby et al., 2012). The true strength of network analyses is that they offer a scalable  
307 method with which to quantify linkages, measure relative centrality or importance of  
308 receivers, explore connectivity and determine the extent to which landscape (structural)  
309 and behaviour (functional) processes facilitate or impede movement between habitat  
310 patches or resources (Baguette & Van Dyck, 2007; Bélisle, 2005). Indeed coupling  
311 movement networks with Stable Isotope Analyses (SIA) has led to important and novel  
312 discoveries around energy landscapes, for example, the classification of permit *Trachinotus*  
313 *falcatus* into two distinct ecotypes within the Florida Keys, US; one, with a heavy reliance on  
314 movements between the Florida reef tract and seagrass beds and their associated prey, and  
315 a second that primarily occupy artificial reefs relying almost exclusively on pelagic prey, with  
316 clear implications for the management of the fishery (Brownscombe *et al.*, 2022).  
317 Consequently, it is becoming increasingly apparent that AT-derived fish movements, in  
318 combination with bioenergetic models, can greatly inform our understanding of nutrient  
319 dynamics with network approaches being adopted to predict the distribution and quantities  
320 of nitrogen egestion by predators on coral reefs (Williams *et al.*, 2018). Using a similar  
321 coupled approach, Eggenberger et al., (2019) were able to demonstrate variation in the  
322 behaviour and habitat selection of Common Snook *Centropomus undecimalis* (Bloch 1792),  
323 despite similar trophic ecology, in response to mesotrophic (higher mobility) and eutrophic  
324 (higher residency) conditions.

325 The application of network analyses to tease apart some of these processes is still in  
326 its relative infancy, particularly the utilisation of edge durations (time associated with  
327 movements from one receiver to another) to explore some of the mechanisms driving  
328 connectivity. These detection 'gaps' have proven useful for inferring different fish  
329 behaviours associated with 'restricted' movements and 'out-of-range' dispersal (Williamson  
330 *et al.*, 2021). To date, network approaches have been successfully applied to AT data to  
331 show how reef-associated shark species connect different management zones in the Great  
332 Barrier Reef (Espinoza *et al.*, 2015a), and how movement strategies can influence species  
333 risk to illegal fishing inside marine protected areas (Jacoby *et al.*, 2020). Furthermore,  
334 network metrics, that capture dynamic movements, appear both consistent with and  
335 complementary to more traditional estimates of space use (Lédée *et al.*, 2015), offering an  
336 extended toolkit to the AT practitioner (Jacoby & Freeman, 2016). For example, the  
337 repeated path use of young *G. morhua* between habitats within a coastal fjord system was  
338 strongly, negatively correlated with water temperature, a finding revealed through  
339 measuring the relative abundance of different types of triadic network motif, or three  
340 receivers linked by directed movements (Staveley *et al.*, 2019).

#### 341 *Segregation*

342 In addition to using AT to quantify space use, we might wish to explore some of the  
343 mechanisms driving this space use. Individual behavioural signatures, whether in two or  
344 three dimensions, may be dictated by their local environment or by the presence of  
345 conspecifics of a different sex or size or individuals of different species altogether,  
346 manifesting itself as spatial and/or temporal differences in habitat use. Realistically, it is  
347 likely to be a combination of factors, yet understanding the dynamics of segregation within

348 a population is important, particularly when considering species that face spatially- or  
349 seasonally-focused exploitation or partial spatial protection (Mucientes *et al.*, 2009). Using  
350 Innovasea's (Amirix Systems, Nova Scotia, Canada) accelerometer and pressure transmitters  
351 (V9AP and V13AP) for example, Payne *et al.* (2015) were able to demonstrate diurnal  
352 segregation on a vertical plane between an estuarine piscivore, mulloway *Argyrosomus*  
353 *japonicus* (Temminck & Schlegel 1844) and benthic carnivore, sand whiting *Sillago ciliata*  
354 (Cuvier 1829) in south-eastern Australia. Interestingly, the authors utilise these multi-  
355 purpose tags to monitor the impact of short-term stochastic weather events on segregation;  
356 the study reveals that rain precedes a switching of spatial segregation to temporal  
357 segregation (increased nocturnal activity in *A. japonicus* and decreased nocturnal activity in  
358 *S. ciliata*), a result compellingly supported by 10 years of commercial set-net CPUE data,  
359 which show increased rainfall produce higher catch rates for *A. japonicus* but lower catch  
360 rates for *S. ciliata* (Payne *et al.*, 2015).

361 Sexual segregation is relatively well documented in marine fishes (Wearmouth & Sims,  
362 2008) and here too AT has played a key role in distinguishing both sexual segregation within  
363 adult populations of elasmobranchs (e.g. Kock *et al.*, 2013), as well as female-only refuging  
364 behaviour as a reproductive strategy for numerous species (e.g. Hight & Lowe, 2007; Sims,  
365 Nash, & Morritt, 2001). Furthermore, mobile, predatory elasmobranchs also have a  
366 tendency to demonstrate segregation by species; processes such as competitive exclusion  
367 within specific habitat types (Papastamatiou, Bodey, *et al.*, 2018) or dynamic, temporal  
368 segregation driven by tidal cycles (Lea *et al.*, 2020) have been demonstrated in remarkably  
369 small systems – relative to the movement capabilities of the study species – such as remote  
370 isolated atolls, using long-term AT data (e.g. Heupel *et al.*, 2018). Despite having similar

371 isotopic niches, AT has also revealed that leopard coral grouper *Plectropomus leopardus*  
372 (Lacépède 1802) and spotted coral grouper *Plectropomus maculatus* (Bloch 1790) had  
373 minimal spatial overlap, yet similar space use patterns, due to vertical segregation in the  
374 water column (Matley et al., 2017). Again, network analyses have been put to good use to  
375 show, for example, that even amongst apparently sympatric species, sharks vary  
376 considerably in their choice of habitat, route choice and connectivity within a gridded  
377 receiver array in the southern Great Barrier Reef, Australia (Heupel et al., 2018). Other  
378 applications include the use of community detection algorithms to networks of movements  
379 between different species and age classes, to explore dissimilarity in movement within  
380 complex fish assemblages (e.g. Casselberry et al., 2020).

381

## 382 *Fish interactions*

### 383 *Aggregation and social structure inference*

384 With enough individuals tagged simultaneously within a population, AT can be hugely  
385 informative for identifying and exploring fish aggregations and their key drivers, most  
386 notably spawning (Domeier & Colin, 1997), predation (Temming *et al.*, 2007), refuging and  
387 nursery behaviours (Bass et al., 2017; Jacoby, Croft, & Sims, 2012). In teleost reef predators  
388 such as grouper, determining the location, timing and composition of reproductive  
389 aggregations is crucial to not only answer fundamental questions about population biology,  
390 but also inform spatial protection measures because aggregations are commonly targeted  
391 by fishers (Keller *et al.*, 2020; Rowell *et al.*, 2015). Indeed, the tendency of numerous pelagic  
392 species, including tropical tuna, to aggregate around floating objects has long been  
393 exploited to aid harvest through the deployment of artificial Fish Aggregating Devices

394 (FADs). The relative ease of instrumenting FADs with acoustic receivers and other sensors  
395 has enabled substantial knowledge gains about movement ecology (Pérez *et al.*, 2020), the  
396 social interactions of individuals (Stehfest *et al.*, 2013), and the vulnerability of target and  
397 bycatch species to exploitation (Forget *et al.*, 2015). In freshwater, the locations of adult  
398 lake trout *Salvelinus namaycush* (Walbaum 1792) aggregations in Lake Huron, North  
399 America, determined from 5 years of acoustic positioning data within an extensive (19 to 27  
400 km<sup>2</sup>) receiver array revealed hitherto unknown putative spawning sites which were  
401 subsequently confirmed by diver surveys of egg deposition (Binder *et al.*, 2018). Several of  
402 these sites were too small or obscure to have been identified by bathymetric survey or did  
403 not conform to the conceptual model of a spawning habitat, so without telemetry would  
404 have otherwise likely been overlooked (Binder *et al.*, 2018). Indeed, temperature and depth  
405 sensors on acoustic transmitters can reveal the abiotic conditions that favour aggregation.  
406 For example, having gained this information through AT, Bajer *et al.* (2011) used the Judas  
407 technique, that is tracking an individual to reveal the location of an aggregation, to assist in  
408 the removal of invasive common carp *Cyprinus carpio* L. aggregations, with an efficiency of  
409 up to 94%.

410 Determining the mechanism driving aggregation or social behaviour from remote,  
411 passive data is in some instances non-trivial and in others near impossible depending on the  
412 ecology of the species. Consequently, a new line of questioning has emerged that uses  
413 machine learning inference to define multi-individual clustering events in acoustic time-  
414 series data that indicate the spatial and temporal co-occurrence of individuals (Jacoby,  
415 Papastamatiou, & Freeman, 2016; Mourier, Lédée, Guttridge, & Jacoby, 2018). Extracting  
416 these events using Bayesian inference reduces the subjectivity around predefining a

417 sampling window with which to measure 'social' behaviour (10 mins? 10 hours?), relying  
418 more on the natural and variable clustering of the visitation patterns produced by  
419 gregarious fishes. Co-occurrence networks can then be generated from the clusters and  
420 worked up using common quantitative network analysis methods (Jacoby & Freeman,  
421 2016), however careful interpretation of social networks produced using these methods is  
422 needed as the distance over which individuals may be socialising (i.e. co-occurring) is not  
423 always known (Mourier, Bass, Guttridge, Day, & Brown, 2017; see *Fine scale social*  
424 *associations* for more discussion around this). Caveats aside, this method has enabled  
425 exploration of the mechanisms behind social behaviour in highly mobile, free-ranging fishes  
426 for the first time, revealing for example stable social bonds in reef sharks that can last for  
427 years and likely function to facilitate information exchange (Papastamatiou et al., 2020).

428

#### 429 *Fine-scale social associations and trophic interactions*

430 The fine-scale co-occurrences of individuals, whether between conspecifics as mutually  
431 beneficial social affiliations, or between predator and prey species as direct interactions and  
432 displacements, are an important factor that can strongly influence population dynamics  
433 and/or spatial distributions of species (Morueta-Holme *et al.*, 2016). The encounter rates of  
434 Atlantic tarpon *Megalops atlanticus* (Valenciennes 1847) with predatory *C. leucas* and great  
435 hammerhead *Sphyrna mokarran* (Rüppell 1837) sharks in the Florida Keys for instance, were  
436 elevated at specific locations and prior to spawning aggregation behaviour, a result  
437 identified using machine learning to quantify spatio-temporal overlap in multi-species AT  
438 tracking data (Griffin *et al.*, 2022). To truly understand fine-scale interactions and  
439 associations, however, requires direct measurement rather than inference methods, and at

440 a precise and known spatial scale (Aspillaga *et al.*, 2021; Mourier *et al.*, 2017). Prototype  
441 methodologies and proof of concept studies have made exciting initial progress towards this  
442 endeavour. For example, recently developed transmitters that switch transmission code  
443 when digested in the stomach of a predator remove much of the uncertainty around  
444 formerly inferring predation events from changes in track characteristics (e.g. Romine *et al.*,  
445 2014), enabling more robust and detailed exploration of fishes' behaviours immediately  
446 prior to predation (Weinz *et al.*, 2020). To reveal social behaviour using AT, a degree of  
447 control is needed over the system. Using model systems of fish constrained to localised  
448 areas or relatively small lakes, high-resolution tracking in combination with Proximity Based  
449 Social Networks, PBSN (temporal network analysis), significant strides have been taken  
450 towards measuring the wild social behaviour of fish. Vanovac *et al.* (2021), for example,  
451 tracked 108 freshwater fish (four species) every few seconds for a year to measure the  
452 location and duration of intra- and interspecific sociality. To measure social behaviour in  
453 wider ranging species, beyond the practical limits of pre-defined static receiver arrays,  
454 prototype 'Business card tags' have been developed; these operate as both transmitters and  
455 receivers for mobile peer-to-peer communication (Holland *et al.*, 2010). Further, proximity  
456 transmitters, miniaturised receivers that can detect conspecific coded transmitters over  
457 distances <10 m (Guttridge *et al.*, 2010) (Fig. 3, specifically d,e), have shown that an  
458 individual's actual social encounters can be logged and stored pending transmitter retrieval.  
459 The need for further technological developments in this area however remains; applications  
460 of devices like the Innovasea Mobile Transceiver (VMT) and Sonotronics' miniSUR - which  
461 are hybrid devices that transmit coded signals like acoustic transmitters, but also record  
462 transmissions from other tagged animals on the same frequency like monitoring receivers –  
463 are currently limited to small numbers on relatively large animals (e.g. Barkley *et al.*, 2020;

464 Haulsee et al., 2016), and in situations where the unit can be recovered to obtain the data.  
465 In all likelihood, advances in the 3D accuracy of spatial positioning of multiple tagged fish  
466 will yield the most insight into fine-scale social behaviours over the next few years (Aspillaga  
467 et al., 2021).

468 As with many aquatic tracking technologies, data retrieval continues to be a significant  
469 hurdle to overcome, particularly for studies involving multiple individuals and their  
470 interactions, as the data can grow exponentially with the addition of every individual. That  
471 said, current off-the-shelf mobile receivers, in combination with other sensors have  
472 provided tantalising insight into the interactions of particularly elusive and cryptic species.  
473 Barkley et al., (2020) for example, use VMTs, accelerometers, radio antennae combined in a  
474 pop-off package to describe increased activity (acceleration and depth changes) in slow  
475 growing, seemingly solitary Greenland sharks *Somniosus microcephalus* (Bloch & Schneider  
476 1801), when in the presence of conspecifics. Furthermore, the encounter rates of  
477 commercially important fish species (*G. morhua*, *Salmo salar* and *A. rostrata*) and  
478 opportunistic mammalian predators have been gleaned through standard tagging (of fishes)  
479 with coded transmitters and the deployment of VMT receivers and GPS tags to grey  
480 seals *Halichoerus grypus* (Fabricius 1791) in Canada (Lidgard et al., 2014). Finally, as we have  
481 already discussed, AT combined with investigations into stable isotope ratios, blood plasma  
482 and other physiological processes, have greatly furthered our understanding of trophic  
483 dynamics, food web structure and niche partitioning within species that share habitat  
484 (Dwyer et al., 2020; Matich & Heithaus, 2014). With the advent of increasingly open-source  
485 tracking technologies, we envisage exciting progress in this area in the next 10 years.

486

487 *Depth preferences and temperature regulation*

488 Detailed knowledge of how fish move through all three dimensions of the space they inhabit  
489 is often pivotal to our understanding of the mechanisms underpinning their behaviour.  
490 Further, the predominance of ectothermy among fishes means depth selection and  
491 thermoregulation are closely coupled. Water temperature together with dissolved oxygen  
492 levels, light, salinity gradients, prey availability, predation risk, and physical habitat features  
493 are among the key factors shown to drive vertical movements (Hussey et al., 2015) ranging  
494 from localised diel migrations for example, in Myliobatid rays (Matern, Cech, & Hopkins,  
495 2000) to large-scale seasonal habitat shifts in *S. vitreus* (e.g. Raby et al., 2018). As we have  
496 seen, ongoing refinement of hardware and analytical techniques can enable sub-metre  
497 positions on the z-axis to be determined directly from the acoustic ping, and in near real-  
498 time, using hyperbolic positioning. This has been used to good effect to elucidate how  
499 different structures, flow field and temperature characteristics around hydropower facilities  
500 affect the vertical distribution and corresponding downstream passage outcome for  
501 migrating juvenile salmonids (Arenas et al., 2015; Deng et al., 2011; Li et al., 2015; Ransom  
502 et al., 2007). However, it is worth highlighting here that different manufacturers use  
503 different transmitter coding systems in an attempt to minimise both tag clashes and false  
504 positive detections and this can impede compatibility and collaboration between networks  
505 of researchers using different technologies (see Reubens et al., (2021) for discussion around  
506 this issue). Further, the comprehensive receiver arrays required for continuous 3D  
507 positioning often render its application unfeasible in the open ocean and large, deep lakes  
508 where species can be far-ranging in all dimensions. While in shallow water there may be too  
509 little vertical separation in the locations of the hydrophones to adequately resolve  
510 transmitter depth (Cooke *et al.*, 2005; Semmens, 2008).

511 Combining pressure and temperature sensors with acoustic transmitters offers a  
512 widely applicable and often more cost-effective alternative (both in terms of hardware and  
513 data processing requirements), and can still provide high accuracy and precision (Baktoft *et*  
514 *al.*, 2015). For example, Schurmann, Claireaux, & Chartois (1998) were able to demonstrate  
515 that a change in the amplitude of diurnal migrations of sea bass *Dicentrarchus labrax* L.  
516 resulted from manipulating vertical oxygen gradients in the water column within an  
517 experimental tank, down to an accuracy of  $\pm 5$  cm using acoustic pressure sensor  
518 transmitters. However, in field environments with extreme variation in environmental  
519 parameters (e.g. salinity, water temperature, flow rate) high accuracy in depth  
520 measurements may require additional field calibration (Brownscombe *et al.*, 2019a; Veilleux  
521 *et al.*, 2016). Technical issues aside, acoustically transmitted temperature and/or depth  
522 sensor data has been used to investigate the influence of feeding regimes on vertical activity  
523 of cage cultured *S. salar* (Føre *et al.*, 2017), vertical thermoregulation in sunfish *Mola mola*  
524 L. (Cartamil & Lowe, 2004), vertical separation of year classes through predator-prey  
525 dynamics in bull trout *Salvelinus confluentus* (Suckley 1859)(Gutowsky *et al.*, 2013), the  
526 impact of seismic surveying on *G. morhua* and saithe *Pollachius virens* L. distribution  
527 (Davidsen *et al.*, 2020) and sea trout *Salmo trutta* L. use of vertical gradients as a response  
528 to parasite loading (Mohn *et al.*, 2020). Direct measurement of the temperatures and  
529 depths that free ranging fish move through has allowed us to move beyond broad  
530 correlational inferences derived from 2D location data alone and advance understanding of  
531 fundamental aspects of fish physiology and environment selection. Nevertheless, there is  
532 the risk that without corresponding environmental data collected at biologically relevant  
533 temporal and spatial resolution, studies will lack the ability to fully contextualise such  
534 animal borne data. For example, despite gaining detailed movement data, including depth,

535 from Mekong giant catfish *Pangasianodon gigas* (Chevey 1931) tracked for up to nine  
536 months in a reservoir, insufficient collection of concurrent temperature and dissolved  
537 oxygen datasets meant it was not possible to draw robust conclusions about the  
538 mechanisms driving their behaviour (Mitamura *et al.*, 2008). Into the future, there is great  
539 potential for repeating tracking studies that have produced well defined relationships  
540 between fish distribution, behaviour and water temperature as a tool to identify and predict  
541 the impacts of a changing climate.

542

#### 543 *Invasion biology*

544 An important prerequisite to applied measures for combating the growing list of fish species  
545 becoming established in non-native locations, is to understand the impact they have on  
546 native species and habitats. This might include monitoring the spread, movement  
547 capabilities, reproductive ecology and competitive interactions with other species (Deacon  
548 *et al.*, 2011; Mills *et al.*, 2004). AT has been pivotal in revealing some of this ecological  
549 information which can then inform more targeted mitigation measures. One of the first fish  
550 to ever be domesticated, the goldfish *Carassius auratus* L., now considered as one of the  
551 world's most invasive species, were tracked in a river in south-western Australia using AT to  
552 show that some individuals were capable of moving >200 km per year; crucially this study  
553 was also able to infer that movements into lentic habitat coincide with spawning behaviour  
554 in this species providing vital knowledge for control programmes (Beatty *et al.*, 2017).  
555 Monitoring a newly-established source population of round goby *Neogobius melanosto-*  
556 *mus* (Pallas 1814) within the Rideau Canal in Ontario, Canada, Bergman *et al.* (2022) were  
557 able to track the invasion front of this species which is normally native to the Black and

558 Caspian Seas. Dispersal amongst a quarter of the tagged individuals was established via  
559 receivers situated within canal locks which were hypothesised to enhance passage  
560 (Bergman *et al.*, 2022). The scale of the challenge facing marine invasive control has been  
561 demonstrated through a study on lionfish *Pterois volitans* L. in the western Atlantic, showing  
562 an eight-fold variation in individual home range estimates (~48000 – 379000 m<sup>2</sup>) and ~40%  
563 of individuals travelling >1 km from the tagging site towards deeper habitat (Green *et al.*,  
564 2021). With the success of species invasion often contingent on species-community  
565 interactions (Lodge, 1993), multispecies AT tagging programmes will be key, as will  
566 developments to overcome the challenges discussed in the previous section around  
567 measuring fine-scale interactions.

568

## 569 2) Applied Research

570 There are many cases in which the ecological information gleaned from AT studies on fish  
571 are an important precursor to applied management measures, mitigation strategies or  
572 conservation interventions. In this section we explore more explicitly how AT has  
573 fundamental application in the management and conservation of aquatic resources.

574

### 575 *Species conservation and management*

#### 576 *Evaluating extinction risk and threat assessments*

577 Continuing data deficiency in even basic population parameters hinders the robust  
578 classification of extinction risk for a fifth of global fish species as assessed by the IUCN

579 (IUCN, 2020) and prevents the potential for their protection within legal frameworks  
580 (VanderZwaag *et al.*, 2013). The assessment of endangerment relies on fundamental  
581 knowledge of demographic parameters to estimate absolute population size, trends in  
582 abundance and geographic range (IUCN, 2012). By tracking individuals from different  
583 components of the population, for extended periods of time, and with the ability to  
584 determine much more precisely when mortality occurs compared to traditional mark-  
585 recapture approaches, AT provides a powerful means of collecting such data for fishes (Lees  
586 *et al.*, 2021). Further, telemetry-derived data can facilitate quantification of the main  
587 processes driving species decline and extinction (habitat loss and alteration,  
588 overexploitation; introduced species; pollution, and climate change), most obviously in the  
589 context of how the spatial ecology of a species predisposes it to specific impacts (Cooke,  
590 2008). In a notably rare example of deep water AT, southern dogfish *Centrophorus zeehaanii*  
591 (White, Ebert & Compagno 2008) were tracked for 15 months at depths of between 300 –  
592 700 m, to demonstrate the effectiveness of a large (100 km long) fishery closure to conserve  
593 this species, extirpated from much of its range off southern Australia (Daley *et al.*, 2015).  
594 Although clearly possible, there remain substantial limitations to tracking wide-ranging  
595 species and/or those that occupy deep water habitats. Technical and logistical challenges in  
596 deploying deep water arrays have constrained the majority of AT studies to depths under 50  
597 m (Loher *et al.*, 2017), and bringing physoclistous species to the surface to tag poses the risk  
598 of damage and mortality due to barotrauma and post-release predation (e.g. Bohaboy *et al.*,  
599 2020; Curtis *et al.*, 2015). The increasing use of in-situ tagging methods at depth and  
600 improvements to surface tagging protocols such as employing descender devices and rapid  
601 tag attachment methods to minimise time at the surface will further unlock the huge

602 potential of AT to study fish movements and population dynamics in the deep sea (Edwards  
603 et al., 2019; Runde & Buckel, 2018).

604 Threats to fishes, especially those with complex lifecycles that undertake migrations  
605 between habitats, vary through their lifetimes, making the study of all life-stages  
606 imperative. Minimum acoustic transmitter size has historically prohibited the study of small,  
607 juvenile life-stages (see *Tracking small species and life-stages*), the population component  
608 which for many endangered fish species, suffers high human-induced mortality (e.g.  
609 Chinook salmon *Oncorhynchus tshawytscha* (Walbaum 1792) Perry et al., 2010). Further, for  
610 long-lived species transmitter life duration may be prohibitively short (Donaldson *et al.*,  
611 2014). Technological advances, the growth of large transnational receiver networks (e.g.  
612 Great Lakes Acoustic Telemetry Observation System [GLATOS], Ocean Tracking Network  
613 [OTN], European Tracking Network [ETN]) and new approaches to data analysis such as  
614 incorporating acoustic data into mark-recapture models (Bird *et al.*, 2014; Dudgeon *et al.*,  
615 2015), as well as the growth of spatially explicit integrated population models (Goethel *et*  
616 *al.*, 2021) that better estimate abundance and predict the impacts of environmental change,  
617 are all expanding the utility of AT for threat assessments and conservation planning.  
618 However, AT remains just one in a suite of necessary tools, as exemplified by studies on *S.*  
619 *microcephalus*, a species for which significant knowledge gaps remain. Effective  
620 management is most likely to be realised through a multi-method approach integrating  
621 biologged physiological, environmental and movement data with population genetics and  
622 genomics, stable isotope analysis and commercial catch data (Edwards et al., 2019).

623

624 *Fisheries management*

625 AT has enabled vast knowledge gains about the spatial ecology of fishes, which in the  
626 context of exploited species, especially those that are wide-ranging and/or straddle national  
627 boundaries, is fundamental to effective fisheries management. In the first instance, AT can  
628 be far more effectively employed to define the stock unit than traditional approaches such  
629 as mark-recapture (Donaldson *et al.*, 2014). For example, acoustic tracking of Greenland  
630 halibut *Reinhardtius hippoglossoides* (Walbaum 1792) revealed connectivity between its use  
631 of inshore fjords and offshore habitats around Baffin Island, Canada, casting doubt on the  
632 status of separate inshore 'resident' and offshore stocks and highlighting the need for a  
633 shared quota (Barkley *et al.*, 2018). Conversely, the discovery of high site fidelity and  
634 presumed natal homing has challenged the assumption of common stocks in many species  
635 including *G. morhua* (Robichaud & Rose, 2001; Svedäng *et al.*, 2007), Pacific cod *Gadus*  
636 *microcephalus* (Tilesius 1810) (Cunningham *et al.*, 2009), and *C. undecimalis* (Young *et al.*,  
637 2014). There is also growing recognition of how individual and ontogenetic variation in  
638 spatial responses to environmental conditions and exploitation, drive the dynamics of  
639 populations (Alós *et al.*, 2019; Goethel *et al.*, 2021). In addition to this increasingly fine-  
640 scale understanding of the structure and spatial dynamics of exploited stocks, many of the  
641 life-history parameters required for stock assessment models can be directly determined  
642 using AT (Crossin *et al.*, 2017). These include instantaneous mortality rate (Block *et al.*,  
643 2019), survival probabilities related to life-stage and migration pattern (Chaput *et al.*, 2019;  
644 Perry *et al.*, 2010), delayed mortality from by-catch or recreational catch and release  
645 activities (Curtis *et al.*, 2015; Halttunen *et al.*, 2010; Yergey *et al.*, 2012), predation  
646 (Berejikian *et al.*, 2016), and the spawning contribution of different stock components (Faust  
647 *et al.*, 2019). Crucially for fisheries management, this information is attainable at the scale of

648 the specific stock (DeCelles & Zemeckis, 2014). By bringing together datasets on spatial  
649 dynamics with these population parameters, spatially explicit integrated population models  
650 offer great potential to more accurately predict species' responses to dynamic processes  
651 such as harvest mortality and climate-induced changes (Goethel *et al.*, 2021). Nonetheless,  
652 despite the versatility and breadth of AT for informing fisheries management, in a review of  
653 global AT studies on all aquatic animals, Matley *et al.*, (2021) found a lack of management  
654 driven applications, with most studies focussed on generating general movement data. They  
655 also highlight key challenges to be addressed such as developing analytical tools and  
656 standardised approaches among research groups to allow the potential of the vast  
657 quantities of AT data being collected globally to be fully realised (Matley *et al.*, 2023, 2021).

658         It is the integration of AT with other approaches and the development of real-time  
659 tracking that offers most promise for more nuanced, creative and adaptive management of  
660 fisheries into the future. The increasing use of additional sensors such as heart-rate and  
661 electromyograms enable quantification of the sub-lethal fitness impacts of fishing activities  
662 such as the stress-induced physiological changes from catch and release (Donaldson,  
663 Arlinghaus, Hanson, & Cooke, 2008 and references therein). Within the context of  
664 ecotoxicological studies that have the dual purpose of understanding the impact of pollution  
665 on exploited stocks, as well as the human health risks of consumption, AT provides the  
666 opportunity to relate individual fish movements to contaminant burden and thereby  
667 manage exposure risk (Taylor *et al.*, 2018). Crucially, AT enables an understanding of trait  
668 variation (e.g. movement) between individuals, relative to the population mean, which for  
669 fisheries that can unknowingly selectively harvest, can have important implications for  
670 ecosystem functioning when combined with physiological data (Allgeier *et al.*, 2020).

671 Further, behavioural change in response to hyperdepletion effects, such as reduced  
672 vulnerability or increased timidity can also be measured with AT, providing critical  
673 information for stock assessments and harvest control (Arlinghaus *et al.*, 2017). Equally,  
674 integration with genomics promises insight into how genetic variation drives individual  
675 behaviour, with applications ranging from predicting the ways in which environmental  
676 change may impact highly locally adapted yet exploited species such as Arctic char  
677 *Salvelinus alpinus* L. (Moore *et al.*, 2017), to understanding the extent to which fishing  
678 exerts a selective pressure on wild populations (Olsen *et al.*, 2012; Villegas-Ríos *et al.*, 2017).  
679 Gaining increasingly detailed information on threats enables continued refinement of  
680 conservation and fisheries management policies. For example, Forget *et al.*, (2015) used AT  
681 to determine the vulnerability of target and non-target species to FADs used in the tuna  
682 purse seine fishery, identifying how impacts on non-target species could be reduced. Finally,  
683 by removing the time lapse associated with periodic receiver download, real-time tracking  
684 opens up huge possibilities for adaptive management, an approach that has also garnered  
685 much attention in aquaculture (Føre *et al.*, 2017; Hassan *et al.*, 2019). In one of the first  
686 examples from a wild fishery, on the Sacramento River, USA, receivers transmitting near  
687 real-time data to a communications centre, alerted water managers to the earlier than  
688 expected migration of *O. tshawytscha* smolts. In response, water diversion structures into  
689 the Delta were closed, greatly reducing the loss of fish through that route (Klimley *et al.*,  
690 2017).

691

692 *Evaluating spatial protection*

693 Integrated data and the organised collaboration of ‘individual’ acoustic telemetry projects  
694 (Taylor *et al.*, 2017), is already proving invaluable for managers to assess connectivity  
695 created by long-range movements between areas of concern (Lédée *et al.*, 2021). This can  
696 also provide important information guiding the restoration of critical habitat (Brooks *et al.*,  
697 2017) and enable adaptive management of river water control structures to enhance  
698 connectivity during key fish migration events (Klimley *et al.*, 2017; Teichert *et al.*, 2020).  
699 Consequently, through either manual tracking or passive arrays, AT remains one of the  
700 primary tools for assessing the space use of imperilled species residing within existing or  
701 proposed aquatic protected areas (Cooke *et al.*, 2005). Novel approaches, for example those  
702 that combine AT with Resource Selection Functions that integrate movement data with data  
703 on resource availability, are beginning to be adopted to assist with the initial prioritisation  
704 and evaluation of habitat to be conserved (Griffin *et al.*, 2021). Additionally, diversification  
705 of environmental DNA (eDNA) approaches to assess the spatio-temporal distribution of  
706 cryptic species will likely require the increasing support of AT to assist in validating positive  
707 eDNA detections (Harris *et al.*, 2022) as this relatively recent methodology continues to be  
708 developed and refined.

709         The ability to accurately assess the efficacy of protected areas using AT, however, is  
710 highly dependent on the size of the area under protection and the ability of the species in  
711 question to make long-range movements. Even for highly mobile species within Very Large  
712 Marine Protected Areas (VLMPPAs), data from array-based acoustic telemetry can be  
713 analysed using dynamic Brownian Bridge Movement Models, which account for the distance  
714 and elapsed time between consecutive detections, and can establish the extent of an

715 animal's home range that is encapsulated within the protected area (e.g. Carlisle et al.,  
716 2019); although note earlier discussion around the challenges in doing this. For the shark  
717 species within this study, it was estimated that grey reef sharks *Carcharhinus amblyrhynchos*  
718 (Bleeker 1856) required at least one year, and silvertip sharks *Carcharhinus albimarginatus*  
719 (Rüppell 1837), two years of monitoring to effectively estimate their activity spaces (Carlisle  
720 et al., 2019). Alternatively, even species capable of making long-distance movements, well  
721 beyond the range of acoustic receivers, may show high levels of residency or site fidelity to  
722 specific places and at specific times of year (Curnick et al., 2020) which may be sufficient to  
723 offer a degree of protection during important behaviours or key life-history stages. Thus,  
724 assessing the space use of multiple species concurrently can help to demonstrate enhanced  
725 efficacy of marine spatial protection, particularly as MPAs are rarely established with a  
726 single species in mind (Casselberry et al., 2020; Hays et al., 2020). Once a tagged fish moves  
727 outside of the range of a receiver however, there is a significant degree of uncertainty; even  
728 notoriously site faithful *C. amblyrhynchos* for example, can appear to undertake different  
729 scales of 'long-range' movements (134 km derived from acoustic telemetry [Heupel,  
730 Simpfendorfer, & Fitzpatrick, 2010] and 926 km derived from satellite tracking [White et al.,  
731 2017]). This is beginning to be remedied, in part, through cross-boundary tracking initiatives  
732 such as the FACT Network, the Integrated Tracking of Aquatic Animals in the Gulf of Mexico  
733 (iTAG), OTN and the Integrated Marine Observing System (IMOS), but remains an issue for  
734 non-networked, isolated or remote protected areas. AT remains a powerful and persuasive  
735 tool for quantifying full or partial space use inside current or proposed protected areas  
736 (Barnett et al., 2012; Knip et al., 2012), movements between different management zones  
737 operating as a network (Espinoza et al., 2015a), estimation of species-specific risk from

738 illegal fishing activity (Jacoby et al., 2020) and for improving spatial conservation by directly  
739 informing policy (Lea *et al.*, 2016).

740

#### 741 *Human-wildlife conflict*

742 Establishing the cause and effect of human-wildlife conflict in aquatic environments remains  
743 challenging and is infrequently documented. Additionally, the (often) passive nature of  
744 more recent AT studies mean that data are rarely available to inform real-time responses to  
745 potential conflict. However, the network of arrays around the coast of Australia, that  
746 comprise the IMOS (formerly the Australian Animal Tagging and Monitoring System,  
747 AATAMS), offer an exception to this general trend. Over the last decade, passive arrays in  
748 Western Australia have been supplemented with satellite-linked Innovasea VR4 Global  
749 (VR4G) receivers at some of the most popular beaches for people (McAuley *et al.*, 2016).  
750 Providing near real-time data retrieval, AT is being linked to social media platforms to  
751 generate 'live alerts' to beach goers when white sharks *Carcharodon carcharias* L. tagged  
752 with acoustic transmitters approach the area. Building on the back of a large collaborative  
753 research programme, the Shark Monitoring Network initiative has informed thousands of  
754 water users about hundreds of potential 'shark hazard events' (McAuley *et al.*, 2016). The  
755 advent of increasingly accessible, real-time data however, is not without its potential  
756 problems, with these same data being used to locate and kill 'problem individual' sharks,  
757 undermining not only the safeguarding intentions of the initiative, but also the science and  
758 the conservation behind the project (Meeuwig *et al.*, 2015). This has led to calls for a more  
759 proactive approach to mitigating the potential unintended consequences of animal tracking,

760 and the associated data use, that may manifest as increased exploitation and disturbance of  
761 threatened species (Cooke *et al.*, 2017).

762         Elsewhere, within recreational catch-and-release fisheries, estimates of post-release  
763 survival are often inaccurate with mortality sometimes occurring immediately, for example  
764 as a result of barotrauma, or a short while after as stress and injury from capture make  
765 individuals more susceptible to depredation (Raby *et al.*, 2014). Quantifying the extent and  
766 timescale of mortality however remains a challenge but fortunately one where AT is  
767 beginning to make inroads. It was recently estimated, using a 3D acoustic positioning array  
768 in the Gulf of Mexico, that 83% of red snapper *Lutjanus campechanus* (Poey 1860) and 100%  
769 of gray triggerfish *Balistes capriscus* (Gmelin 1789) mortality was a result of post-release  
770 depredation. However, for snapper at least, releasing individuals with descender devices  
771 (weighted devices that assist in returning the fish to depth), did significantly reduce  
772 mortality (Bohaboy *et al.*, 2020). It is important to remember of course that once collected,  
773 AT data might also reveal unintended insight. The near simultaneous loss in December 2014  
774 of 15 acoustic transmitters from an array in a protected area in the central Indian Ocean for  
775 example, was found to be indicative of a suspected illegal fishing event, once natural tag  
776 loss from the system had been controlled for (Tickler *et al.*, 2019). As pressure on aquatic  
777 resources continue to increase, as well as increasing potential for distributional shifts of  
778 species in response to climate change, we envision that issues around human-wildlife  
779 conflict will continue to increase, presenting further opportunities for AT to play a role in  
780 monitoring and mitigation.

781

782 *Kinematics, energetics and physiological impacts of human modified systems*

783 In its simplest form, AT enables an individual to be detected at two spatially and temporally  
784 separated points allowing estimation of minimum distance moved over time, i.e. swim  
785 speed over ground, and thus broad inference about behavioural state and energy costs in  
786 free-swimming fish (e.g. Madison, Horrall, Stasko, & Hasler, 1972). The more spatially  
787 and/or temporally separated these detection events are, the larger the error in such  
788 estimates due to failure to capture variations in path curvature and depth, as well as  
789 behaviours such as resting and burst swimming (Cooke *et al.*, 2004b). The increasing  
790 resolution and near-continuous positioning afforded by dense passive receiver arrays and  
791 active tracking technologies enables more accurate determination of swim path metrics  
792 such as speed, turn angle and direction of movement; although active tracking can  
793 practically only achieve this for a small number of individuals over limited temporal and  
794 spatial scales (Meese & Lowe, 2020). From these, key descriptors of path characteristics  
795 (e.g. tortuosity) can be derived to determine how well a track conforms to established  
796 movement models (e.g. correlated random walk, biased correlated random walk, Lévy  
797 walk), helping to develop more accurate models of dispersal (Papastamatiou *et al.*, 2011).

798       Overlaying fine-scale ( $\pm <5$  m) 2D and 3D individual trajectories from acoustic  
799 positioning with concomitant environmental data, has proven key to understanding the  
800 mechanisms underpinning individual behavioural responses to anthropogenic perturbations.  
801 For example, near-continuous tracks of migratory European eel *Anguilla anguilla* and *S.*  
802 *salar* have been analysed in relation to flow fields on their approach to hydropower and  
803 water withdrawal facilities. These study systems have proven significant in unravelling the  
804 complex interactions between fish and the multiple hydrodynamic variables that elicit

805 behaviours such as rejection on the approach to accelerating flows (Piper *et al.*, 2015),  
806 milling (Svendsen *et al.*, 2011b) and fine-scale adjustments in swimming direction and speed  
807 (Silva *et al.*, 2020). Further, precise, real-world data are invaluable for the parametrisation  
808 and validation of agent-based models. Predictive behavioural models, that enable testing of  
809 different management scenarios aimed to reduce fish mortality and delay, are a key area of  
810 focus for hydropower, water abstraction and flood defence managers (Goodwin *et al.*,  
811 2006, 2014).

812           Even at fine resolution however, inferences about the energetics of movements and  
813 behaviours derived from position data alone will be inherently lacking through failure to  
814 consider the dynamics of the fluid in which the fish is moving and the physiological state of  
815 the individual. Thorough understanding of the biomechanics and energetics of free-  
816 swimming fish therefore requires moving beyond an animal's track characteristics.

817 Measurement and modelling of salient metrics of the surrounding hydrodynamic  
818 environment such as flow velocity, turbulence intensity and hydraulic strain have revealed  
819 much about how migrating fish attempt to optimise energy usage (Piper *et al.*, 2015; Silva *et*  
820 *al.*, 2020; Svendsen, Aarestrup, Malte, Thygesen, Baktoft, Koed, Deacon, Cubitt, *et al.*, 2011).  
821 For example, the modelled energy costs of a pallid sturgeon *Scaphirhynchus albus* (Forbes &  
822 Richardson 1905) actively tracked during its upstream spawning migration through a  
823 velocity-surveyed section of the Missouri River, USA, were lower than those calculated for  
824  $10^5$  random paths in the same reach (McElroy *et al.*, 2012). A suite of fish-borne sensors  
825 enable time-stamped monitoring of an individual's physiological processes such as muscle  
826 activity (Cooke *et al.*, 2004b), heart rate (Lucas *et al.*, 1991) and tail beat frequency  
827 (Watanabe *et al.*, 2012), while accelerometers and speedometers provide a measure of

828 speed (Block et al., 1992). These have been used successfully alongside acoustic positioning  
829 techniques to explore fish activity patterns and their associated energy expenditures  
830 (Meese & Lowe, 2020), as well as the stress responses and energy costs resulting from  
831 human disturbances such as recreational fishing (McLean *et al.*, 2019), hydropower  
832 generation (Burnett *et al.*, 2014) and seismic surveying (Davidsen *et al.*, 2020). While such  
833 technologies began as stand-alone and typically data storage devices (Cooke *et al.*, 2004b),  
834 the evolution of transmitting sensors and those integrated within acoustic positioning  
835 technologies offer much greater scope to derive detailed data from free-swimming fish  
836 without the need for recapture (Cooke *et al.*, 2016; Lennox *et al.*, 2017). Further, rapidly  
837 evolving data compression and transfer techniques to embed additional sensor data within  
838 the transmitted acoustic signals will serve to deepen our mechanistic understanding of  
839 fishes' behaviours as they move through their increasingly human-impacted environments  
840 (Cooke *et al.*, 2022).

841

### 842 3) Future directions and considerations

843 In this section we look ahead to some of the innovations that we envisage will further  
844 enhance the application of AT in fish biology. We highlight areas in which innovations are  
845 likely to have the biggest impact, and discuss some of the more generic issues and  
846 considerations that still present a challenge for AT.

847

848 *Tracking small species and life-stages*

849 Historically, the large size of transmitters has biased the application of AT towards adult life-  
850 stages and/or juveniles of large taxa only. Further, for species that exhibit sexual body size  
851 dimorphism such as anguillid eels, acoustic tracking has been skewed towards larger  
852 females (Bultel *et al.*, 2014; Piper *et al.*, 2013). This challenges the principal assumption that  
853 studied individuals are representative of the wider population and risks the erroneous  
854 extrapolation of findings. In applied research, this can have serious negative consequences  
855 such as misdirection of conservation funds or ineffective mitigation measures. To remedy  
856 this, continuing efforts towards transmitter miniaturisation, aided by substantial  
857 improvements in battery and microprocessor technologies, are greatly increasing the range  
858 of life-stages and species that can be tracked (Fig 3)(Lennox *et al.*, 2017). When studying  
859 small species and life-stages for which commercially available transmitters may approach  
860 the limits of the acceptable tag to body weight ratio (traditionally the 2% rule, [Winter,  
861 1983], although this is increasingly being questioned, [e.g. Brown, Cooke, Anderson, &  
862 McKinley, 1999]), body morphology also becomes an important consideration. The narrower  
863 body cavity relative to fish size among species with an elongated shape requires even  
864 smaller transmitters. New transmitters as small as 12.0 x 2.0 mm, weighing as little as 0.08  
865 grams in air and lasting 30 days at a 5-second ping rate interval have been recently tested in  
866 juvenile lamprey *Entosphenus tridentatus* (Richardson 1836) and *A. rostrata* (Mueller, Liss, &  
867 Deng, 2019, Fig 3a). Although AT has been used across a wide range of taxa, the scale of  
868 investment directed towards juvenile salmonid research to assess stocks (see *Fisheries*  
869 *management*) and quantify anthropogenic impacts such as hydropower facilities continues  
870 to drive much of the innovation within the field (Cooke *et al.*, 2013; Walker *et al.*, 2016). For  
871 example, injectable acoustic transmitters have been developed for small fish sizes but also

872 the volume of individuals and speed required to tag statistically meaningful samples, given  
873 the high mortality rate of juvenile out-migrating salmon smolts (Deng et al., 2015).

874 Long battery lives are required to track species across multiple life-history stages. The  
875 lifetime of an acoustic transmitter however, reflects the trade-off between battery power  
876 and the frequency and strength of transmissions, along with any additional power burden  
877 from integrated sensors. For smaller species and life-stages, the need for miniaturisation  
878 inevitably results in a transmitter with a shorter battery life and typically smaller detection  
879 range. Currently the smallest available acoustic transmitters are best suited to capturing  
880 brief windows of activity rather than providing near whole lifecycle data. Life-time tracking  
881 will significantly improve our understanding of small and cryptic species conservation  
882 however, and small battery-less tag technologies, for example passive integrated  
883 transponders (PIT) remain viable on a multi-decadal scale, enabling near whole lifetime  
884 studies. Near whole lifetime, AT studies of small individuals may be possible in the future  
885 using self-powered transmitters that incorporate a transducer to use the energy from fish  
886 locomotion to power the tag (Li et al., 2016). More sophisticated programming regimes,  
887 such as multiple time-limited transmission rates and dormancy, offers researchers  
888 increasing flexibility to extend the life of small transmitters to capture discrete periods of  
889 interest. These are, at present, pre-programmed and so require detailed *a priori* knowledge  
890 of predictable behaviours and/or life histories to be of most use (Davies *et al.*, 2020;  
891 Stevenson *et al.*, 2019). Further development of responsive acoustic transmitters that can  
892 dynamically adapt settings, for example transmission frequency or dormancy, in response to  
893 distinct changes in activity or environmental conditions such as the transition between fresh

894 and saltwater, as has been trialled in Combined Acoustic and Radio Transmitter tags (Deary  
895 *et al.*, 1998), would vastly improve their usefulness.

896 Notwithstanding the restrictions posed by transmitter size, our application of AT to  
897 small species and/or life-stages is often limited by their inherent spatial ecology. The  
898 microscale movements relevant to many small fish species, for example, anemonefish  
899 *Amphiprion sp.* whose home range is often less than a metre (Kobayashi & Hattori, 2006),  
900 are smaller than can be effectively studied given the current accuracy of most technologies.  
901 Advancements in hyperbolic positioning systems have enabled researchers to reliably  
902 achieve 2D and 3D positions at sub-metre accuracy and precision in small individuals (e.g.  
903 Leclercq, Zerafa, Brooker, Davie, & Migaud, 2018)(Fig. 2). In a novel study, the JSATS,  
904 Juvenile Salmon Acoustic Telemetry system (Lotek Wireless, Canada), was employed in a  
905 challenging open marine environment to simultaneously track large numbers of individuals  
906 as small as 90 mm (Aspillaga *et al.*, 2021). But challenges remain for many applications,  
907 especially in complex habitats such as rocky areas, coral reefs and macrophyte beds where  
908 detections are impeded (Baktoft *et al.*, 2015).

909

#### 910 *Multi-sensor transmitters, combined technologies and surrogates*

911 Multi-sensor acoustic transmitters and AT studies that integrate additional biologging  
912 technologies (accelerometers, magnetometers, physiological sensors etc), and in some  
913 instances, direct observations, clearly facilitate broader research questions (Fig. 3). This has  
914 promoted greater exploration, for example, of the proximate mechanisms underpinning  
915 specific population level processes such as group living, social behaviour or individual  
916 behavioural variation/consistency through time (Villegas-Ríos *et al.*, 2017; Wilson *et al.*,

917 2015). Knowledge of these mechanisms for specific fish populations has the potential to  
918 greatly advance how we conserve and manage commercially important or highly threatened  
919 species (Villegas-Ríos *et al.*, 2022). Importantly, the four major AT manufacturers (Thelma  
920 Biotel; Lotek; Innovasea, Sonotronics), offer different sensor combinations with some  
921 facilitating bespoke sensor integration into transmitters. Careful consideration of the end  
922 user of AT data and anticipated collaborations with other research groups is needed prior to  
923 deciding on where to source equipment. Currently, not all suppliers provide integration of  
924 all sensor combinations into their transmitters, and restrictions remain around the  
925 compatibility between transmitters and receivers from different suppliers.

926         The recent modification and miniaturisation of RAFOS technology (a form of sound  
927 fixing and ranging) has presented the potential to track relatively small marine fish species  
928 across large areas of the ocean. The ROAM (RAFOS Ocean Acoustic Monitoring) approach  
929 uses moored acoustic transmitting units emitting acoustic signals that carry up to 1000 km,  
930 offering potential to conduct whole ocean scale tracking studies. Individual study fish are  
931 equipped with a RAFOS float receiver that detects the sound pulses from fixed stations and  
932 triangulates position. This logged information is either recovered by recapturing fish  
933 returning to known areas e.g. salmonid spawning rivers (which permits a significantly  
934 smaller tag than PSAT technologies), or can be transmitted to land via satellite after the  
935 float pops-up at a predefined time for species able to accommodate the larger tag this  
936 requires (Bronger & Sheehan, 2019). Clearly, these innovations have the potential to  
937 provide much greater insight into highly migratory species, particularly those that face  
938 multiple threats during long-distance movements.

939 Yet despite many encouraging examples within the literature where technological  
940 innovation or integration of sensors has provided true insight and/or policy-relevant data,  
941 combining technologies may not be a viable solution in instances where mortality is high  
942 (Klinard & Matley, 2020). Ethical, logistical and financial drivers are increasingly promoting  
943 approaches that reduce, or even remove, the requirement to capture and tag live fish to  
944 derive biologically meaningful data. For example, in perilous scenarios such as during transit  
945 of water control and power generation infrastructure, multi-sensor passively conveyed  
946 devices have been employed to collect environmental data on the likely experience and fate  
947 of fish (Deng et al., 2017; Pflugrath, Boys, Cathers, & Deng, 2019). By incorporating key  
948 locomotory and behavioural characteristics, it is hoped that evolving robotic fish surrogates  
949 (Fig. 3c), combined with computational fluid mechanics and predictive modelling, will  
950 ultimately eliminate the need for live fish transit experiments at hydropower facilities  
951 (RETERO project - <https://retero.org/>). Many of the research areas discussed may be  
952 advanced by applying increasingly sophisticated analyses to historic acoustic telemetry  
953 datasets, and by combining biological, physiological and behavioural data to produce  
954 predictive models to allow scenario testing of management interventions, thus greatly  
955 reducing the costs and animal use associated with the traditional 'build and test' approach  
956 (Goodwin *et al.*, 2014; Snyder *et al.*, 2019).

957

#### 958 *Live data for near real-time management*

959 AT systems which instantaneously relay detection data to a computer or data transfer unit  
960 at the surface present an opportunity for assessment of and dynamic adaptation to  
961 activities that may be stressful, harmful or fatal to fish. So-called 'live' AT technologies mean

962 fish tracks can be reconstructed, in near real-time, to measure the impact on fish of human  
963 disturbance activities such as marine infrastructure development (e.g. pile driving, gas and  
964 oil exploration and extraction, wind farms and port development). The potential for this  
965 approach is in its infancy but has been installed as part of the innovative adaptive planning  
966 consent process for a major road/airport infrastructure scheme with potential to disrupt  
967 important salmonid migration routes in a Norwegian fiord (Davidsen et al., 2021). Data  
968 retrieval however, continues to be a limiting factor for many AT studies that would benefit  
969 from live or near-live upload. In many instances, it can be extremely expensive and/or  
970 unreliable. Consequently, there has been significant interest in innovation that can provide  
971 reliable, real-time, long-range wireless access to AT systems. A recent proof of concept of  
972 the Internet of Fish (IoF), uses Low Power Wide Area Networks (LPWANs) and LoRa (Long  
973 Range wireless data protocol with low power modulation) to achieve just this, presenting an  
974 exciting opportunity for long-term, real-time behavioural monitoring of fish in commercial  
975 settings for example (Hassan *et al.*, 2019). The implications of this innovation could be huge  
976 for improving fish welfare in intensive aquaculture. With increased global scrutiny around  
977 the ethics of intensive fish farming it seems likely that AT technologies could become a  
978 routine tool to manage and demonstrate fish welfare (Matley et al., 2021).

979

#### 980 *Accuracy, precision and validation*

981 Irrespective of the scale and complexity of a receiver array, or the study question being  
982 addressed, robust interpretation of animal movement data requires some quantitative  
983 measure of the accuracy and precision at which a transmitter can be detected. Crucially, this  
984 should capture the influence of spatial and temporal variation on detections within the

985 specific study environment. Such sources of detection error are frequently overlooked or  
986 only partially accounted for in acoustic tracking studies (Brownscombe, Griffin, et al., 2019;  
987 Kessel et al., 2014; Klinard, Halfyard, Matley, Fisk, & Johnson, 2019). Equally, reflecting on  
988 detection efficiency during a study might also reveal redundancy within the array design  
989 (Gabriel *et al.*, 2021) that once identified, might free up a proportion of valuable receivers to  
990 monitor new locations.

991 Advances in transmitter and receiver design and data processing techniques provide  
992 increasing capability to achieve high accuracy and precision from both cabled and non-  
993 cabled arrays. For example, more sophisticated transmitter programming has reduced data  
994 loss from transmission collision when multiple transmitters are present and increased  
995 detection probability and positioning accuracy (Cooke *et al.*, 2005), even in acoustically  
996 noisy environments (Bergé *et al.*, 2012; Leander *et al.*, 2019; Weiland *et al.*, 2011). Fine-  
997 scale positioning studies typically require substantial post-processing to derive 2D or 3D  
998 positions from detection data, but the continual refinement of positioning methods is  
999 improving accuracy and reducing data omission during this process. For example, by  
1000 employing a time-of-arrival rather than time-difference-of-arrival algorithm and  
1001 incorporating a random walk movement model, the YAPS (Yet Another Positioning Solver)  
1002 approach developed by Baktoft, Gjelland, Økland, & Thygesen (2017) out-performed  
1003 comparable methods in terms of both accuracy and number of positions resolved, a method  
1004 that has been successfully applied to acoustically reflective environments (Vergeynst *et al.*,  
1005 2020). On a broader scale, where receivers may be dispersed over a wide area, model  
1006 simulations that predict each receiver's theoretical detection range based on site-specific  
1007 architecture, environmental variables and target species characteristics can be useful at the

1008 design stage (Gjelland & Hedger, 2013; Hobday & Pincock, 2011). Subsequent  
1009 parametrisation with empirical environmental datasets and detection range tests collected  
1010 within the study, enables calibration of live animal detection data post-collection.  
1011 Brownscombe, Griffin, et al. (2019) developed an approach that uses variation in the  
1012 detection efficiency of fixed reference transmitters collected at a subset of representative  
1013 'sentinel receivers' as a proxy measure for detection range across the whole array.  
1014 Application of the detection range correction factors they generated to a data set on *T.*  
1015 *falcatus* from the Florida Keys, showed substantial departure from the raw data (up to  
1016 127%) with most difference in the space use patterns associated with habitat and diel  
1017 differences (Brownscombe *et al.*, 2019b).

1018

## 1019 **Conclusions**

1020 Meeting the needs required of our rapidly changing aquatic environments, and doing so in  
1021 ways that are fair, equitable, sustainable and responsive, is not trivial. In 2017, Lennox et al.,  
1022 (2017) set out a vision for how multiplatform tracking systems will be utilised in the future  
1023 to monitor simultaneously the position, physiology and activity of aquatic animals and their  
1024 environment. They highlight the four pillars of progress required to achieve this as "(1)  
1025 technological and infrastructural innovations; (2) transdisciplinary integration of collected  
1026 data and new methods of analysis; (3) emergent applications for telemetry data in fisheries,  
1027 ecosystems, and the global management of aquatic animals; and (4) looking forward to  
1028 solving challenges that currently inhibit progress in telemetry research" (Lennox *et al.*,  
1029 2017). Since then, there have been advances in AT technology, data integration, analyses

1030 and application, many of which we have tried to cover in this review, but all of which have  
1031 significantly progressed research within the key themes discussed (see summary in Table 1).

1032 As AT users continue to diversify, alongside an ever-growing list of analyses and  
1033 packages designed to handle the associated data, there is a need to consolidate the current  
1034 state of the field of AT which remains a 'go to' approach for addressing key questions within  
1035 fish biology and conservation. This comes at a time when the pathway from fundamental  
1036 species ecology to end-user management and policy making is clearer than ever before;  
1037 careful consideration of AT application, study design and interpretation, including the  
1038 potential pitfalls, is needed to ensure transparency during all stages of this process  
1039 (Brownscombe *et al.*, 2019a). As we outline here, AT is both broadly applicable and highly  
1040 nuanced, enabling us to tease apart patterns of space use, segregation and migration, and  
1041 through increasingly more accurate high-resolution tracking, interactions and associations  
1042 between individual fish. Combined with machine learning approaches, physiological or  
1043 energetic sensors, or by coupling with ecotoxicology, eDNA or stable isotope analyses, AT  
1044 can be even more powerful an approach for monitoring the behaviour of individuals and  
1045 groups of fish. As both technological and analytical developments continue apace, this is an  
1046 exciting time to track fish using acoustics. We hope that the field will continue to attract  
1047 innovation that will generate new insight for mitigating threats, managing our stocks and  
1048 protecting the species occupying imperilled aquatic environments.

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1054

#### 1055 **Data Availability Statement**

1056 No data were used in this review paper which discusses work that is already published.

1057

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