Electronic tagging and tracking aquatic animals to understand a world increasingly

shaped by a changing climate and extreme weather events

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12	Lennox RJ, Afonso P, Birnie-Gauvin K, Dahlmo LS, Nilsen CI, Arlinghaus R, Cooke SJ,
13	Souza AT, Jaric I, Prchalova M, Riha M, Westrelin S, Twardek W, Aspillaga E, Kraft S,
14	Smejkal M, Baktoft H, Brodin T, Hellstrom G, Villegas-Rios D, Vollset KW, Adam T,
15	Sortland LK, Bertram MG, Crossa M, Vogel EF, Gillies N, Reubens J. 2023. Electronic
16	tagging and tracking aquatic animals to understand a world increasingly shaped by a changing
17	climate and extreme weather events. Canadian Journal of Fisheries and Aquatic Sciences
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73 Abstract

74 75 Despite great promise for understanding the impacts and extent of climate change and 76 extreme weather events on aquatic animals, their species, and ecological communities, it is 77 surprising that electronic tagging and tracking tools, like biotelemetry and biologging, have 78 not been extensively used to understand climate change or develop and evaluate potential 79 interventions that may help adapt to its impacts. In this review, we provide an overview of 80 methodologies and study designs that leverage available electronic tracking tools to 81 investigate aspects of climate change and extreme weather events on aquatic ecosystems. Key 82 interventions to protect aquatic life from the impacts of climate change, including habitat 83 restoration, protected areas, conservation translocations, mitigations against interactive effects 84 of climate change, and simulation of future scenarios can all be greatly facilitated by using 85 electronic tagging and tracking. We anticipate that adopting animal tracking to identify 86 phenotypes, species, or ecosystems that are vulnerable or resilient to climate change will help 87 in applying management interventions such as fisheries management, habitat restoration, 88 invasive species control, or enhancement measures that prevent extinction and strengthen 89 resilience of communities against the most damaging effects of climate change. Given the 90 scalability and increasing accessibility of animal tracking tools for researchers, tracking of 91 individual organisms will hopefully also facilitate research into effective solutions and 92 interventions against the most extreme and acute impacts on species, populations, and 93 ecosystems.

Keywords: global warming, electronic tagging, acoustic telemetry, PSAT, applied ecology

1. Introduction

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99 Anthropogenic-driven climate change will likely continue to intensify, at least in the near-100 term, regardless of international agreements to cut harmful emissions. Indeed, the climate 101 system has a time lag such that the effects of emissions cuts now will not be able to 102 completely mitigate the future amount of these gases in the atmosphere (Samset et al. 2020). 103 Evolutionary adaptation of animals to future climate scenarios is therefore needed as 104 ecosystems continue to change (Nagelkerken et al. 2023). The consensus is that climate 105 change will generally lead to a net loss of biodiversity, which yields biotic homogenization in 106 most areas (Malhi et al. 2020). Extreme habitats where specialists have evolved will likely 107 accept more generalist species, driving a loss of endemism and further homogenization 108 (Gordó-Vilaseca et al. 2023). Physiological tolerance to stressors, phenotypic plasticity and 109 capacity to adapt, both physiologically and behaviourally, in response to climate stress will 110 determine the winners and losers of climate change (Somero 2011; Pecl et al. 2017; Webster 111 et al. 2017; Andreasson et al. 2022). Identifying the likely losers, and managing for their 112 resilience is one of few options available to mitigate or forestall the impacts of climate change 113 (Schuurmann et al. 2022). Tackling the climate crisis is an enormous challenge but the focus 114 must be on adaptation to the new realities imposed by the changes. In actionable terms, this 115 means identifying the phenotypes, species, or ecosystems that are most vulnerable to climate 116 change, and using tools and actions such as fisheries management, habitat restoration, 117 invasive species control, or enhancement measures to forestall extinctions and fortify 118 ecological communities against the most damaging impacts.

119 Essential to managing under the constraints of a changing climate in inland and marine 120 waters are data that accurately describe the responses of biological units to change. In water, 121 behavioural changes play a key role because the initial response of individuals to human-122 induced environmental change is often behavioural (Toumainen and Candolin 2011). In many 123 ways, behaviour is the first line of defense for most aquatic organisms. Such responses can 124 then initiate a predictable sequence of observable changes (e.g. alteration of individual fitness 125 and population dynamics) that manifest as changes in population abundance (Cerini et al. 126 2023). The role of aquatic animal electronic tagging and tracking tools (including both 127 biotelemetry and biologging; herein E3Ts) in informing how wild animal populations react to 128 these global changes occurring in lakes, rivers, and seas is therefore important, allowing 129 researchers to identify, and understand and preview the resilience of species and ecosystems 130 to climate change. Investigating how aquatic tagging and tracking can make an actionable 131 and enduring contribution to climate research requires a suitable framework of climate change 132 impacts with which to consider the study designs that could be implemented. Pörtner and 133 Peck (2010) provided a simple framework to scale climate change impacts from individuals to 134 communities, which was created for causal inference about the impacts of climate change on 135 fish. In their framework, they suggest three scales at which climate affects fish: the individual 136 (physiology and behaviour), its population, and their ecosystem. Other researchers have 137 drawn similar frameworks based on these fundamental levels of organization (also 138 Nagelkerken et al. 2023), including the hierarchical response framework proposed by Smith et 139 al. (2009), where individual, within-ecosystem, and between-ecosystems effects of climate are 140 considered. Here, we consider the role of aquatic E3Ts within existing climate change impact 141 frameworks, focusing on aquatic animals that are at particularly high risk due to climate 142 change and extreme weather events (Pinsky et al. 2022; Figure 1). 143

2. Applying animal tracking to studying climate change

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146 2.1 Impacts of climate change on the performance of individuals

147 148 Background for linking the framework to electronic tagging and tracking: Physiological rates 149 controlled by the environment (aka the Fry Paradigm; Fry 1959) dictate progress towards life 150 history checkpoints. Laboratory experiments have demonstrated the importance of 151 temperature as a mediator of individual life histories; in fact, temperature is often referred to 152 as the 'master factor' controlling biological rates (Fry 1971; Hochchka and Somero 2002; 153 Sunday et al. 2012; Nakayama et al. 2016). However, field data from tracking can offer a much more comprehensive view of individual ecologies (Metcalfe et al. 2012, 2016; Šmejkal 154 155 et al. 2021). Major effects of climate change include extremification of water temperature 156 (including cold shock; Szekeres et al. 2016) and pH, and hypoxia in many areas, which 157 determine vital rates (including rates of physiological functioning and rates of movement), 158 and constrain activities to hospitable water conditions. All of these processes may in turn 159 drive competition for space and access to resources, as well as vulnerability to capture by 160 people and predators. For example, Vedor et al. (2021) demonstrated that climate-induced 161 hypoxia will promote habitat compression for blue sharks (*Prionace glauca*) and enhanced 162 vulnerability to surface-oriented fisheries. Better individual data from tagging may provide 163 insights into the maturation of fish as they initiate spawning migrations inferred from 164 movement patterns (Griffin et al. 2022) and lifespans of species based on tag detections that 165 can be linked to environmental experiences. E3Ts can also be used to explain how 166 exploitation removes high-performing metabolic phenotypes from populations (Duncan et al. 167 2019). Animal tracking can also help identify mortality events and specific responses of 168 animals to extreme scenarios that operate at a population scale (floods, heat waves, warm 169 winters, swells, etc.; Clark et al. 2020; Jarić et al. 2022; Sarkar and Borah, 2018; Smejkal et 170 al. 2023; Williams et al., 2017; Lempidakis et al. 2022) as well as the impacts of more gradual 171 changes (e.g. increased accumulated thermal units) on life histories. Such questions can be 172 directly answered by logging the environmental temperatures experienced by fish throughout 173 their lifespans. Using individual tagging data, analysts can query: where are the animals, how 174 do they use micro- and macro-habitats, how does their behaviour change during extreme 175 weather (e.g. heat waves, drought, natural disasters), how heritable are the phenotypes that 176 persist through climatic bottlenecks, and how does behaviour affect competition, predation, 177 reproduction, and senescence? Beyond behaviour, E3Ts can also help to assess the 178 physiological constraints and demands that environmental conditions pose, including for 179 example, measures of metabolism (Metcalfe et al. 2016). 180 *Examples:* Several studies have combined track and sensor data to investigate climate 181 vulnerabilities of individual animals. Depth-temperature records have been used to identify 182 environmental windows where loggerhead turtles (*Caretta caretta*) thrive (Patel et al. 2021), 183 and to compare chinook salmon (Oncorhynchus tshawytscha) and lake trout (Salvelinus 184 *namaycush*) habitat partitioning in a lake (Raby et al. 2020). Combining habitat, temperature 185 and tracking data, Freitas et al. (2016) showed that given favourable sea surface temperatures, 186 Atlantic cod (*Gadus morhua*) individuals selected shallow, food-rich vegetated habitats; 187 however, with warmer surface waters such as those predicted under future climate scenarios, 188 individuals remained at deeper waters in less productive habitats. Matching the thermal niche 189 of species to the future available thermal habitat using climate models can provide projections 190 for species' ranges under climate change using species distribution modeling (e.g. Legrand et 191 al. 2021; Patel et al. 2021). Movement tracks can be used to link abiotic features to

energetically sensitive behaviours, for example, revealing the importance of moderate ice
cover to the foraging behaviour of bowhead whales (*Balaena mysticetus*) in Nunavut, Canada
(Pomerleau et al. 2011). Similarly, Hamilton et al. (2017) found that sea ice decline

195 effectively reduced the degree of spatial overlap between polar bears (Ursus maritimus) and

196 their prey, ringed seals (*Pusa hispida*). Payne et al. (2018) used accelerometer loggers to 197 reveal that tiger sharks (Galeocerdo cuvier) had peak activity and, consequently, were more 198 vulnerable to fisheries bycatch at 22 °C. Kneebone et al. (2018) observed juvenile sand tiger 199 sharks (Carcharias taurus) in a bay (Massachusetts, USA) with acoustic transmitters outfitted 200 with accelerometer sensors and implemented Gaussian Markov random fields to model areas 201 with high activity and energy expenditure. Direct calibration of acceleration metrics to oxygen 202 consumption can provide estimates of oxygen consumption and energy landscapes, revealing 203 how habitat and climate interact to shape the metabolic demands and life course (aka pace of 204 life) of individuals. Such methods must be extended beyond temperature for aquatic species to 205 see how other water parameters affect energetics, to fully appreciate how climate change 206 affects aquatic animals across a range of climate-related impacts, including water volume loss 207 (i.e. drought), flow regimes, cyclones/hurricanes, pH extremification, or hypoxia. E3Ts can 208 also be used to study winter ecology, under the assumption that cold-water adapted fish show 209 elevated fitness in harsh winters and lose performance as winters warm (McMeans et al. 210 2020).

211 *Designing studies:* With careful planning and the availability of environmental data at relevant spatial and temporal scales, it is possible to assess relationships between individual 212 213 animal movement and environmental change. Simulations can facilitate projections describing 214 how niches (estimated from computer models) correspond to expected changes in 215 distributions (e.g., Patel et al. 2021). However, direct manipulations including habitat 216 alterations, such as studies with experimentally warmed outflows (e.g. from power plants), 217 and experimental displacement can be useful to test resilience and climate vulnerability across 218 species or phenotypes within species. There is a need to seek tools that will help make more 219 thorough assessments of the individual's status and fitness (e.g., survival) when exposed to 220 climate stressors, such as heart rate loggers and transmitters that measure indicators of 221 physiology (i.e., stress) that may be independent of other metabolic demands (e.g., 222 movement). Studying the impacts of climate change on individuals requires some control over 223 the habitat or the animals, which can be achieved using ponds or lakes to better understand 224 climate change impacts at this scale (Lennox et al. 2021). If combined with physiological 225 metrics of thermal performance and tolerance, E3Ts could provide us with a powerful tool to 226 predict climate impacts on individuals and species. Physiological measures of performance 227 and tolerance have predominantly been undertaken in the lab, creating opportunities to expand 228 the testing of temperature-mediated performance hypotheses in the field (Rezende et al. 229 2014). In this regard, E3Ts could be pivotal in elucidating whether these metrics are, in fact, 230 relevant in the wild.

2.2 Species responses to climate change

Background for linking the framework to electronic tagging and tracking: Detecting responses to climate change at the species level depends on distributional models that treat individual replication, the inherent unit at which E3Ts is conducted, as a means to understand a representative sample of a species. Using tracking data and models that account for individual variation (i.e. mixed effects), it can be possible to assess the species-scale responses of animals to climate change. It is logical that inferences made at the individual level can be extrapolated to the species scale, but specific approaches and aims will guide researchers to use E3T data at the species scale. Indeed, the changing habitats and the impact climate change will have on physiological processes will influence mass movements of animals, transferring matter and nutrients in bulk across boundaries (Nathan et al. 2008). Warmer water temperatures will force poleward or vertical changes in distribution as animals seek thermal refuge (Perry et al. 2005). Changes in river hydromorphology or ocean currents

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246 will alter species assemblages (Vannote et al. 1980) or species distributions (e.g. Gardner et 247 al. 2015). Diel vertical behaviour might also be influenced, as the northward distribution will 248 lead to shifts in seasonal variability in light availability, both impacting foraging for food and 249 predation risks, an impact on one of the planet's major biological pumps (Ljugstrøm et al. 250 2021). Beyond species-specific effects, climate change can cause spatiotemporal alterations to 251 the interactions between species or populations, which ultimately affect the structure of 252 ecosystems and their functioning (van Zuiden et al. 2016; Tunney et al. 2014). 253 *Examples:* To be relevant at the species scale, E3T experiments should aim to identify broad-254 scale movement and behavioural shifts representative of the species, including spatial or 255 temporal shifts, meaning data series that are broad in geographic scale or long in term are 256 most robust. Models using E3Ts can be used to generate distribution or niche models that are 257 built on representatives of a population and focus less so on intraspecific variation. This can 258 be accomplished by using individual data to generate models or predictions, such as in 259 Aspillaga et al. (2017) where a general northward shift of common dentex (*Dentex dentex*) 260 was projected based on mechanistic niche data established from tracking. Spatial shifts at the 261 species level have been revealed from tracking data in a lake, where Ríha et al. (2022) 262 identified a collective shift in the depth use of wels catfish (Silurus glanis) in response to 263 bottom hypoxia. As the climate continues to change, the centroid of animal distributions may 264 shift over time, which can be tracked from E3T data using archived data in a time series. 265 Moreover, migration routes could also shift; however, Horton et al. (2020) found that 15 years 266 of satellite tracking data did not reveal any significant changes in the migration routes of 267 humpback whales (Megaptera novaeangliae) despite changes in the oceanography and 268 magnetic fields during that period. This contrasts with 15 years of bluefin tuna (Thunnus 269 *thynnus*) tracking data from the Pacific, where tunas were observed to adapt their distributions 270 according to marine temperatures, including an extreme anomaly during a heatwave (Carroll 271 et al. 2022). In terms of timing of key life history events, Douglas et al. (2011) observed 272 phenological shifts in striped bass (Morone saxatilis) in the Miramichi River, while Hauser et 273 al. (2017) used time series data from satellite telemetry of beluga whales (Delphinapterus 274 *leucas*) to identify changing migration timing in the Arctic. 275 Designing studies: Understanding how species are responding (and will respond) to climate 276 change using E3Ts likely needs a reliance on temporal comparisons with long-term time 277 series for tracking changes at a relevant scale. Time series can identify gradual or stepped 278 changes in the phenology of key events, or may simply provide insights from aberrant events 279 such as heat waves or extreme weather that cannot be planned for (e.g. Heupel et al. 2002; 280 Carroll et al. 2021). Projects with several years of data sampling are likely to include some 281 periods of abnormally warm temperature or extreme weather, and data sampled during such 282 events are valuable to explain or even predict potential shifts in behaviour (e.g., refuge 283 seeking, foraging areas) that a population/species will face in the future (Westrelin et al. 2022, 284 2023). Experiments at the population scale using tracking may include randomized control 285 treatment trials in which control fish are systematically released and compared to a treatment 286 group that is reared under projected future environmental scenarios such as warming. Such 287 designs are possible using E3Ts to track the fate of a suitable fraction of a population to draw 288 inferences at scale using experimental rearing or challenge tests combined with fate tracking. 289 Interventions that could be considered include acute exposure or chronic immersion in warm 290 temperatures or acidified water, simulating the rearing conditions likely to be encountered by 291 fish experiencing climate change. Long-term tracking of these fish and comparison with a 292 control group will be instructive to understand the magnitude of the challenges faced by these 293 animals and proactively adopt management actions. For most studies aiming to generate

results at the population scale, customisation of battery lifetime to be long enough to detect

295 animals later in life, or addition of sensors to the tags for tracking days or total activity, can 296 greatly improve current data collection. 297

One important methodological possibility at the population scale is to track offspring and assign them to different parents, thereby tracking how exposure to different environments affects reproduction and fitness. In Caspian terns (*Hydroprogne caspia*), cultural transmission of migration routes was inferred from tracking birds with their own offspring and with fosters (Byholm et al. 2022). Genotyping tagged individuals could then allow us to also follow the temperature preferences across intraspecific genetic lines, and study evolutionary adaptations to climate change over time. Although designs using electronic tagging to better understand population responses to climate change are promising, caution is warranted when attempting to scale observations of individuals to establish trends about species or populations.

2.3 Global influence of climate change on ecosystems and communities

309 Background for linking the framework to electronic tagging and tracking: Climate change has 310 the potential to induce ecosystem-level changes, such altering the ecology, density, and 311 phenotypic structure of keystone species, creating mismatches between the migration 312 phenology of keystone species and their prey (Renner and Zohner, 2018), changing the 313 outcome of interspecific competition (Helland et al., 2011; Carmona-Catot et al., 2013), 314 increasing ecosystem vulnerability to invasive species (Ilarri et al., 2022; Souza et al., 2022), 315 shifting temporal and spatial niches of thermal specialists (Santiago et al., 2016), affecting 316 parasite-host interactions (Lõhmus and Björklund, 2015; Cable et al., 2017), increasing the 317 frequency and intensity of ecosystem perturbations, and ultimately causing interconnected 318 cascading effects that can disrupt ecosystem functioning (Durant et al., 2007; Thackeray et al., 319 2010). Climate change impacts can be further exacerbated through synergistic interactions 320 with other stressors such as eutrophication, pollution, water regulation, and biological 321 invasions (Woodward et al. 2010). Climate change can also create novel heterogeneity 322 through asymmetrically altering environmental conditions in space, which can alter mobile generalist consumer species behaviour and broadly reorganize food webs (Bartley et al. 2019). However, to fully track impacts, detailed ecosystem information has to be collected, starting with abiotic variables, food resources, and various organismal responses, representing a subset of taxa and trophic levels in the ecosystem (recognizing that not all species are suitable for tagging). Detailed animal tracking, in combination with other monitoring tools, can provide valuable insights into the extent of resulting changes in reproductive phenology, the level of their synchronization across different animal taxa, and how they affect the timing of food supply (Reglero et al., 2018; Renner and Zohner, 2018; Beltran et al. 2019, 2022). For larger organisms, E3Ts can effectively track responses to climate change that affect migration timing, nesting behavior, or small-scale habitat shifts due to migration. *Examples:* Despite a broad agreement that ecosystem approaches are needed to understand and manage environmental resources, incorporating animal tracking into whole-ecosystem research is still quite rare, and only a few ecosystem studies have used E3Ts. Yet, the movements and distributions of animals are crucial, as evidenced by the little auk (Alle alle), which deposits guano in lakes that yield such eutrophic conditions that invertebrates and fish are excluded; climate-induced range shifts would therefore induce landscape-scale changes in freshwater ecosystems (González-Bergonzoni et al. 2017). However, the highlighted

examples demonstrate the enormous potential of tracking data to reveal ecosystem consequences of climate change-induced alterations of animal behaviour. Guzzo et al. (2017)

combined long-term acoustic telemetry with diet analysis to show that warming reduced lake trout use of the nearshore areas, and thus reduced exploitation of limnetic food resources. This

resulted in a reduction in the growth and condition factor of lake trout and significant changes

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345 in carbon flux throughout the lake ecosystem. Caldwell et al. (2020) examined the effects of 346 earlier ice breakup on water temperatures and habitat production, as well as the consequences 347 for habitat use, behaviour, and fitness of brook trout (Salvelinus fontinalis). The study showed 348 that earlier ice breakup created resource-rich littoral-benthic habitat compared to pelagic 349 habitat. Nevertheless, movement data revealed that brook trout did not exploit the littoral 350 habitat due to warm temperature avoidance, which reduced their fitness. Thus, changes in ice 351 break-up drive multi-directional results for resource production within lake habitats and have 352 important consequences for predators.

353 The effects of climate change on the coupling between terrestrial and aquatic 354 ecosystems were studied by Hamilton et al. (2016) and Deacy et al. (2017). Hamilton et al. 355 (2016) used satellite telemetry to show that polar bears (Ursus maritimus) spent more time on 356 land during periods of reduced sea ice, spatially isolated from their preferred prey, ringed 357 seals (*Pusa hispida*). While on land, polar bears spent more time near ground-nesting bird 358 colonies and predated more on nesting seabirds. Deacy et al. (2017) used GPS telemetry in 359 Kodiak brown bears (Ursus arctos) to examine the response of bear behaviour to global 360 warming-induced changes in the availability of two important food resources, red elderberry 361 (Sambucus racemosa) and sockeye salmon (Oncorhynchus nerka). Climate warming 362 advanced the elderberry blooming to align with the spawning of sockeye, causing bears to 363 prioritize elderberry, and weakening the link between salmon and its contributions to the 364 surrounding land by fertilizing the earth and enhancing local biodiversity. 365 Designing studies: The ecosystem approach can be challenging because it requires 366 consideration of other trophic levels and how changes in focal animal behavior translate to 367 population, species, or community scales. Behavioral changes can alter ecological interactions 368 (e.g., predator-prey dynamics, competition, social behaviors), and these consequences can be 369 tracked using a suite of complementary tools that link tracking data to metrics collected at 370 different levels of the ecosystem. For example, approaches may require examining population 371 and life history parameters of key species, system productivity, and the strength or direction 372 of ecological interactions prior to, or during, movement tracking. In this way, the impacts of 373 climate change can be comprehensively studied using animal tracking. Effects of climate 374 change on ecosystems and communities could be studied through experiments involving 375 islands or small pond ecosystems using telemetry where manipulations can be undertaken, 376 including experimental warming. Space or time replication (e.g., across lakes) and reciprocal 377 transplant studies can be used to study evolutionary adaptation to climate change at an ecosystem scale. For example, ponds could be warmed at different temperatures, exposed to 378 379 different water levels or fluctuations, different nutrient loads, as well as different levels of pH 380 and dissolved oxygen. Alternative designs could involve tracking in replicated tracts, such as 381 whole lakes, along a latitudinal gradient that would treat climatic variation as a component of 382 the behavioural variation (Lennox et al. 2022). Experiments could additionally address 383 changes to physiological and behavioural phenotypic frequencies related to changing 384 environments, including activity, phenology, and interspecific interactions (e.g., predation 385 rates). Of special relevance would be multi-species experiments that integrate fish behaviour 386 with physiology (Cooke et al. 2008; Komoroske and Birnie-Gauvin 2022), to infer responses 387 at the level of communities, as well as effects on ecosystem metabolism. Where possible, 388 there should be an increasing emphasis on building models with multiple species to better 389 understand how different species respond when confronted by changes not in isolation, but in 390 the presence of competitors or predators. Experiments using predation tags-tools that 391 continue to be developed for identifying the fate of animals and a key ecological interaction— 392 should become a tool that helps reveal some of the most important aspects of ecological 393 dynamics symptomatic of climate change in both experimental and observational studies 394 (Lennox et al. 2023).

3. Testing climate resilience and management

3.1 Habitat restoration

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400 Physicochemical habitat is linked to climate and therefore measures aimed at improving 401 habitat suitability or availability can play a key role in buffering climate change effects for 402 individuals (Timpane-Padgham et al. 2017). For aquatic species reliant on physical habitats, 403 the most important mitigation effort is to conserve or restore essential habitats that minimize 404 impacts of climate change. Some of the most concrete examples are canopy shelters in rivers 405 (Fullerton et al. 2022; Kirk et al. 2022), artificial reef construction in the sea (Getz and Kline 406 2019), or artificial nests for seabirds (Burke et al. 2022). Indeed, animals may find refuge in 407 the landscape that helps them cope with climate change, but how this process operates in 408 nature may be challenging to understand for aquatic species. In an effective illustration of 409 this, Freitas et al. (2021) tracked several species of a fish community in a Norwegian fjord to 410 find that their depth distribution responded to environmental temperatures, showing that they 411 were allocating their time to spatial areas in the landscape that provided thermal refuge. 412 Tracking animals and their temporal and spatial use of habitat in various climate scenarios is 413 therefore an important avenue of research to inform restoration efforts that can be engineered 414 in a way to minimise climate effects. Indeed, our knowledge of what constitutes an effective 415 refuge for aquatic species may be biased or incomplete without empirical data from the field. 416 Opportunistic data may be key to generating new knowledge where experiments are not 417 feasible. For example, tracking animals can help identify areas of high use during weather 418 anomalies that provide refuge, or strategic use of areas that help maintain homeostasis and 419 that are key to protect, restore or even expand to face climate change (e.g. Henesy et al. 420 2022). Amat-Trigo et al. (2022) suggested that behavioural thermoregulation may provide an 421 innate mechanism of resilience to fish encountering a changing climate. Effective behavioural 422 thermoregulation, however, depends on the availability of suitable habitat, which may require 423 spatial planning measures in rivers, lakes, and coasts. Using this knowledge, action can be 424 taken to generate heterogeneity that buffers warming and protects important inflows and seeps 425 and upwellings.

3.2 Protected areas to facilitate persistence of vulnerable species

429 Protected areas (PAs) are often used as a management intervention to protect species against 430 disturbance (Agardy 1994; Edgar et al. 2014). Although marine PAs are widely known, 431 freshwater PAs are equally valuable and actionable (Saunders et al. 2002). PAs are globally 432 used to buffer exposure of animals to stressors, but their role in mitigating climate change 433 effects should be further explored (Hannah et al. 2008; Soares-Filho et al. 2010; Roberts et al. 434 2017). Adapting PAs to buffer vulnerable species from climate change may be a viable option 435 to mitigate the effects of temperature warming. Most advice suggests that marine PAs need to 436 be larger and better connected (McLeod et al. 2009) to effectively benefit species 437 experiencing climate change. However, there is an opportunity for gathering additional 438 evidence using tracking tools. Animal tracking is vital to understand how the functionality of 439 PAs will change as animals migrate and change their movements according to climate, 440 especially in open aquatic systems, where range shifting can alter the protection afforded by 441 area-based measures. In a climate change scenario, where the conditions in the ecosystems are 442 in constant change, the effectiveness of PAs might be challenged, as temperature fluctuations 443 can alter the suitability of certain habitats for constituent species (Hooker et al., 2011; Sahri et 444 al. 2022: Freitas et al., 2016). E3T studies can be designed to monitor how species respond to

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warming conditions with and without protections from potential synergistic stressors, which
in turn can inform conservation efforts and potentially lead to reconsideration and reallocation
of PAs and even the option for dynamic PAs based on seasonally changing needs of animals
(Sequeira et al. 2019).

3.3 Translocations or assisted migration

452 Climate change is challenging species to respond to rapidly changing conditions in their local 453 environments. Species may not have the capacity to adapt at a sufficient pace to these changes 454 (i.e. evolutionary adaptational lag) or may lack the dispersal capacity to colonise suitable 455 habitats (Schloss et al., 2012; Fréjaville et al., 2020). To overcome these limitations, "assisted 456 migration" (see Twardek et al. 2023 for definition) of animals to more suitable areas has been 457 proposed as a means of facilitating the resilience of a population impacted by climate change 458 by providing suitable habitats faster than they could reach them by natural range expansion 459 (Hällfors et al., 2014). Typically, these movements occur into areas where those individuals 460 would be predicted to move, provided they had sufficient time and connectivity between the 461 habitats, as they might be expected to in a slower climate change scenario (Hällfors et al., 462 2014). Assisted migration is gaining increased attention as a potential conservation tactic 463 (Twardek et al. 2023; Benomar et al., 2022), though much uncertainty and controversy 464 remains regarding the potential ecological risks and benefits (Ricciardi and Simberloff 2009; 465 Aitken and Whitlock 2013; Bucharova 2017). Thus far, successful cases of assisted migration 466 for conservation have been very limited, with most movements pertaining to trees and other 467 vascular plants in the context of forestry (Pedlar et al. 2012). Aquatic animals have rarely 468 been the subjects of assisted migration studies (Twardek et al. 2023), though there is 469 recognition of the values these movements may have in supporting fisheries (Green et al. 470 2010), and it seems likely that these movements will be increasingly considered to abate the 471 impacts of climate change on highly valued species, possibly at the cost of less economically 472 valued counterparts. Careful study and monitoring will be critical to this endeavour given that 473 it would not be desirable to have assisted migration become a broad-scale invasion (Mueller 474 and Hellmann 2008). Electronic tagging and tracking will be uniquely positioned to inform 475 how introduced species are using their newfound environments, expanding their ranges, and 476 interacting with the broader aquatic ecosystem. As a unique example of this, western swamp 477 turtles (Pseudemydura umbrina), Australia's rarest herptile, were outfitted with 478 radiotelemetry transmitters and temperature loggers and were introduced into a wetland 479 located 300 km south of the species' native range (Bouma et al. 2020). Over a six month 480 period, researchers gained insights into habitat use, movement, growth rates, mortality rates, 481 and microclimate conditions, providing important knowledge for future assisted migration 482 efforts for the species. Although fish have not been the focus of many assisted migration 483 studies, humans have inadvertently conducted assisted migration of fish at a large scale 484 through the stocking of fish throughout freshwater systems around the world (Halverson 485 2010). Whereas most of these movements would not constitute assisted migration, there is 486 great potential to study these movements in the context of assisted migration (see Banting et 487 al. 2021). As E3Ts continue to revolutionize how we understand aquatic animal movements 488 and species interactions (e.g. predation tags), it will undoubtedly be at the forefront of efforts 489 to study and monitor assisted migration. 490

3.4 Mitigation of interactive effects

Although the intensity of future climate change can be mitigated, aquatic temperatures will continue to warm, with limited potential for direct intervention for abatement. Climate change

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495 may, however, be an exacerbating factor for other stressors such as invasive species or 496 pollution (Bertram et al. 2022), that is operating interactively with warming; in many cases, 497 the other factors may be easier to address than the climate impacts (Brook et al. 2008). 498 Litchman and Thomas (2023) reviewed the role of several exacerbating factors that affect 499 species' metabolism and can interactively affect the vulnerability to warming. In such cases, 500 identification and removal of the interactive stressor will be an efficient remedy for the 501 species or population. For such interactive effects, it may be possible to mitigate the impact of 502 climate change on species by removing or addressing the interacting stressor, for example 503 invasive species removal or pollution remediation could enhance climate resilience of species 504 exposed to warming. In general, appreciation that climate vulnerability can be interactive is 505 still developing and we submit that animal tracking can help to reveal where interactions exist 506 and what actionable solutions can intervene to buffer the impacts of climate change. Such 507 approaches will necessarily rely on multi-disciplinary methods, and likely experimentation, to 508 identify and test how interactive effects operate. 509

3.5 Simulation of future scenarios

At a larger spatial scale, some studies suggest using global change projections together with predictive species distribution models (Santos et al. 2020). To predict species distributions using models, a first step is to understand the tolerance of individuals and populations to different environmental conditions, including for instance how individual performance (e.g. survival, reproduction) is affected by warming temperatures. Remote observation of thermal experiences by animals can be more important than theoretical or laboratory challenge tests for understanding the temperature selections made by aquatic animals, in large part because of plasticity that they may exhibit to cope with such changes (e.g. Levy et al. 2019). The relevance of thermal tolerance metrics derived from laboratory experiments have been debated (Rezende et al. 2014). The collation of animal tracking data into large databases allows for such synthetic modelling exercises and should be an important product of such open access products (Iverson et al. 2019). This is already being put into practice to prepare for climate change with a stronger understanding of likely animal responses (e.g. Hückstädt et al. 2020; Reisinger et al. 2022a,b; Chambault et al 2022).

4. Future directions

Aquatic E3Ts are part of a rapidly advancing field in movement ecology, with continually expanding use in ecological research and management (Hellström et al. 2022; Nathan et al. 2022). Examples of these technological advances include continuous improvements in battery technology that enable the miniaturisation of transmitters, permitting researchers to track smaller species (Hazen et al. 2012) and younger age-classes of aquatic organisms (Li et al. 2020). Emerging technologies such as self-powered tags that can harness the biomechanical energy of the host animal may allow for the study of individual fish over their entire life-span in the wild, across ontogenetic shifts, maturation, and eventual death (Liss et al. 2022). Parallel advances in on-board processing capabilities coupled with artificial intelligence programming make the next generation of transmitters able to remotely analyse large amounts of high-resolution sensor data to identify complex behaviours and physiological states, which can be quantified, summarised, and transmitted. Such on-board data-processing would bypass the current bottleneck posed by the narrow bandwidth in underwater communication, and further integrate big data science with animal tracking (Figure 2; Nathan et al. 2022; e.g. Adachi et al. 2023). In addition, new communication protocols and transmission techniques are being developed to reduce false detections and

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545 signal collisions, making it possible to track large numbers of fish simultaneously with very 546 high spatial and temporal resolution (Lennox et al. 2023). Technological advances, in 547 combination with real-time transmission of detection data, creates the potential for automated 548 tracking systems that function at resolutions comparable to terrestrial GPS (Yang et al. 2022). 549 Such real-time tracking can be applied in experimental contexts to facilitate manipulation 550 treatments, as well as improving adaptive management by allowing for data-driven decision 551 making with minimal delay when data are made available and accessible to end-users 552 efficiently. It would also allow the expanded capacity to detect routinely-tagged animal 553 behavioral responses to unpredicted climate-change related events, such as extreme weather 554 regional/localized events.

555 Innovative use of acoustic tags capable of both transmitting and receiving signals, 556 particularly in combination with GPS technology, will generate exciting opportunities to 557 study social interactions and predation dynamics between tagged animals across scales and 558 contexts not previously possible (Krause et al. 2013; Lidgard et al. 2014; Nathan et al. 2022). 559 Autonomous underwater and surface vehicles can be used for mobile tracking of tagged fish 560 outside receiver arrays (Nash et al. 2021). There have also been solutions introduced to 561 facilitate remote off-loading of data from deployed receivers, such as using autonomous 562 vehicles and daisy-chained receiver links (Dagorn et al. 2007), which promise to drastically 563 cut maintenance costs of remote receiver networks and increase the update frequency of 564 detection data. At the same time, expanding networks of receiver infrastructure globally, 565 organised via data-sharing hubs such as the Ocean Tracking Network (Iverson et al. 2019), 566 are increasing the areas of the world's oceans where aquatic species can be tracked and 567 studied. Extremely high-power transmitters that can be detected thousands of kilometres away 568 may in the future reduce the need for dense receiver networks when tracking large-bodied fish 569 across oceans (Bronger and Sheean 2019). All of these developments will enable long-lived 570 and highly migratory species such as whales, seabirds, pelagic sharks, billfishes, and tunas, 571 that cross vast expanses of water, and potentially experience very different climate-impacted 572 habitats over their life-span, to be tracked with increased detail, including into areas of the 573 deep-sea to track their use of oxythermal habitat at a global scale. Overall, the continued 574 advancement of E3T tools has the potential to revolutionise research on the impacts of climate 575 change on aquatic wildlife and prepare for implementing solutions and interventions where 576 possible. By harnessing the full capabilities of these technologies, researchers can gain a 577 better understanding of how climate change is affecting these species and develop strategies 578 to protect and conserve them.

5. Limitations

Whereas tracking the movements of aquatic animals can provide valuable insight into their spawning aggregations, migration routes, and barriers to movement, aquatic E3Ts have mostly been applied to adult organisms, due to the limitation of the tag size with decreasing body size until quite recently. Many aquatic species have a planktonic stage, during which they disperse and inhabit different habitats before reaching adulthood. By mainly having tracked adult aquatic animals, we have missed crucial information about the connectivity between metapopulations and shifts mediated by climate change in dispersion and nursery areas. In order to fully understand the movements and behaviours of aquatic species, we must also track the movement of these earlier, smaller stages.

The importance of tracking all life stages can be extended to further scales, including 592 investigations of different personalities within a life stage. Indeed, larger variations in 593 behaviour among individuals could be expected with warming temperatures as a function of 594 differences in personality, but it has been found that seabirds encountering stressful conditions

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595 may become more homogenous in their behaviour (Gillies et al. 2023), as do fish exposed to 596 certain pollutants (Tan et al. 2020; Polverino et al. 2021). To capture the whole spectrum of 597 behaviours and gather an unbiased representation of responses of the population to 598 environmental changes, it is then of utmost importance to track a representative sample of all 599 personalities and thermal preferences within the considered population (Villegas-Rios et al. 600 2018; Cooper et al. 2018), strengthening the importance of obtaining affordable tracking 601 technologies adapted to large samples. For acoustic telemetry, this may mean adopting more 602 CDMA (code division multiple access) or BPSK (binary phase shift key) systems to allow for 603 more animals to be tagged simultaneously within an area, without false detections (e.g. 604 Aspillaga et al. 2017)

6. Conclusions

Here, we have presented a case for how animal trackers can design studies to reveal how aquatic organisms respond to climate-related changes in their environment while providing a useful tool to inform management and human adaptation strategies. Climate change will result in more dynamic environmental conditions that span warming waters, cold shock events, changing ocean currents, varied runoff conditions, and extreme weather events (e.g., storms, hurricanes, blizzards), which will undoubtedly impact aquatic animals in diverse ways, many of which are unpredictable without empirical data. E3T data are able to provide unprecedented information on animal-environment interactions, and these baseline data are already being used to understand contemporary climate change impacts, and to predict how future climate change may impact aquatic animals.

618 Simply documenting changes in the distribution, timing, and survival of aquatic 619 animals in the face of climate change will not fully realise the potential of E3T data to support 620 climate change adaptation efforts. Moreover, waiting for decades to do so will mean that we will continue to invest in management strategies that may be ineffective. Reliance on 622 observational data as the climate gradually changes will nevertheless be valuable, and there 623 should be investment in long-term data series for tracking key species in climate-sensitive 624 areas. Indeed, despite the high-throughput nature of E3T data and the capacity to provide 625 immensely valuable and highly detailed data from remote observations of animals that are 626 otherwise very hard to observe, there seems to be a lack of long-term time series using 627 tracking of electronic tags that could be used to identify inter-annual or decadal responses to 628 climate, as well as the magnitude of changes to behaviour in anomalous years. Fortunately, 629 time series can be assembled *post hoc* from international databases, albeit with limitations of 630 study design interoperability to overcome. Notwithstanding, time series alone will provide limited power unless there is a great adoption of manipulative experiments that reduce 632 uncertainty and accelerate our understanding of climate change impacts on aquatic species, 633 populations, and ecosystems.

There is a dire need to future-proof today's management initiatives so that they provide resilience to aquatic systems and resource users in the face of a more dynamic future. Consequently, it is necessary to develop science-based climate change human adaptation strategies from tracking data that will provide decision makers with a new management toolbox to ensure that aquatic animals are managed in a sustainable manner. We are confident that biotelemetry and biologging tools for tracking aquatic animals can be used to generate novel information to support such efforts and do so at scales relevant to environmental decision makers.

Acknowledgements

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645 The project was conceived through the project "Multi-Lake Research of Fish Ecology and 646 Management using High-Resolution 3D Telemetry Systems", funded by ALTER-Net within 647 the MultiSite Research (MSR) initiative. Afonso was supported by the European Union's Horizon Europe research and innovation programmes 'MEESO' (contract number 817669) and 648 649 'Mission Atlantic' (862428), and by the Azorean Regional Government program 'MoniCo'. 650 Reubens acknowledges support by the Research Foundation Flanders (FWO) as part of the 651 Belgian contribution to LifeWatch. This work is supported by the COST Action - The European 652 Animal Tracking Network (CA18102), supported by COST (European Cooperation in Science 653 and Technology). Vollset and Dahlmo were supported by the Norwegian Research Council 654 project LOST (325840). Nilsen was supported by the Norwegian Research Council project 655 LaKES (320726). Lennox and Birnie-Gauvin were supported by the European Union's Horizon 656 Europe research and innovation programme STRAITS project (grant agreement No. 657 101094649). Villegas-Ríos was supported by the Ramón y Cajal programme from the Spanish 658 Ministry of Science and Innovation (RYC2021-032594-I). There is no particular order of the 659 author names aside from the first and last authors.

Competing Interests

The authors have no interests in competition

Data Availability

There are no data in this manuscript.

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1106 Figure Captions

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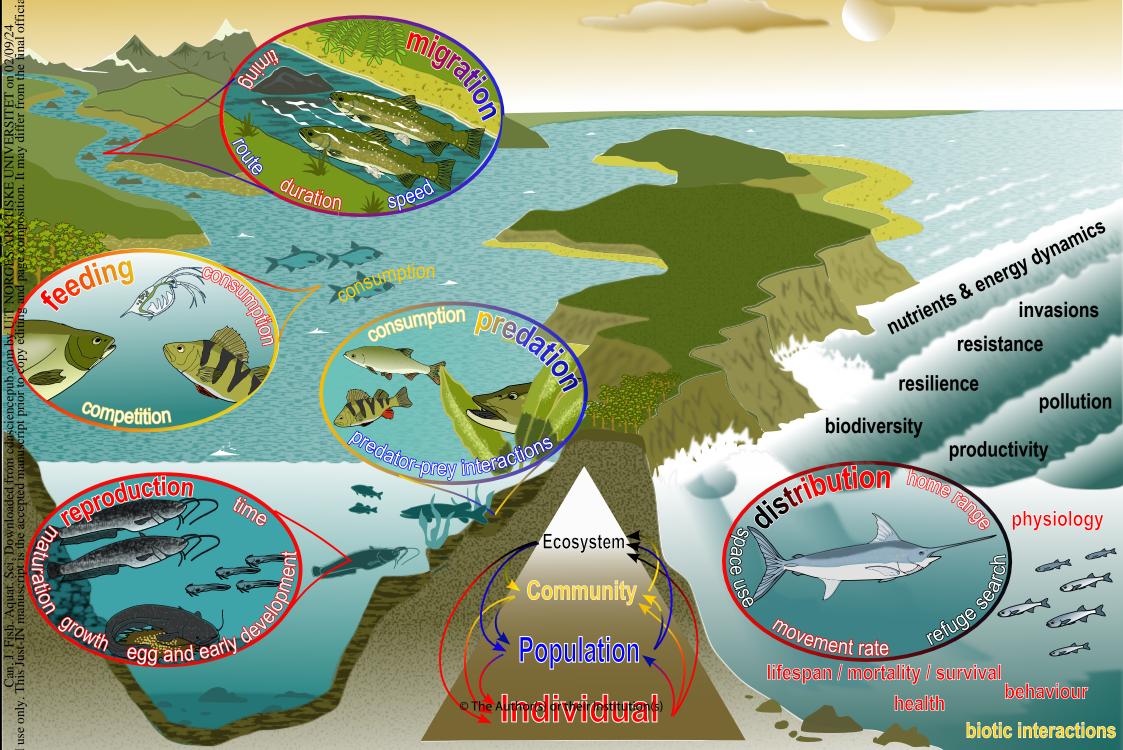
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Figure 1. Illustration of the complexity of aquatic ecosystems down to the individual level. The features likely to be affected by climate change and into which telemetry can give insight are highlighted in ellipses. Each ellipse presents a feature (larger font) and the variables that can be estimated by acoustic telemetry (smaller font). The features listed on the figure are coloured according to the level they are concerned with (ecosystem in black, community in orange, population in blue, and individual in red). The pyramid displays the hierarchical order of the levels with arrows to show the interactions among them. Artwork by Zuzana Sajdlová.

Figure 2. Currently available sensors for acoustic tags and their study objectives. The types of tags are indicated in the inner circles with uppercase text and colour coded. The features that can be studied in the context of climate change using one or more of these tags are detailed in the smaller outer circles with lowercase text.

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