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


























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Electronic tagging and tracking aquatic animals to understand a world increasingly shaped by a changing climate and extreme weather events

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Abstract

Despite great promise for understanding the impacts and extent of climate change and extreme weather events on aquatic animals, their species, and ecological communities, it is surprising that electronic tagging and tracking tools, like biotelemetry and biologging, have not been extensively used to understand climate change or develop and evaluate potential interventions that may help adapt to its impacts. In this review, we provide an overview of methodologies and study designs that leverage available electronic tracking tools to investigate aspects of climate change and extreme weather events in aquatic ecosystems. Key interventions to protect aquatic life from the impacts of climate change, including habitat restoration, protected areas, conservation translocations, mitigations against interactive effects of climate change, and simulation of future scenarios, can all be greatly facilitated by using electronic tagging and tracking. We anticipate that adopting animal tracking to identify phenotypes, species, or ecosystems that are vulnerable or resilient to climate change will help in applying management interventions such as fisheries management, habitat restoration, invasive species control, or enhancement measures that prevent

extinction and strengthen the resilience of communities against the most damaging effects of climate change. Given the scalability and increasing accessibility of animal tracking tools for researchers, tracking individual organisms will hopefully also facilitate research into effective solutions and interventions against the most extreme and acute impacts on species, populations, and ecosystems.

Key words: global warming, electronic tagging, acoustic telemetry, PSAT, applied ecology

1. Introduction

Anthropogenic-driven climate change will likely continue to intensify, at least in the near-term, regardless of international agreements to cut harmful emissions. Indeed, the climate system has a time lag such that the effects of emissions cuts now will not be able to completely mitigate the future amount of these gases in the atmosphere (Samset et al. 2020). Phenotypic plasticity or evolutionary adaptation of animals to future climate scenarios is therefore needed as ecosystems continue to change (Nagelkerken et al. 2023). The consensus is that climate change will generally lead to a net loss of biodiversity, which yields biotic homogenization in most areas (Malhi et al. 2020). Extreme habitats where specialists have evolved will likely accept more generalist species, driving a loss of endemism and further homogenization (Gordó-Vilaseca et al. 2023). Physiological tolerance to stressors, phenotypic plasticity, and capacity to adapt, both physiologically and behaviourally, in response to climate stress will determine the winners and losers of climate change (Somero 2011; Pecl et al. 2017; Webster et al. 2017; Andreasson et al. 2022). Identifying the likely losers and managing their resilience is one of the few options available to mitigate or forestall the impacts of climate change (Schuurmann et al. 2022). Tackling the climate crisis is an enormous challenge. In actionable terms, it is necessary to identify phenotypes, species, or ecosystems that are most vulnerable to climate change and using tools and actions such as fisheries management, habitat restoration, invasive species control, or enhancement measures to forestall extinctions and fortify ecological communities against the most damaging impacts.

Essential to managing under the constraints of a changing climate in inland and marine waters are data that accurately describe the responses of biological units to change. In water, behavioural changes play a key role because the initial response of individuals to human-induced environmental change is often behavioural (Toumainen and Candolin 2011). In many ways, behaviour is the first line of defense for most aquatic organisms. Such responses can then initiate a predictable sequence of observable changes (e.g., alteration of individual fitness and population dynamics) that manifest as changes in population abundance (Cerini et al. 2023). The role of aquatic animal electronic tagging and tracking tools (including both biotelemetry and biologging; herein E3Ts) in informing how wild animal populations react to these global changes occurring in lakes, rivers, and seas is therefore important, allowing researchers to identify, understand, and preview the resilience of species and ecosystems to climate change. Investigating how aquatic tagging and tracking can make an actionable and enduring contribution to climate research requires a suitable framework of climate change impacts with which to consider the study designs that could be implemented. Pörtner and Peck (2010) provided a sim-

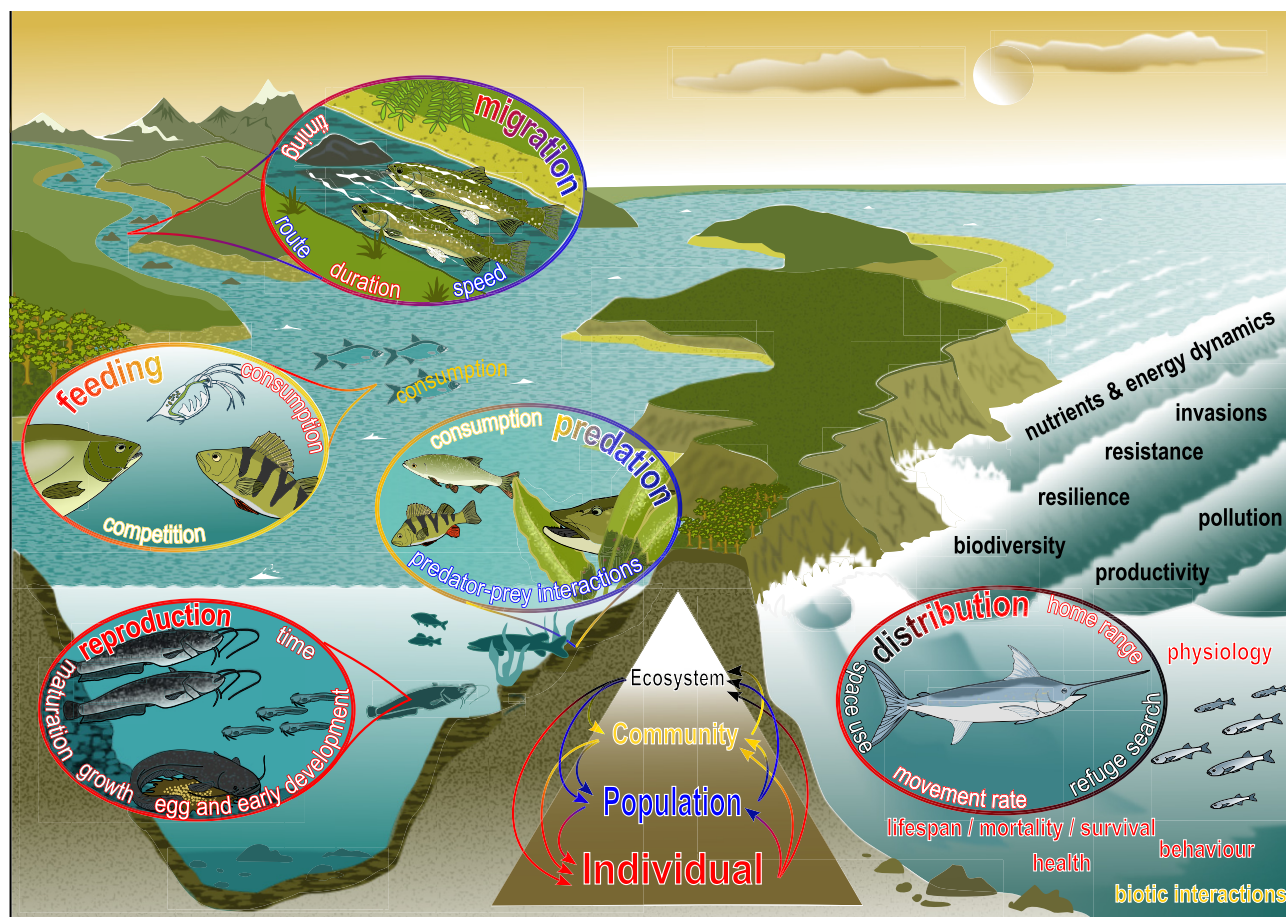
ple framework to scale climate change impacts from individuals to communities, which was created for causal inference about the impacts of climate change on fish. In their framework, they suggest three scales at which climate affects fish: the individual (physiology and behaviour), its population, and their ecosystem. Other researchers have drawn similar frameworks based on these fundamental levels of organization (also Nagelkerken et al. 2023), including the hierarchical response framework proposed by Smith et al. (2015), where individual, within-ecosystem, and between-ecosystem effects of climate are considered. Here, we consider the role of aquatic E3Ts within existing climate change impact frameworks, focusing on aquatic animals that are at particularly high risk due to climate change and extreme weather events (Pinsky et al. 2022; Fig. 1).

2. Applying animal tracking to studying climate change

2.1. Impacts of climate change on the performance of individuals

Background for linking the framework to electronic tagging and tracking: Physiological rates controlled by the environment (aka the Fry Paradigm; Fry 1959) dictate progress towards life history checkpoints. Laboratory experiments have demonstrated the importance of temperature as a mediator of individual life histories; in fact, temperature is often referred to as the “master factor” controlling biological rates (Fry 1971; Hochchka and Somero 2002; 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 et al. 2021). Major effects of climate change include extremification of water temperature (including cold shock; Szekeres et al. 2016), and pH, and hypoxia in many areas, which determine vital rates (including rates of physiological functioning and rates of movement) and constrain activities to hospitable water conditions. All of these processes may in turn drive competition for space and access to resources, as well as vulnerability to capture by people and predators. For example, Vedor et al. (2021) demonstrated that climate-induced hypoxia will promote habitat compression for blue sharks (*Prionace glauca*) and enhance their vulnerability to surface-oriented fisheries. Better individual data from tagging may provide insights into the maturation of fish as they initiate spawning migrations inferred from movement patterns (Griffin et al. 2022) and the lifespans of species based on tag detections that can be linked to environmental experiences. E3Ts can also be used to explain how exploitation removes high-performing metabolic phenotypes from populations (Duncan et al. 2019). Animal

Fig. 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.



tracking can also help identify mortality events and specific responses of animals to extreme scenarios that operate at a population scale (floods, heat waves, warm winters, swells, etc.; Williams et al. 2017; Sarkar and Borah 2018; Clark et al. 2020; Jarić et al. 2022; Lempidakis et al. 2022; Šmejkal et al. 2023) as well as the impacts of more gradual changes (e.g., accumulation of thermal units) on life histories. Such questions can be directly answered by logging the environmental temperatures experienced by fish throughout their lifespans. Using individual tagging data, analysts can query: where are the animals, how do they use micro- and macro-habitats, how does their behaviour change during extreme weather (e.g., heat waves, droughts, and natural disasters), how heritable are the phenotypes that persist through climatic bottlenecks, and how does behaviour affect competition, predation, reproduction, and senescence? Beyond behaviour, E3Ts can also help to assess the physiological constraints and demands that environmental conditions pose, including, for example, measures of metabolism (Metcalf et al. 2016).

Examples: Several studies have combined location and sensor data (e.g. physiologging) to investigate the climate vulnerabilities of individual animals. Depth-temperature records have been used to identify environmental windows where loggerhead turtles (*Caretta caretta*) thrive (Patel et al. 2021) and to compare chinook salmon (*Oncorhynchus tshawytscha*) and lake trout (*Salvelinus namaycush*) habitat partitioning in a lake (Raby et al. 2020). Combining habitat, temperature, and tracking data, Freitas et al. (2016) showed that given favourable sea surface temperatures, Atlantic cod (*Gadus morhua*) individuals selected shallow, food-rich vegetated habitats; however, with warmer surface waters such as those predicted under future climate scenarios, individuals remained in deeper waters in less productive habitats. Matching the thermal niche of species to the future available thermal habitat using climate models can provide projections for species' ranges under climate change using species distribution modelling (e.g., Legrand et al. 2016; Patel et al. 2021). Movement tracks can be used to link abiotic features to energetically sensitive behaviours, for example, revealing

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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 recession effectively reduced the degree of spatial overlap between polar bears (*Ursus maritimus*) and a key prey species, the ringed seal (*Pusa hispida*). Moreover, Payne et al. (2018) used accelerometer loggers to reveal that tiger sharks (*Galeocerdo cuvier*) had peak activity and, consequently, were more vulnerable to fisheries bycatch at 22 °C. Kneebone et al. (2018) observed juvenile sand tiger sharks (*Carcharias taurus*) in a bay (Massachusetts, USA) with acoustic transmitters outfitted with accelerometer sensors and modeled posterior spatial distributions highlighting activity and energy expenditure hotspots. Direct calibration of acceleration metrics to oxygen consumption can provide estimates of oxygen consumption and energy landscapes, revealing how habitat and climate interact to shape the metabolic demands and life course (aka pace of life) of individuals. Such methods must be extended beyond temperature for aquatic species to see how other water parameters affect energetics to fully appreciate how climate change affects aquatic animals across a range of climate-related impacts, including water volume loss (i.e., drought), flow regimes, cyclones/hurricanes, pH extremification, or hypoxia. E3Ts can also be used to study winter ecology, under the assumption that cold-water-adapted fish show elevated fitness in harsh winters and lose performance as winters warm (McMeans et al. 2020).

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 animal movements and environmental change. Simulations can facilitate projections describing how niches (estimated from computer models) correspond to expected changes in distributions (e.g., Patel et al. 2021). However, direct manipulations, including habitat alterations, such as studies with experimentally warmed outflows (e.g., from power plants), and experimental displacement can be useful to test resilience and climate vulnerability across species or phenotypes within species. There is a need to seek tools that will help make more thorough assessments of the individual's status and fitness (e.g., survival) when exposed to climate stressors, such as heart rate loggers and transmitters that measure indicators of physiology (i.e., stress) that may be independent of other metabolic demands (e.g., movement). Studying the impacts of climate change on individuals requires some control over the habitat or the animals, which can be achieved using ponds or lakes to better understand climate change impacts at this scale (Lennox et al. 2021). If combined with physiological metrics of thermal performance and tolerance, E3Ts could provide us with a powerful tool to predict climate impacts on individuals and species. Physiological measures of performance and tolerance have predominantly been undertaken in the lab, creating opportunities to expand the testing of temperature-mediated performance hypotheses in the field (Rezende et al. 2014). In this regard, E3Ts could be pivotal in elucidating whether these metrics are, in fact, 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 will alter species assemblages (Vannote et al. 1980) or species distributions (e.g., Gardner et al. 2015). Diel vertical behaviour might also be influenced, as the northward distribution will lead to shifts in seasonal variability in light availability, both impacting foraging for food and predation risks, an impact on one of the planet's major biological pumps (Ljugström et al. 2021). Beyond species-specific effects, climate change can cause spatiotemporal alterations to the interactions between species or populations, which ultimately affect the structure of ecosystems and their functioning (van Zuiden et al. 2016; Tunney et al. 2014).

Examples: To be relevant at the species scale, E3T experiments should aim to identify broad-scale movement and behavioural shifts representative of the species, including spatial or temporal shifts, meaning data series that are broad in geographic scale or long-term are most robust. Models using E3Ts can be used to generate distribution or niche models that are built on representatives of a population and focus less on intraspecific variation. This can be accomplished by using individual data to generate models or predictions, such as in Aspillaga et al. (2017) where a general northward shift of common dentex (*Dentex dentex*) at the species level was projected based on mechanistic niche data established from tracking. Spatial shifts at the species level have been revealed from tracking data in a lake, where identified a collective shift in the depth use of wels catfish (*Silurus glanis*) in response to bottom hypoxia (Westrelin 2022). As the climate continues to change, the centroid of animal distributions may shift over time, which can be tracked from E3T data using archived data in a time series. Migration routes could also shift, although few examples exist and Horton et al. (2020) found that 15 years of satellite tracking data did not reveal any significant changes in the migration routes of humpback whales (*Megaptera novaeangliae*) despite changes in the oceanography and magnetic fields during that period. This contrasts with 15 years of bluefin tuna (*Thunnus thynnus*) tracking data from the Pacific, where tunas were observed to adapt their distributions according to marine temperatures, including an extreme anomaly during a heatwave (Carroll et

al. 2021). In terms of the timing of key life history events, Douglas et al. (2011) observed phenological shifts in striped bass (*Morone saxatilis*) in the Miramichi River, while Hauser et al. (2017) used time series data from satellite telemetry of beluga whales (*Delphinapterus leucas*) to identify changing migration timing in the Arctic.

Designing studies: Understanding how species are responding (and will respond) to climate change using E3Ts likely needs a reliance on temporal comparisons with long-term time series for tracking changes at a relevant scale. Time series can identify gradual or stepped changes in the phenology of key events or may simply provide insights from aberrant events such as heat waves or extreme weather that cannot be planned for (e.g., Heupel et al. 2003; Carroll et al. 2021). Projects with several years of data sampling are likely to include some periods of abnormally warm temperatures or extreme weather, and data sampled during such events are valuable to explain or even predict potential shifts in behaviour (e.g., refuge seeking, foraging areas) that a population/species will face in the future (Westrelin et al. 2022, 2023). Experiments at the population scale using tracking may include randomized control treatment trials in which control fish are systematically released and compared to a treatment group that is reared under projected future environmental scenarios such as warming. Such designs are possible using E3Ts to track the fate of a suitable fraction of a population to draw inferences at scale using experimental rearing or challenge tests combined with fate tracking. Interventions that could be considered include acute exposure or chronic immersion in warm temperatures or acidified water, simulating the rearing conditions likely to be encountered by fish experiencing climate change. Long-term tracking of these fish and comparison with a control group will be instructive to understand the magnitude of the challenges faced by these animals and proactively adopt management actions. For most studies aiming to generate results at the population scale, customizing the battery lifetime to be long enough to detect animals later in life or adding sensors to the tags for tracking days or total activity can greatly improve current data collection.

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 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

Background for linking the framework to electronic tagging and tracking: Climate change has the potential to induce

ecosystem-level changes, such as altering the ecology, density, and phenotypic structure of keystone species, creating mismatches between the migration phenology of keystone species and their prey (Renner and Zohner 2018), changing the outcome of interspecific competition (Helland et al. 2011; Carmona-Catot et al. 2013), increasing ecosystem vulnerability to invasive species (Ilarri et al. 2022; Souza et al. 2022), shifting temporal and spatial niches of thermal specialists (Santiago et al. 2016), affecting parasite-host interactions (Löhmus and Björklund 2015; Cable et al. 2017), increasing the frequency and intensity of ecosystem perturbations, and ultimately causing interconnected cascading effects that can disrupt ecosystem functioning (Durant et al. 2007; Thackeray et al. 2010). Climate change impacts can be further exacerbated through synergistic interactions with other stressors such as eutrophication, pollution, water regulation, and biological invasions (Woodward et al. 2010). Climate change can also create novel heterogeneity 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 behaviour, 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 the ecosystem consequences of climate change-induced alterations in 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 the exploitation of limnetic food resources. This resulted in a reduction in the growth and condition factors of lake trout and significant changes in carbon flux throughout the lake ecosystem. Caldwell et al. (2020) examined the effects of earlier ice breakup on water temperatures and habitat production, as well as the consequences for habitat use, behaviour, and fitness of brook trout (*Salvelinus fontinalis*). The study showed that earlier ice breakup created resource-rich

littoral-benthic habitat compared to pelagic habitat. Nevertheless, movement data revealed that brook trout did not exploit the littoral habitat due to warm temperature avoidance, which reduced their fitness. Thus, changes in ice break-up drive multi-directional results for resource production within lake habitats and have important consequences for predators.

The effects of climate change on the coupling between terrestrial and aquatic ecosystems were studied by [Hamilton et al. \(2017\)](#) and [Deacy et al. \(2017\)](#). [Hamilton et al. \(2017\)](#) used satellite telemetry to show that polar bears (*U. maritimus*) spent more time on land during periods of reduced sea ice, spatially isolated from their preferred prey, ringed seals (*Pusa hispida*). While on land, polar bears spent more time near ground-nesting bird colonies and preyed more on nesting seabirds. [Deacy et al. \(2017\)](#) used GPS telemetry in Kodiak brown bears (*Ursus arctos*) to examine the response of bear behaviour to global warming-induced changes in the availability of two important food resources, red elderberry (*Sambucus racemosa*) and sockeye salmon (*Oncorhynchus nerka*). Climate warming advanced the elderberry blooming to align with the spawning of sockeye, causing bears to prioritize elderberry and weakening the link between salmon and its contributions to the surrounding land by fertilizing the earth and enhancing local biodiversity.

Designing studies: The ecosystem approach can be challenging because it requires consideration of other trophic levels and how changes in focal animal behaviour translate to population, species, or community scales. Behavioural changes can alter ecological interactions (e.g., predator-prey dynamics, competition, and social behaviours), and these consequences can be tracked using a suite of complementary tools that link tracking data to metrics collected at different levels of the ecosystem. For example, approaches may require examining population and life history parameters of key species, system productivity, and the strength or direction of ecological interactions prior to, or during, movement tracking. In this way, the impacts of climate change can be comprehensively studied using animal tracking. The effects of climate change on ecosystems and communities could be studied through experiments involving islands or small pond ecosystems using telemetry where manipulations can be undertaken, including experimental warming. Space or time replication (e.g., across lakes) and reciprocal 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 and exposed to different water levels or fluctuations, different nutrient loads, as well as different levels of pH and dissolved oxygen. Alternative designs could involve tracking in replicated tracts, such as whole lakes, along a latitudinal gradient that would treat climatic variation as a component of the behavioural variation ([Lennox et al. 2021](#)). Experiments could additionally address changes to physiological and behavioural phenotypic frequencies related to changing environments, including activity, phenology, and interspecific interactions (e.g., predation rates). Of special relevance would be multi-species experiments that integrate fish behaviour with physiology ([Cooke et al. 2008](#); [Komotoroske and Birnie-Gauvin 2022](#)) to in-

fer responses at the level of communities as well as effects on ecosystem metabolism. Where possible, there should be an increasing emphasis on building models with multiple species to better understand how different species respond when confronted by changes not in isolation but in the presence of competitors or predators. Experiments using predation tags—tools that continue to be developed for identifying the fate of animals and a key ecological interaction—should become a tool that helps reveal some of the most important aspects of ecological dynamics symptomatic of climate change in both experimental and observational studies ([Lennox et al. 2023](#)).

3. Testing climate resilience and management

3.1. Habitat restoration

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

3.2. Protected areas to facilitate persistence of vulnerable species

Protected areas (PAs) are often used as a management intervention to protect species against disturbance (Agardy 1994; Edgar et al. 2014). Although marine PAs are widely known, freshwater PAs are equally valuable and actionable (Saunders et al. 2002). PAs are globally used to buffer the exposure of animals to stressors, but their role in mitigating climate change effects should be further explored (Hannah 2008; Soares-Filho et al. 2010; Roberts et al. 2017). Adapting PAs to buffer vulnerable species from climate change may be a viable option to mitigate the effects of temperature. Most advice suggests that marine PAs need to be larger and better connected (McLeod et al. 2009) to effectively benefit species experiencing climate change. However, there is an opportunity to gather additional evidence using tracking tools. Animal tracking is vital to understanding how the functionality of PAs will change as animals migrate and change their movements according to climate, especially in open aquatic systems, where range shifting can alter the protection afforded by area-based measures. In a climate change scenario, where the conditions in the ecosystems are in constant change, the effectiveness of PAs might be challenged, as temperature fluctuations can alter the suitability of certain habitats for constituent species (Hooker et al. 2011; Freitas et al. 2016; Sahri et al. 2022). E3T studies can be designed to monitor how species respond to 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 the seasonally changing needs of animals (Sequeira et al. 2019).

3.3. Translocations or assisted migration

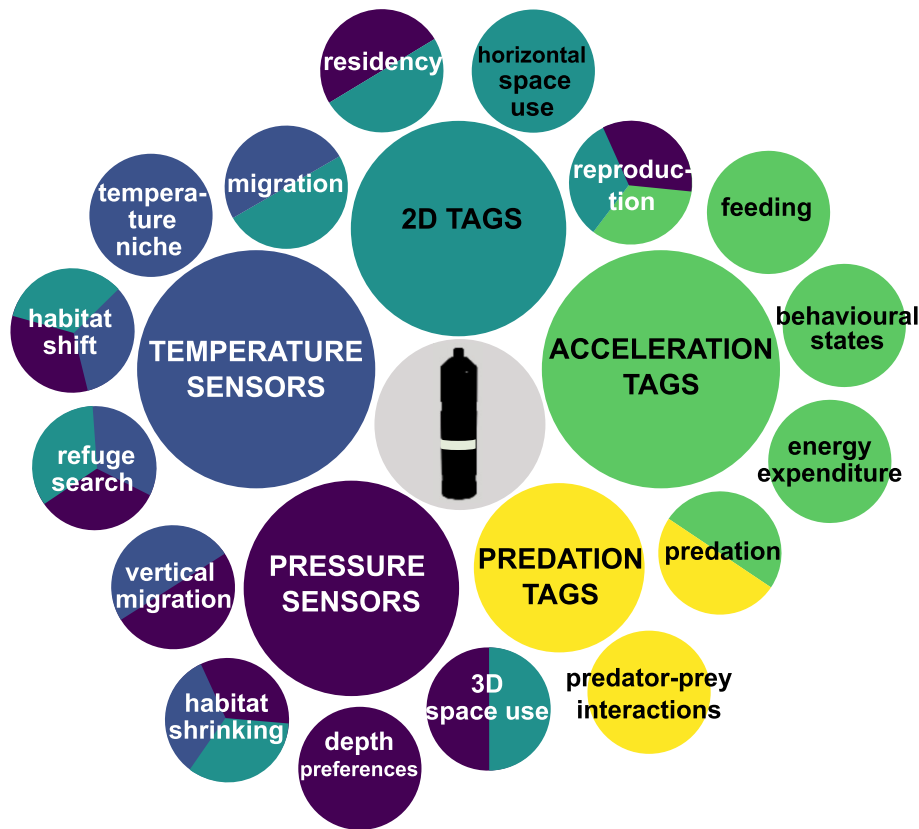
Climate change is challenging species to respond to rapidly changing conditions in their local environments. Species may not have the capacity to adapt at a sufficient pace to these changes (i.e., evolutionary adaptational lag) or may lack the dispersal capacity to colonize suitable habitats (Schloss et al. 2012; Fréjaville et al. 2020). To overcome these limitations, “assisted migration” (see Twardek et al. 2023 for definition) of animals to more suitable areas has been proposed as a means of facilitating the resilience of a population impacted by climate change by providing suitable habitats faster than they could reach them by natural range expansion (Hällfors et al. 2014). Typically, these movements occur in areas where those individuals would be predicted to move, provided they had sufficient time and connectivity between the habitats, as they might be expected to in a slower climate change scenario (Hällfors et al. 2014). Assisted migration is gaining increased attention as a potential conservation tactic (Benomar et al. 2022; Twardek et al. 2023), though much uncertainty and controversy remain regarding the potential ecological risks and benefits (Ricciardi and Simberloff 2009; Aitken and Whitlock 2013; Bucharova 2017). Thus far, successful cases of assisted migration for conservation have been very limited, with most movements pertaining to trees and other vascular plants in the context of forestry (Pedlar et al. 2012). Aquatic

animals have rarely been the subjects of assisted migration studies (Twardek et al. 2023), though there is recognition of the values these movements may have in supporting fisheries (Green et al. 2010), and it seems likely that these movements will be increasingly considered to abate the impacts of climate change on highly valued species, possibly at the cost of less economically valued counterparts. Careful study and monitoring will be critical to this endeavour, given that it would not be desirable to have assisted migration become a broad-scale invasion (Mueller and Hellmann 2008). Electronic tagging and tracking will be uniquely positioned to inform how introduced species are using their newfound environments, expanding their ranges, and interacting with the broader aquatic ecosystem. As a unique example of this, western swamp turtles (*Pseudemys umbrina*), Australia’s rarest herpetile, were outfitted with radiotelemetry transmitters and temperature loggers and were introduced into a wetland located 300 km south of the species’ native range (Bouma et al. 2020). Across a 6-month period, researchers gained insights into habitat use, movement, growth rates, mortality events, and microclimate conditions, providing important knowledge for future assisted migration efforts for the species. Although fish have not been the focus of many assisted migration studies, humans have inadvertently conducted assisted migration of fish at a large scale through the stocking of fish throughout freshwater systems around the world (Halverson 2010). While most of these movements would not constitute assisted migration, there is great potential to study these movements in the context of assisted migration (see Banting et al. 2021). As E3Ts continue to revolutionize how we understand aquatic animal movements and species interactions (e.g., predation tags), it will undoubtedly be at the forefront of efforts to study and monitor assisted migration in the context of climate change.

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 may, however, be an exacerbating factor for other stressors, such as invasive species or pollution (Bertram et al. 2022), that are operating interactively with warming; in many cases, the other factors may be easier to address than the climate impacts (Brook et al. 2008). Litchman and Thomas (2023) reviewed the role of several exacerbating factors that affect species’ metabolism and can interactively affect their vulnerability to warming. In such cases, identification and removal of the interactive stressor will be an efficient remedy for the species or population even if climate change cannot be effectively addressed. For such interactive effects, it may be possible to mitigate the impact of climate change on species by removing or addressing the secondary stressor; for example invasive species removal or pollution remediation could enhance the climate resilience of species exposed to warming. In general, appreciation that climate vulnerability can be interactive is still developing, and we submit that animal tracking can help to reveal where interactions exist and what actionable solutions can intervene to buffer the impacts of cli-

Fig. 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.



mate change. Such approaches will necessarily rely on multi-disciplinary methods, and likely experimentation, to identify and test how interactive effects operate.

3.5. Simulation of future scenarios

At a larger spatial scale, some studies suggest using global change projections together with predictive species distribution models (Frazão 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 the 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 has 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 output of tracking efforts (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; Chambault et al. 2022; Reisinger et al. 2022a, 2022b).

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 miniaturization of transmitters, permitting researchers to track smaller species (Hazen et al. 2012) and younger age classes of aquatic organisms (Li et al. 2023). 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, summarized, 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 (Fig. 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 signal collisions, making it possible to track large numbers of fish si-

multaneously with very high spatial and temporal resolution (Lennox et al. 2023). Technological advances, in combination with real-time transmission of detection data, create the potential for automated tracking systems that function at resolutions comparable to terrestrial GPS. Such real-time tracking can be applied in experimental contexts to facilitate manipulation treatments, as well as improve adaptive management by allowing for data-driven decision-making with minimal delay when data are made available and accessible to end-users efficiently. It would also allow the expanded capacity to detect routinely tagged animal behavioural responses to unpredicted climate-change-related events, such as extreme weather regional/localized events.

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

5. Limitations

While 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 tracking adult aquatic animals, we have missed crucial information about the connectivity between

metapopulations and shifts mediated by climate change in dispersion and nursery areas. 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 investigations of different personalities within a life stage. Indeed, larger variations in behaviour among individuals could be expected with warming temperatures as a function of differences in personality, but it has been found that seabirds encountering stressful conditions may become more homogenous in their behaviour (Gillies et al. 2023), as do fish exposed to certain pollutants (Tan et al. 2020; Poverino et al. 2021). To capture the whole spectrum of behaviours and gather an unbiased representation of responses of the population to environmental changes, it is then of utmost importance to track a representative sample of all personalities and thermal preferences within the considered population (Cooper et al. 2018; Villegas-Rios et al. 2018), strengthening the importance of obtaining affordable tracking technologies adapted to large samples. For acoustic telemetry, this may mean adopting more CDMA (code division multiple access) or BPSK (binary phase shift key) type systems to allow for more animals to be tagged simultaneously within an area, without false detections (e.g., 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, and 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.

Simply documenting changes in the distribution, timing, and survival of aquatic animals in the face of climate change will not fully realize the potential of E3T data to support 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 observational data as the climate gradually changes will nevertheless be valuable, and there should be investment in long-term data series for tracking key species in climate-sensitive areas. Indeed, despite the high-throughput nature of E3T data and the capacity to provide immensely valuable and highly detailed data from remote observations of animals that are otherwise very hard to observe, there seems to be a lack of long-term time series using tracking of electronic tags that could be used to identify inter-annual or decadal responses to climate, as well as the magnitude of changes to behaviour in

anomalous years. Fortunately, time series can be assembled post hoc from international databases, albeit with limitations of study design interoperability to overcome. Notwithstanding, time series alone will provide limited power unless there is a great adoption of manipulative experiments that reduce uncertainty and accelerate our understanding of climate change impacts on aquatic species, 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 logging 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.

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