What acoustic telemetry can and can’t tell us about fish biology

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Abstract

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

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

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Introduction

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

In essence, animal borne tags (hereafter 'transmitters') that transmit coded signals at a specific frequency, can be logged by a researcher directly with a hydrophone from a boat (active tracking) or by stationary, *in situ* 'receivers' with hydrophones attached, recording the presence of an individual within a particular, and highly variable range. Since the early days of active, continuous ultrasonic tracking in the 1950s, the field of AT has undergone a number of significant phase transitions; perhaps most significantly, the implementation of passive tracking using arrays of fixed receivers, which revolutionised the scope and scale of research question that could be tackled (Cote et al., 1998; Heupel & Hueter, 2001). This development put the onus firmly on study design, dramatically increasing the number of individuals that could contribute to a given study by reducing the effort required to collect data for each. Nowadays, depending on the spatial arrangement and type of receivers installed within an array, data returned can either be presence only, recording the identification, time and date of a fish anywhere within an ellipsoid that represents the detection range of a particular receiver; or alternatively, by closely-spacing receivers, such that their detection ranges overlap considerably, high-resolution tracking can be conducted whereby sub-meter positional estimates of fish can be achieved (Brownscombe, Lédée, et al., 2019). Nuances in the placement of acoustic receiver arrays are often dictated by the geography or environmental conditions of specific study sites. Arrays therefore can be highly variable leading to placements of receiver gates within bottlenecks, grided arrays within enclosed lakes or embayments or receiver 'chains' that track the shape of a coastline, island or river bed (Heupel et al., 2006). With recent advances in both transmitter and receiver technologies comes the opportunity to track fishes for longer, with higher precision or greater spatial coverage, follow them in deeper habitat or in near real-time, while also gathering physiological data on the individuals that carry tags (Lennox et al., 2017). Perhaps then, it is unsurprising that this toolkit has become more attractive in recent years, to the diversity of people that work directly and indirectly with fish.

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

Recent developments within AT offer new and more diverse opportunities to explore different aspects of fish biology. The increasing miniaturisation, reduced cost and improved battery life of current acoustic transmitters for instance, has ensured that AT has become a vital part of the toolkit for those seeking to influence the conservation of imperilled aquatic species (Cooke, 2008) or inform management practices to mitigate pressures on their ecosystems (Matley et al., 2021). Alongside hardware developments, data management strategies, once rare and often unstandardized (Heupel, Semmens, & Hobday, 2006), today have shifted from localised to global data sharing initiatives (Abecasis et al., 2018; Cooke et al., 2011); where analyses were largely descriptive, they have started to become considerably more hypothesis-driven and quantitative (Donaldson et al., 2014). Even the very description of the field now goes beyond referring simply to tags that transmit a unique ID code to passive monitoring stations, to incorporate multifunctional temperature, pressure, acceleration and even heart-rate sensors (e.g. Kadar, Ladds, Mourier, Day, & Brown, 2019; Payne et al., 2015), with the option to retrieve real-time updates on detections via satellite (e.g. Forget et al., 2015). For those relatively new to the field, this diversification and continuing development can offer up a daunting array of challenges and decisions (summarised in Figure 1), and as a growing number of excellent reviews will attest, the applications of these technologies are broad (Brownscombe, Lédée, et al., 2019; Donaldson et al., 2014; Heupel et al., 2006; Hussey et al., 2015; Matley et al., 2021).

In light of the transition of AT from a very specialised methodology to more of a generalist toolkit, our intention for this paper is to take stock of where the field is at in its capacity to reveal crucial information about fishes occupying an increasingly unpredictable and impacted world – our marine and freshwater ecosystems. As increasingly diverse practitioners enter the field, we wish to address the impact that AT can have on both fundamental ecological and applied research themes. We discuss these themes in turn breaking them down into more specific areas, utilising key papers that exemplify progress in each of these research areas. At the same time, we aim to discuss some of the current limitations and future advances of AT, as well as celebrate the progress the field has and continues to make within fish biology.

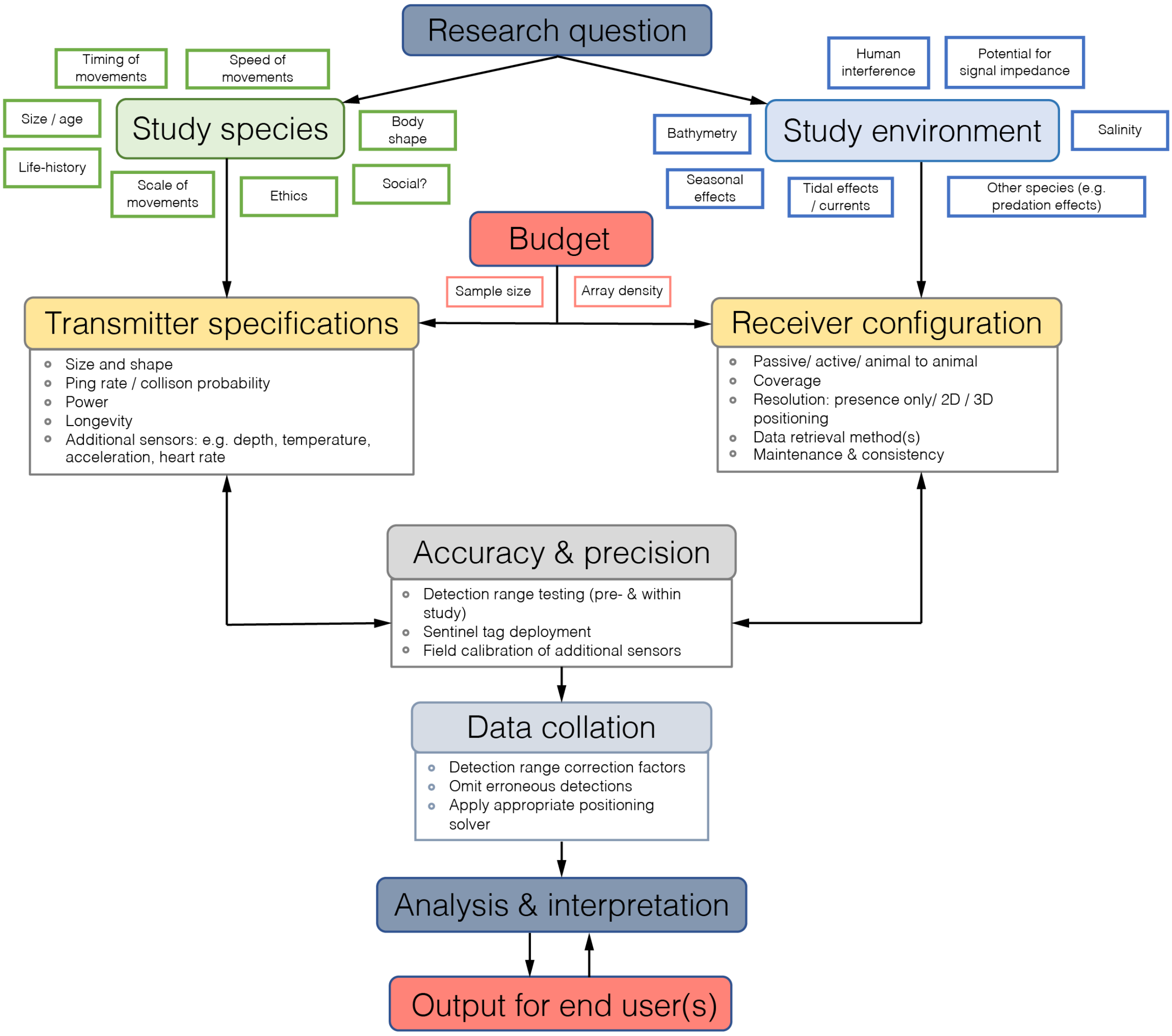

Figure 1. Plotting a course to accurately address a research question. Acoustic telemetry studies are typically highly nuanced and species or site specific which requires an ordered flow of decisions to help better link the research question with the end user and/or the practical application of the data for conservation and management of aquatic species.

1) Fundamental Ecological Research

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

Migration patterns

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

For fishes that migrate either entirely in freshwater (potadromy) or between freshwater and marine environments (diadromy), the use of AT has proven critical for revealing the scale and variability associated with migration, particularly in the freshwater component of this behaviour. Strategic use of receiver 'lines' or check points that span waterways and reliably capture both upstream and downstream movements of tagged individuals, enable estimates of migration distance, timing and relative survivorship (Clements et al., 2005; Melnychuk et al., 2007). Indeed, the mechanics of moving between salinity gradients for diadromous species have only really been fully understood by combining AT with otolith microchemistry. Telemetry defined migratory behaviour, in combination with otolith analyses, have been used to validate or disregard chemical signatures associated with transitions in pinkeye mullet (*Trachystoma petard*, Miles et al., 2018) but also to determine partial anadromy in non-native rainbow trout (*Oncorhynchus mykiss,* Roloson et al., 2020).

These combined, interdisciplinary approaches provide new levels of ecological understanding, particularly for complex migratory species, helping to better link the influence of flexibility in migration strategy to threats that may impact individuals/groups within populations disproportionately (Tamario et al., 2019). A closer look from a recent study however, suggests that 50% of published articles that use AT to understand fish movement or ecology, fail to incorporate or consider mortality within their study, while those that did estimate an ~11% loss on average of tagged individuals from the system

(Klinard & Matley, 2020). This is pertinent as transmitters will continue to be detected even after depredation, leading to movement patterns that reflect the predator rather than the prey species (Bohaboy et al., 2020). Even those that survive but leave the array, and thus exhibit different behaviour to individuals typically included in analyses, remain rarely discussed in studies on movement. Yet despite these important caveats, AT continues to prove invaluable for understanding fish migration. Hayden et al. (2014) for example, used receiver lines situated in the nearshore waters of Lake Huron and a multi-state mark-recapture model to describe three migratory pathways for walleye (*Sander vitreus*), demonstrating that males spent significantly longer in the rivers before migrating out into a bay than females, despite no sex preferences for specific pathways. Acoustic tracking of lake sturgeon (*Acipenser fulvescens*) in the same region (Huron-Erie Corridor, HEC) has also proven instrumental in highlighting intraspecific variability in freshwater migrants, known as divergent migration (Kessel et al., 2018). As anthropogenic barriers continue to pose one of the biggest threats to riverine migration, the identification of consistent migratory behavioural states, including partial migration and non-migratory residency within populations, illuminates the need for separate management strategies as well as the potential for species to respond to continued change to their habitat (Kessel et al., 2018).

As indicated, moving from a freshwater environment to marine imposes considerable physiological demands on fishes but also our ability to utilise AT to monitor migration, without the natural ‘bottleneck’ that rivers provide. Array design between habitats can vary substantially (Fig. 2) highlighting the need to carefully consider species ecology. For diadromous species like freshwater eels (*Anguilla spp.*) that mature in rivers and estuaries before undertaking their only spawning migration to the open ocean, understanding the timing, drivers and threats to migration is vital for conserving these imperilled species (Jacoby et al., 2015). Béguer-Pon et al. (2014) successfully deployed acoustic receivers covering a distance of 420 km to monitor the ‘silver eel’ escapement of mature America eels (*Anguilla rostrata*) as they headed out towards the Sargasso Sea to spawn from the St Lawrence River. The acoustic data revealed substantial individual variation in the timing and speed of migration, but for the first time a strong reliance on nocturnal, ebb tide transport by silver eels to escape the estuary (Béguer-Pon et al., 2014). When tracking species in the marine environment, horizontal migration is typically detected on departure and arrival by strategically-deployed receiver arrays, as documented for example in bull sharks, *Carcharhinus leuca* (Daly, Smale, Cowley, & Froneman, 2014; Heupel et al., 2015). Alternatively, active acoustic tracking can provide a window into the short-term vertical migrations (e.g. diel vertical migration) of highly-mobile species of pelagic fishes (Block, Booth, & Carey, 1992; Nakano, Matsunaga, Okamoto, & Okazaki, 2003). Finally, long-distance movements in the marine environment, normally outside the capabilities of passive AT, are beginning to be captured via coordinated networks of acoustic arrays operating data sharing agreements to track cross-jurisdictional migration of wide ranging, commercially important or threatened species (Lédée et al., 2021).

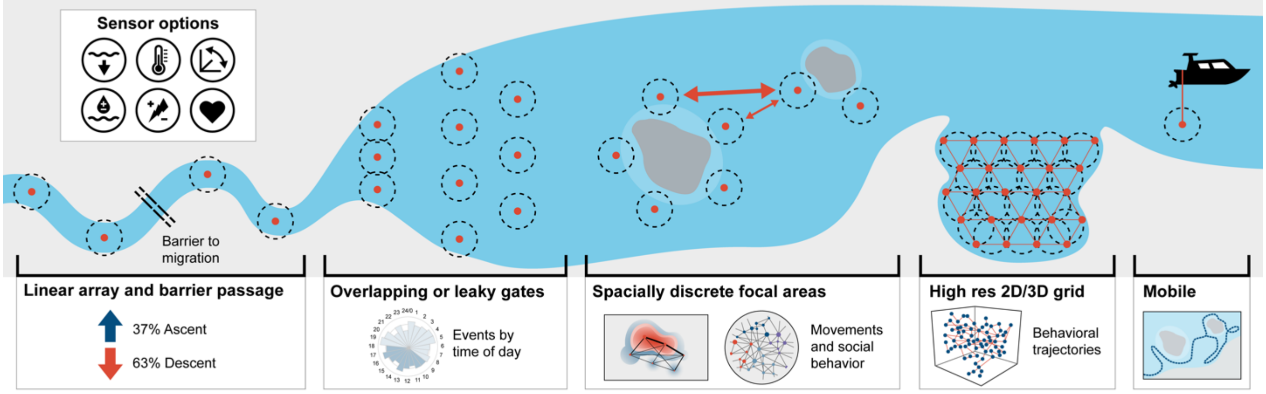

Figure 2. Variation in array configuration, complexity and tag sensor 'add-ons'. Outside of active, boat-based tracking, passive arrays can vary from linear, non-overlapping arrays to gridded, overlapping, high resolution arrays, each shaped by infrastructure, cost, geography, species and other logistical constraints. Further, fish can be tagged with transmitters that offer additional functionality such as depth, temperature, activity, salinity, conductivity or heart rate (left to right, top to bottom). Red dots indicate acoustic receivers and the dotted lines, estimated detection ranges.

Space use and fine-scale movement strategies

Across most aquatic environments, AT has been used to great effect to estimate fish activity space, home range, core areas or 'central places' and residency patterns, in addition to how these parameters vary by species, sex or time of day, month or year (Garcia, Mourier, & Lenfant, 2015; Heupel, Simpfendorfer, & Hueter, 2004; Heupel, Lédée, & Simpfendorfer, 2018; Kirby, Johnson, & Ringler, 2017; Nakayama et al., 2018; Papastamatiou et al., 2018; Simpfendorfer, Heupel, & Hueter, 2002; Watson et al., 2019). The accuracy of space use estimates derived from passive telemetry data are very much dependent on the metric used (Dwyer et al., 2015). Some of the most widely used are now built into bespoke packages, such as those in the R statistical environment (e.g. *VTrack*), offering standardised tools for deriving and comparing these metrics between locations (Udyawer et al., 2018). It is important to stress however, that there remain a number of challenges associated with estimating space use from AT data, not least that estimates are constrained by the size of the array, limiting reliability to species that use smaller areas than are being monitored. Accurate estimation of space use and home range of fishes is first contingent on precise estimation of location (Hostetter & Royle, 2020), and must consider biases that include autocorrelation, small numbers of tagged individuals (sample size) and irregular data collection. The pros and cons of home range estimator methods are discussed in detail by Silva et al. (2022) who offer a useful guide to choosing between the different options, in addition to *R* code for applying autocorrelated kernel density estimators (AKDEs) for home range analyses. With these caveats in mind, and for species that show some form of site-attachment or fidelity, AT has remained invaluable for understanding space use at multiple spatial scales, particularly in recent years with the advent of open source data platforms enabling the coordination of data streams from multiple acoustic arrays to cover significantly broader spatial ranges for more mobile species (Brownscombe, Lédée, et al., 2019; Campbell et al., 2012; Harcourt et al., 2019; Heupel, Kessel, Matley & Simpfendorfer, 2018; Udyawer et al., 2018).

Aggregated by species or sex, movement metrics (including range and dispersal) provide an important overview of space use at the population level. However, metrics from individual animals inform another important area of research; the role of individual variability or personalities (consistent individual behaviours) and behavioural syndromes (a correlated suite of behaviours) on population stability and adaptive resilience (Villegas-Ríos et al., 2017). Using Atlantic cod (*Gadus morhua*) as a model species, Villegas-Ríos, Réale, Freitas, Moland, & Olsen (2018) exposed individuals to repeated and standardised behavioural laboratory assays prior to releasing them with acoustic tags into a high-resolution, acoustic tracking array (Innovasea Positioning System, VPS) to monitor their movements in response to changes in sea surface temperature. From hyperbolic positioning within the VPS array and depth-sensing tags, fine-scale reconstructions of three-dimensional (3D) movements were modelled against individual home range across the proactive (bold) to reactive (shy) behavioural spectrum. In short, one of the key results to come from this novel work was that personality was found to be a significant predictor of changes in home range size (Villegas-Ríos et al., 2018).

Habitat connectivity and energy landscapes

Depending on the design of a passive acoustic array and the equipment used, data can be generated as discrete, presence-only packages associated with important monitoring locations or in the other extreme, as discussed, near-continuous, high-resolution 3D individual tracks reliant on receiver overlap and considerable post-processing of the data to determine fine-scale position. Particularly when tracking species in the marine environment or in very large water bodies, positional accuracy is regularly sacrificed for spatial coverage as arrays are designed around habitats of interest such as reefs, islands or atolls (Espinoza, Heupel, Tobin, & Simpfendorfer, 2015; Papastamatiou, Meyer, Kosaki, Wallsgrove, & Popp, 2015); that said, gridded arrays and receiver lines are sometimes adopted where the physical geography of the study location and the research question permits, such as bottlenecks or enclosed embayments (Block et al., 2019; Braccini, Rensing, Langlois, & McAuley, 2017; Farmer & Ault, 2011; Hussey et al., 2017)(Fig. 2).

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

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

Segregation

In addition to using AT to quantify space use, we might wish to explore some of the mechanisms driving this space use. Individual behavioural signatures, whether in two or three dimensions, may be dictated by their local environment or by the presence of conspecifics of a different sex or size or individuals of different species altogether, manifesting itself as spatial and/or temporal differences in habitat use. Realistically, it's likely to be a combination of factors, yet understanding the dynamics of segregation within a population is important, particularly when considering species that face spatially- or seasonally-focused exploitation or partial spatial protection (Mucientes et al., 2009). Using Innovasea's (Amirix Systems, Nova Scotia, Canada) accelerometer and pressure transmitters (V9AP and V13AP) for example, Payne et al. (2015) were able to demonstrate diurnal segregation on a vertical plane between an estuarine piscivore (mulloway, *Argyrosomus japonicus*) and benthic carnivore (sand whiting, *Sillago ciliata*) in south-eastern Australia. Interestingly, the authors utilise these multi-purpose tags to monitor the impact of short-term stochastic weather events on segregation; the study reveals that rain precedes a switching of spatial segregation to temporal segregation (increased nocturnal activity in *A. japonicus* and decreased nocturnal activity in *S. ciliata*), a result compellingly supported by 10 years of commercial set-net CPUE data, which show increased rainfall produce higher catch rates for *A. japonicus* but lower catch rates for *S. ciliata* (Payne et al., 2015).

Sexual segregation is relatively well documented in marine fishes (Wearmouth & Sims, 2008) and here too AT has played a key role in distinguishing both sexual segregation within adult populations of elasmobranchs (e.g. Kock et al., 2013), as well as female-only refuging behaviour as a reproductive strategy for numerous species (e.g. Hight & Lowe, 2007; Sims, Nash, & Morritt, 2001). Furthermore, mobile, predatory elasmobranchs also have a tendency to demonstrate segregation by species; processes such as competitive exclusion within specific habitat types (Papastamatiou, Bodey, et al., 2018) or dynamic, temporal segregation driven by tidal cycles (Lea et al., 2020) have been demonstrated in remarkably small systems – relative to the movement capabilities of the study species – such as remote isolated atolls, using long-term AT data (e.g. Heupel et al., 2018). Despite having similar isotopic niches, AT has also revealed that leopard coral grouper (Plectropomus leopardus) and spotted coral group (Plectropomus maculatus) had minimal spatial overlap, yet similar space use patterns, due to vertical segregation in the water column (Matley et al., 2017). Again, network analyses have been put to good use to show, for example, that even amongst apparently sympatric species, sharks vary considerably in their choice of habitat, route choice and connectivity within a gridded receiver array in the southern Great Barrier

Reef (Heupel et al., 2018). Other applications include the use of community detection algorithms to networks of movements between different species and age classes, to explore dissimilarity in movement within complex fish assemblages (e.g. Casselberry et al., 2020).

Fish interactions

Aggregation and social structure inference

With enough individuals tagged simultaneously within a population, AT can be hugely informative for identifying and exploring fish aggregations and their key drivers, most notably spawning (Domeier & Colin, 1997), predation (Temming et al., 2007), refuging and nursery behaviours (Bass et al., 2017; Jacoby, Croft, & Sims, 2012). In teleost reef predators such as grouper, determining the location, timing and composition of reproductive aggregations is crucial to not only answer fundamental questions about population biology, but also inform spatial protection measures because aggregations are commonly targeted by fishers (Keller et al., 2020; Rowell et al., 2015). Indeed, the tendency of numerous pelagic species, including tropical tuna, to aggregate around floating objects has long been exploited to aid harvest through the deployment of artificial Fish Aggregating Devices (FADs). The relative ease of instrumenting FADs with acoustic receivers and other sensors has enabled substantial knowledge gains about movement ecology (Pérez et al., 2020), the social interactions of individuals (Stehfest et al., 2013), and the vulnerability of target and bycatch species to exploitation (Forget et al., 2015). In freshwater, the locations of adult lake trout (*Salvelinus namaycush*) aggregations in Lake Huron, North America, determined from 5 years of acoustic positioning data within an extensive (19 to 27 km^2) receiver array revealed hitherto unknown putative spawning sites which were subsequently confirmed by diver surveys of egg deposition (Binder et al., 2018). Several of these sites were too small or obscure to have been identified by bathymetric survey or did not conform to the conceptual model of a spawning habitat, so without telemetry would have otherwise likely been overlooked (Binder et al., 2018). Indeed temperature and depth sensors on acoustic transmitters can reveal the abiotic conditions that favour aggregation. For example, having gained this information through AT, Bajer et al. (2011) used the Judas technique, that is tracking an individual to reveal the location of an aggregation, to assist in the removal of invasive common carp (*Cyprinus carpio*) aggregations, with an efficiency of up to 94%.

Determining the mechanism driving aggregation or social behaviour from remote, passive data is in some instances non-trivial and in others near impossible depending on the ecology of the species. Consequently, a new line of questioning has emerged that uses machine learning inference to define multi-individual clustering events in acoustic time-series data that indicate the spatial and temporal co-occurrence of individuals (Jacoby, Papastamatiou, & Freeman, 2016; Mourier, Lédée, Guttridge, & Jacoby, 2018). Extracting these events using Bayesian inference reduces the subjectivity around predefining a sampling window with which to measure 'social' behaviour (10 mins? 10 hours?), relying more on the natural and variable clustering of the visitation patterns produced by gregarious fishes. Co-occurrence networks can then be generated from the clusters and worked up using common quantitative network analysis methods (Jacoby & Freeman, 2016), however careful interpretation of social networks produced using these methods is needed as the distance over which individuals may be socialising (i.e. co-occurring) is not always known (Mourier, Bass, Guttridge, Day, & Brown, 2017; see *Fine scale social associations* for more discussion around this). Caveats aside, this method has enabled exploration of the mechanisms behind social behaviour in highly mobile, free-ranging fishes for the first time, revealing for example stable social bonds in reef sharks that can last for years and likely function to facilitate information exchange (Papastamatiou et al., 2020).

Fine-scale social associations and trophic interactions

The fine-scale co-occurrences of individuals, whether between conspecifics as mutually beneficial social affiliations, or between predator and prey species as direct interactions and displacements, are an important factor that can strongly influence population dynamics and/or spatial distributions of species (Morueta-Holme et al., 2016). The encounter rates of Atlantic tarpon (*Megalops atlanticus*) with predatory bull (*Carcharhinus leucas*) and great hammerhead (*Sphyrna mokarran*) sharks in the Florida Keys for instance, were elevated at specific locations and prior to spawning aggregation behaviour, a result identified using machine learning to quantify spatio-temporal overlap in multi-species AT tracking data (Griffin et al., 2022). To truly understand fine-scale interactions and associations, however, requires direct measurement rather than inference methods, and at a precise and known spatial scale (Aspillaga et al., 2021; Mourier et al., 2017). Prototype methodologies and proof of concept studies have made exciting initial progress towards this endeavour. For example, recently developed transmitters that switch transmission code when digested in the stomach of a predator remove much of the uncertainty around formerly inferring predation events from changes in track characteristics (e.g. Romine et al., 2014), enabling more robust and detailed exploration of fishes' behaviours immediately prior to predation (Weinz et al., 2020). To reveal social behaviour using AT, a degree of control is needed over the system. Using model systems of fish constrained to localised areas or relatively small lakes, high-resolution tracking in combination with Proximity Based Social Networks, PBSN (temporal network analysis), significant strides have been taken towards measuring the wild social behaviour of fish. Vanovac et al. (2021), for example, tracked 108 freshwater fish (four species) every few seconds for a year to measure the location and duration of intra- and interspecific sociality. To measure social behaviour in wider ranging species, beyond the practical limits of pre-defined static receiver arrays, prototype 'Business card tags' have been developed; these operate as both transmitters and receivers for mobile peer-to-peer communication (Holland et al., 2010). Further, proximity transmitters, miniaturised receivers that can detect conspecific coded transmitters over distances <10 m (Guttridge et al., 2010)(Fig. 3, specifically d,e), have shown that an individual's actual social encounters can be logged and stored pending transmitter retrieval. The need for further technological developments in this area however remains; applications of devices like the Innovasea Mobile Transceiver (VMT) and Sonotronics' miniSUR - which are hybrid devices that transmit coded signals like acoustic transmitters, but also record transmissions from other tagged animals on the same frequency like monitoring receivers – are currently limited to small numbers on relatively large animals (e.g. Barkley et al., 2020; Haulsee et al., 2016), and in situations where the unit can be recovered to obtain the data. In all likelihood, advances in the 3D accuracy of spatial positioning of multiple tagged fish will yield the most insight into fine-scale social behaviours over the next few years (Aspillaga et al., 2021).

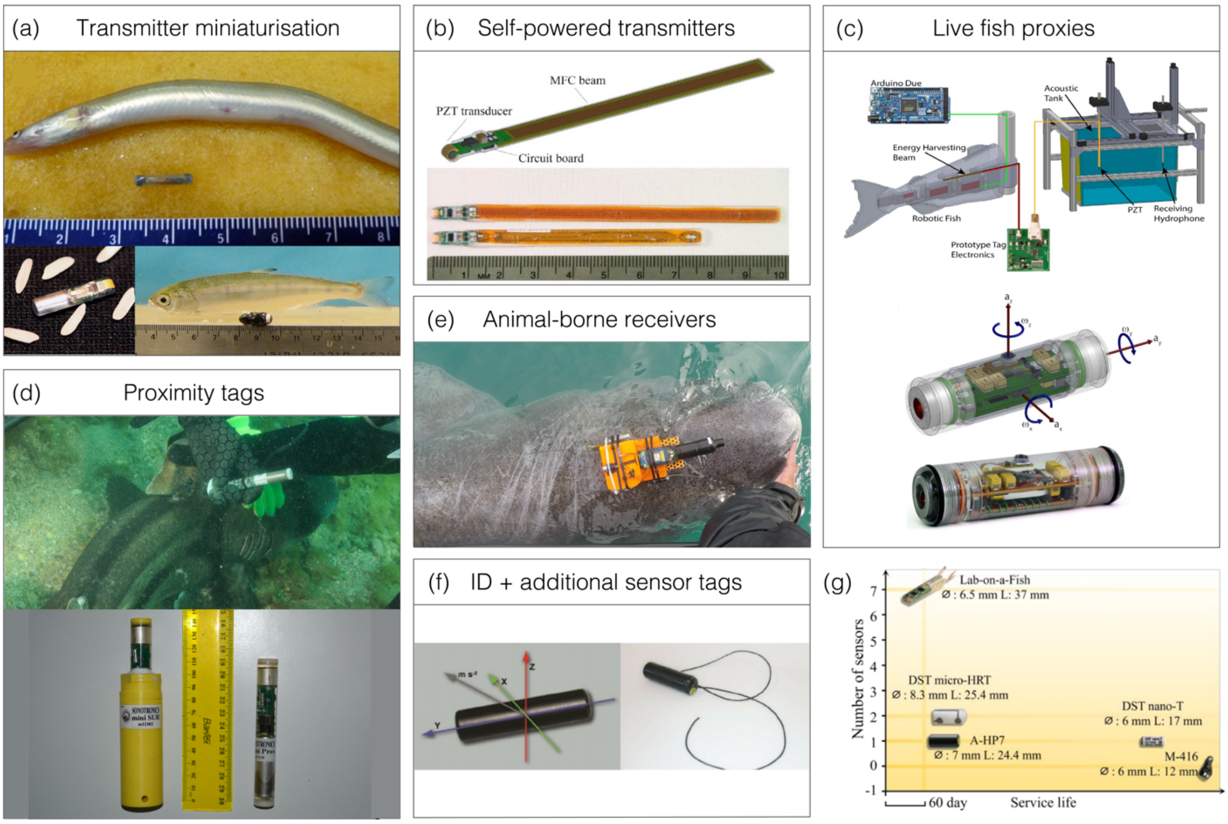

Figure 3. Important areas of transmitter development. a) Micro acoustic transmitter (0.08 g) developed for small/juvenile eel and lamprey research (top); needle injectable acoustic transmitter (0.22g) (lower left), and juvenile Sockeye salmon with 0.7g micro acoustic tag (lower right). b) Long life, self-powered acoustic transmitter employs a flexible piezoelectric beam to harvest energy from fish swimming to power direct acoustic transmission or re-charge onboard batteries. c) Robotic fish tail developed to replace the need for live fish testing in early phase tag development (top), and Sensor Fish, live fish surrogate which uses multiple sensors to approximate salmon smolt experience (e.g. shear forces, collisions with structures, acceleration, and pressure) when transiting deleterious route such as turbines, spillways, and sluiceways (bottom). d & e) Proximity loggers and animal-borne receivers record other fish in close proximity to one another (at a scale of metres). These have been trialled on Port Jackson sharks (d, top) to understand social networks and aggregation behaviour (images: Justin Gill; Nathan Bass) and on Greenland sharks (e), as part of a telemetry package to explore interactions, behaviour and encounter rates between individual sharks (image: Nigel Hussey). f) acoustic transmitters now offer additional sensors including for example, aceleration and heart rate monitors. g) Indication of how state-of-the-art Lab-on-a-Fish technologies fair against other commercial miniturised biotelemetric devices (reproduced with permission from Yang et al. 2021). All images unless otherwise stated kindly provided by Daniel Deng.

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

Depth preferences and temperature regulation

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

Combining pressure and temperature sensors with acoustic transmitters offers a widely applicable and often more cost-effective alternative (both in terms of hardware and data processing requirements), and can still provide high accuracy and precision (Baktoft et al., 2015). For example, Schurmann, Claireaux, & Chartois (1998) were able to demonstrate that a change in the amplitude of diurnal migrations of sea bass (*Dicentrarchus labrax* L.) resulted from manipulating vertical oxygen gradients in the water column within an experimental tank, down to an accuracy of +/-5 cm using acoustic pressure sensor transmitters. However, in field environments with extreme variation in environmental parameters (e.g. salinity, water temperature, flow rate) high accuracy in depth measurements may require additional field calibration (Brownscombe, Lédée, et al., 2019; Veilleux et al., 2016). Technical issues aside, acoustically transmitted temperature and/or depth sensor data has been used to investigate the influence of feeding regimes on vertical activity of cage cultured Atlantic salmon (Føre et al., 2017), vertical thermoregulation in sunfish (*Mola mola*) (Cartamil & Lowe, 2004), vertical separation of year classes through predator-prey dynamics in bulltrout (*Salvelinus confluentus*) (Gutowsky et al., 2013), the impact of seismic surveying on cod (*G. morhua*) and saithe (*Pollachius virens*) distribution (Jan G Davidsen et al., 2020) and seatrout (*Salmo trutta*) use of vertical gradients as a response to parasite loading (Mohn et al., 2020). Direct measurement of the temperatures and depths that free ranging fish move through has allowed us to move beyond broad correlational inferences derived from 2D location data alone and advance understanding of fundamental aspects of fish physiology and environment selection. Nevertheless, there is the risk that without corresponding environmental data collected at biologically relevant temporal and spatial resolution, studies will lack the ability to fully contextualise such animal borne data. For example, despite gaining detailed movement data, including depth, from Mekong giant catfish (*Pangasianodon gigas*) tracked for up to nine months in a reservoir, insufficient collection of concurrent temperature and dissolved oxygen datasets meant it was not possible to draw robust conclusions about the mechanisms driving their behaviour (Mitamura et al., 2008). Into the future, there is great potential for repeating tracking studies that have produced well defined relationships between fish distribution, behaviour and water temperature as a tool to identify and predict the impacts of a changing climate.

Invasion biology

An important prerequisite to applied measures for combating the growing list of fish species becoming established in non-native locations, is to understand the impact they have on native species and habitats. This might include monitoring the spread, movement capabilities, reproductive ecology and competitive interactions with other species (Deacon et al., 2011; Mills et al., 2004). AT has been pivotal in revealing some of this ecological information which can then inform more targeted mitigation measures. One of the first fish to ever be domesticated, the goldfish (*Carassius auratus*), now considered as one of the world's most invasive species, were tracked in a river in south-western Australia using AT to show that some individuals were capable of moving >200 km per year; crucially this study was also able to infer that movements into lentic habitat coincide with spawning behaviour in this species providing vital knowledge for control programmes (Beatty et al., 2017). Monitoring a newly-established source population of round goby (*Neogobius melanostomus*) within the Rideau Canal in Ontario, Canada, Bergman et al. (2022) were able to track the invasion front of this species which is normally native to the Black and Caspian Seas. Dispersal amongst a quarter of the tagged individuals was established via receivers situated within canal locks which were hypothesised to enhance passage (Bergman et al., 2022). The scale of the challenge facing marine invasive control has been demonstrated through a study on lionfish (*Pterois volitans*) in the western Atlantic, showing an eight-fold variation in individual home range estimates (~48000 – 379000 m^2) and ~40% of individuals travelling >1 km from the tagging site towards deeper habitat (Green et al., 2021). With the success of species invasion often contingent on species-community interactions (Lodge, 1993), multispecies AT tagging programmes will be key, as will developments to overcome the challenges discussed in the previous section around measuring fine-scale interactions.

2) Applied Research

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

Species conservation and management

Evaluating extinction risk and threat assessments

Continuing data deficiency in even basic population parameters hinders the robust classification of extinction risk for a fifth of global fish species as assessed by the IUCN (IUCN, 2020) and prevents the potential for their protection within legal frameworks (VanderZwaag et al., 2013). The assessment of endangerment relies on fundamental knowledge of demographic parameters to estimate absolute population size, trends in abundance and geographic range (IUCN, 2012). By tracking individuals from different components of the population, for extended periods of time, and with the ability to determine much more precisely when mortality occurs compared to traditional mark-recapture approaches, AT provides a powerful means of collecting such data for fishes (Lees et al., 2021). Further, telemetry-derived data can facilitate quantification of the main processes driving species decline and extinction (habitat loss and alteration, overexploitation; introduced species; pollution, and climate change), most obviously in the context of how the spatial ecology of a species predisposes it to specific impacts (Cooke, 2008). In a notably rare example of deep water AT, southern dogfish (*Centrophorus* *zeehaanii*) were tracked for 15 months at depths of between 300 – 700 m, to demonstrate the effectiveness of a large (100 km long) fishery closure to conserve this species, extirpated from much of its range off southern Australia (Daley et al., 2015). Although clearly possible, there remain substantial limitations to tracking wide-ranging species and/or those that occupy deep water habitats. Technical and logistical challenges in deploying deep water arrays have constrained the majority of AT studies to depths under 50 m (Loher et al., 2017), and bringing physoclistous species to the surface to tag poses the risk of damage and mortality due to barotrauma and post-release predation (e.g. Bohaboy et al., 2020; Curtis et al., 2015). The increasing use of in-situ tagging methods at depth and improvements to surface tagging protocols such as employing descender devices and rapid tag attachment methods to minimise time at the surface will further unlock the huge potential of AT to study fish movements and population dynamics in the deep sea (Edwards et al., 2019; Runde & Buckel, 2018).

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

Fisheries management

AT has enabled vast knowledge gains about the spatial ecology of fishes, which in the context of exploited species, especially those that are wide-ranging and/or straddle national boundaries, is fundamental to effective fisheries management. In the first instance, AT can be far more effectively employed to define the stock unit than traditional approaches such as mark-recapture (Donaldson et al., 2014). For example, acoustic tracking of Greenland halibut (*Reinhardtius hippoglossoide*) revealed connectivity between its use of inshore fjords and offshore habitats around Baffin Island, Canada, casting doubt on the status of separate inshore ‘resident’ and offshore stocks and highlighting the need for a shared quota (Barkley et al., 2018). Conversely, the discovery of high site fidelity and presumed natal homing has challenged the assumption of common stocks in many species including Atlantic cod *G. morhua* (Robichaud & Rose, 2001; Svedäng et al., 2007), Pacific cod *Gadus microcephalus* (Cunningham et al., 2009), and common snook *Centropomus undecimalis* (Young et al., 2014). There is also growing recognition of how individual and ontogenetic variation in spatial responses to environmental conditions and exploitation, drive the dynamics of populations (Alós et al., 2019; Goethel et al., 2021). In addition to this increasingly fine-scale understanding of the structure and spatial dynamics of exploited stocks, many of the life-history parameters required for stock assessment models can be directly determined using AT (Crossin et al., 2017). These include instantaneous mortality rate (Block et al., 2019), survival probabilities related to life-stage and migration pattern (Chaput et al., 2019; Perry et al., 2010), delayed mortality from by-catch or recreational catch and release activities (Curtis et al., 2015; Halttunen et al., 2010; Yergey et al., 2012), predation (Berejikian et al., 2016), and the spawning contribution of different stock components (Faust et al., 2019). Crucially for fisheries management, this information is attainable at the scale of the specific stock (DeCelles & Zemeckis, 2014). By bringing together datasets on spatial dynamics with these population parameters, spatially explicit integrated population models offer great potential to more accurately predict species’ responses to dynamic processes such as harvest mortality and climate-induced changes (Goethel et al., 2021). Nonetheless, despite the versatility and breadth of AT for informing fisheries management, in a review of global AT studies on all aquatic animals, Matley et al., (2021) found a lack of management driven applications, with most studies focussed on generating general movement data. They also highlight key challenges to be addressed such as developing analytical tools and standardised approaches among research groups to allow the potential of the vast quantities of AT data being collected globally to be fully realised (Matley et al., 2021).

It is the integration of AT with other approaches and the development of real-time tracking that offers most promise for more nuanced, creative and adaptive management of fisheries into the future. The increasing use of additional sensors such as heart-rate and electromyograms enable quantification of the sub-lethal fitness impacts of fishing activities such as the stress-induced physiological changes from catch and release (Donaldson, Arlinghaus, Hanson, & Cooke, 2008 and references therein). Within the context of ecotoxicological studies that have the dual purpose of understanding the impact of pollution on exploited stocks, as well as the human health risks of consumption, AT provides the opportunity to relate individual fish movements to contaminant burden and thereby manage exposure risk (Taylor et al., 2018). Crucially, AT enables an understanding of trait variation (e.g. movement) between individuals, relative to the population mean, which for fisheries that can unknowingly selectively harvest, can have important implications for ecosystem functioning when combined with physiological data (Allgeier et al., 2020). Further, behavioural change in response to hyperdepletion effects, such as reduced vulnerability or increased timidity can also be measured with AT, providing critical information for sock assessments and harvest control (Arlinghaus et al., 2017). Equally, integration with genomics promises insight into how genetic variation drives individual behaviour, with applications ranging from predicting the ways in which environmental change may impact highly locally adapted yet exploited species such as Arctic char (*Salvelinus alpinus*) (Moore et al., 2017), to understanding the extent to which fishing exerts a selective pressure on wild populations (Olsen et al., 2012; Villegas-Ríos et al., 2017). Gaining increasingly detailed information on threats enables continued refinement of conservation and fisheries management policies. For example, Forget et al., (2015) used AT to determine the vulnerability of target and non-target species to FADs used in the tuna purse seine fishery, identifying how impacts on non-target species could be reduced. Finally, by removing the time lapse associated with periodic receiver download, real-time tracking opens up huge possibilities for adaptive management, an approach that has also garnered much attention in aquaculture (Føre et al., 2017; Hassan et al., 2019). In one of the first examples from a wild fishery, on the Sacramento River, USA, receivers transmitting near real-time data to a communications centre, alerted water managers to the earlier than expected migration of Chinook salmon (*Oncorhynchus tshawytscha*) smolts. In response, water diversion structures into the Delta were closed, greatly reducing the loss of fish through that route (Klimley et al., 2017).

Evaluating spatial protection

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

The ability to accurately assess the efficacy of protected areas using AT however, is highly dependent on the size of the area under protection and the ability of the species in question to make long-range movements. Even for highly mobile species within Very Large Marine

Protected Areas (VLMPAs), data from array-based acoustic telemetry can be analysed using dynamic Brownian Bridge Movement Models, which account for the distance and elapsed time between consecutive detections, and can establish the extent of an animal's home range that is encapsulated within the protected area (e.g. Carlisle et al., 2019); although note earlier discussion around the challenges in doing this. For the shark species within this study, it was estimated that grey reef sharks (*Carcharhinus amblyrhynchos*) required at least one year, and silvertip sharks (*Carcharhinus albimarginatus*), two years of monitoring to effectively estimate their activity spaces (Carlisle et al., 2019). Alternatively, even species capable of making long-distance movements, well beyond the range of acoustic receivers, may show high levels of residency or site fidelity to specific places and at specific times of year (Curnick et al., 2020) which may be sufficient to offer a degree of protection during important behaviours or key life-history stages. Thus, assessing the space use of multiple species concurrently can help to demonstrate enhanced efficacy of marine spatial protection, particularly as MPAs are rarely established with a single species in mind (Casselberry et al., 2020; Hays et al., 2020). Once a tagged fish moves outside of the range of a receiver however, there is a significant degree of uncertainty; even notoriously site faithful grey reef sharks for example, can appear to undertake different scales of 'long-range' movements (134 km derived from acoustic telemetry [Heupel, Simpfendorfer, & Fitzpatrick, 2010] and 926 km derived from satellite tracking [White et al., 2017]). This is beginning to be remedied, in part, through cross-boundary tracking initiatives such as the FACT (Florida Atlantic Coast Telemetry) Network, the Integrated Tracking of Aquatic Animals in the Gulf of Mexico (iTAG), OTN and IMOS, but remains an issue for non-networked, isolated or remote protected areas. AT remains a powerful and persuasive tool for quantifying full or partial space use inside current or proposed protected areas (Barnett et al., 2012; Knip et al., 2012), movements between different management zones operating as a network (Espinoza, Lédée, et al., 2015), estimation of species-specific risk from illegal fishing activity (Jacoby et al., 2020) and for improving spatial conservation by directly informing policy (Lea et al., 2016).

Human-wildlife conflict

Establishing the cause and effect of human-wildlife conflict in aquatic environments remains challenging and is infrequently documented. Additionally, the (often) passive nature of more recent AT studies mean that data are rarely available to inform real-time responses to potential conflict. However, the network of arrays around the coast of Australia, that comprise the Australian Animal Tagging and Monitoring System (AATAMS) and the Integrated Marine Observing System (IMOS) offer an exception to this general trend. Over the last decade, passive arrays in Western Australia have been supplemented with satellite-linked Innovasea VR4 Global (VR4G) receivers at some of the most popular beaches for people (McAuley et al., 2016). Providing near real-time data retrieval, AT is being linked to social media platforms to generate 'live alerts' to beach goers when white sharks (*Carcharodon carcharias*) tagged with acoustic transmitters approach the area. Building on the back of a large collaborative research programme, the Shark Monitoring Network initiative has informed thousands of water users about hundreds of potential 'shark hazard events' (McAuley et al., 2016). The advent of increasingly accessible, real-time data however, is not without its potential problems, with these same data being used to locate and kill 'problem individual' sharks, undermining not only the safeguarding intentions of the initiative, but also the science and the conservation behind the project (Meeuwig et al., 2015). This has led to calls for a more proactive approach to mitigating the potential unintended consequences of animal tracking, and the associated data use, that may manifest as increased exploitation and disturbance of threatened species (Cooke et al., 2017).

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

Kinematics, energetics and physiological impacts of human modified systems

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

Overlaying fine-scale (± <5 m) 2D and 3D individual trajectories from acoustic positioning with concomitant environmental data, has proven key to understanding the mechanisms underpinning individual behavioural responses to anthropogenic perturbations. For example, near-continuous tracks of migratory European eel (*Anguilla anguilla*) and Atlantic salmon (*Salmo salar*) have been analysed in relation to flow fields on their approach to hydropower and water withdrawal facilities. These study systems have proven significant in unravelling the complex interactions between fish and the multiple hydrodynamic variables that elicit behaviours such as rejection on the approach to accelerating flows (Piper et al., 2015), milling (Svendsen, Aarestrup, Malte, Thygesen, Baktoft, Koed, Deacon, Fiona Cubitt, et al., 2011) and fine-scale adjustments in swimming direction and speed (Silva et al., 2020). Further, precise, real-world data are invaluable for the parametrisation and validation of agent-based models. Predictive behavioural models, that enable testing of different management scenarios aimed to reduce fish mortality and delay, are a key area of focus for hydropower, water abstraction and flood defence managers (Goodwin et al., 2006, 2014).

Even at fine resolution however, inferences about the energetics of movements and behaviours derived from position data alone will be inherently lacking through failure to consider the dynamics of the fluid in which the fish is moving and the physiological state of the individual. Thorough understanding of the biomechanics and energetics of free-swimming fish therefore requires moving beyond an animal's track characteristics. Measurement and modelling of salient metrics of the surrounding hydrodynamic environment such as flow velocity, turbulence intensity and hydraulic strain have revealed much about how migrating fish attempt to optimise energy usage (Piper et al., 2015; Silva et al., 2020; Svendsen, Aarestrup, Malte, Thygesen, Baktoft, Koed, Deacon, Cubitt, et al., 2011). For example, the modelled energy costs of a pallid sturgeon (*Scaphirhynchus albus*) actively tracked during its upstream spawning migration through a velocity-surveyed section of the Missouri River, USA, were lower than those calculated for 10^5 random paths in the same reach (McElroy et al., 2012). A suite of fish-borne sensors enable time-stamped monitoring of an individual's physiological processes such as muscle activity (Cooke, Thorstad, et al., 2004), heart rate (Lucas et al., 1991) and tail beat frequency (Watanabe et al., 2012), while accelerometers and speedometers provide a measure of speed (Block et al., 1992). These have been used successfully alongside acoustic positioning techniques to explore fish activity patterns and their associated energy expenditures (Meese & Lowe, 2020), as well as the stress responses and energy costs resulting from human disturbances such as recreational fishing (McLean et al., 2019), hydropower generation (Burnett et al., 2014) and seismic surveying (Jan G Davidsen et al., 2020). While such technologies began as stand-alone and typically data storage devices (Cooke, Thorstad, et al., 2004), the evolution of transmitting sensors and those integrated within acoustic positioning technologies offer much greater scope to derive detailed data from free-swimming fish without the need for recapture (Cooke et al., 2016; Lennox et al., 2017). Further, rapidly evolving data compression and transfer techniques to embed additional sensor data within the transmitted acoustic signals will serve to deepen our mechanistic understanding of fishes' behaviours as they move through their increasingly human-impacted environments (Cooke et al., 2022).

3) Future directions and considerations

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

Tracking small species and life-stages

Historically, the large size of transmitters has biased the application of AT towards adult life-stages and/or juveniles of large taxa only. Further, for species that exhibit sexual body size dimorphism such as anguillid eels, acoustic tracking has been skewed towards larger females (Bultel et al., 2014; Piper et al., 2013). This challenges the principal assumption that studied individuals are representative of the wider population and risks the erroneous extrapolation of findings. In applied research, this can have serious negative consequences such as misdirection of conservation funds or ineffective mitigation measures. To remedy this, continuing efforts towards transmitter miniaturisation, aided by substantial improvements in battery and microprocessor technologies, are greatly increasing the range of life-stages and species that can be tracked (Fig 3)(Lennox et al., 2017). When studying small species and life-stages for which commercially available transmitters may approach the limits of the acceptable tag to body weight ratio (traditionally the 2% rule, [Winter, 1983], although this is increasingly being questioned, [e.g. Brown, Cooke, Anderson, & McKinley, 1999]), body morphology also becomes an important consideration. The narrower body cavity relative to fish size among species with an elongated shape requires even smaller transmitters. New transmitters as small as 12.0 x 2.0 mm, weighing as little as 0.08 grams in air and lasting 30 days at a 5-second ping rate interval have been recently tested in juvenile lamprey (*Entosphenus tridentatus*) and American eel (*A. rostrata*) (Mueller, Liss, & Deng, 2019, Fig 3a). Although AT has been used across a wide range of taxa, the scale of investment directed towards juvenile salmonid research to assess stocks (see *Fisheries management*) and quantify anthropogenic impacts such as hydropower facilities continues to drive much of the innovation within the field (Cooke et al., 2013; Walker et al., 2016). For example, injectable acoustic transmitters have been developed for small fish sizes but also the volume of individuals and speed required to tag statistically meaningful samples, given the high mortality rate of juvenile out-migrating salmon smolts (Deng et al., 2015).

Long battery lives are required to track species across multiple life-history stages. The lifetime of an acoustic transmitter however, reflects the trade-off between battery power and the frequency and strength of transmissions, along with any additional power burden from integrated sensors. For smaller species and life-stages, the need for miniaturisation inevitably results in a transmitter with a shorter battery life and typically smaller detection range. Currently the smallest available acoustic transmitters are best suited to capturing brief windows of activity rather than providing near whole lifecycle data. Life-time tracking will significantly improve our understanding of small and cryptic species conservation however, and small battery-less tag technologies, for example passive integrated transponders (PIT) remain viable on a multi-decadal scale, enabling near whole lifetime studies. Near whole lifetime, AT studies of small individuals may be possible in the future using self-powered transmitters that incorporate a transducer to use the energy from fish locomotion to power the tag (Li et al., 2016). More sophisticated programming regimes, such as multiple time-limited transmission rates and dormancy, offers researchers increasing flexibility to extend the life of small transmitters to capture discrete periods of interest. These are, at present, pre-programmed and so require detailed *a priori* knowledge of predictable behaviours and/or life histories to be of most use (Davies et al., 2020; Stevenson et al., 2019). Further development of responsive acoustic transmitters that can dynamically adapt settings, for example transmission frequency or dormancy, in response to distinct changes in activity or environmental conditions such as the transition between fresh and saltwater, as has been trialled in Combined Acoustic and Radio Transmitter tags (Deary et al., 1998), would vastly improve their usefulness.

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

Multi-sensor transmitters, combined technologies and surrogates

Multi-sensor acoustic transmitters and AT studies that integrate additional biologging technologies (accelerometers, magnetometers, physiological sensors etc), and in some instances, direct observations, clearly facilitate broader research questions (Fig. 3). This has promoted greater exploration, for example, of the proximate mechanisms underpinning specific population level processes such as group living, social behaviour or individual behavioural variation/consistency through time (Villegas-Ríos et al., 2017; Wilson et al., 2015). Knowledge of these mechanisms for specific fish populations has the potential to greatly advance how we conserve and manage commercially important or highly threatened species (Villegas-Ríos et al., 2022).

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

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

Live data for near real-time management

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

Accuracy, precision and validation

Irrespective of the scale and complexity of a receiver array, or the study question being addressed, robust interpretation of animal movement data requires some quantitative measure of the accuracy and precision at which a transmitter can be detected. Crucially, this should capture the influence of spatial and temporal variation on detections within the specific study environment. Such sources of detection error are frequently overlooked or only partially accounted for in acoustic tracking studies (Brownscombe, Griffin, et al., 2019; Kessel et al., 2014; Klinard, Halfyard, Matley, Fisk, & Johnson, 2019). Equally, reflecting on detection efficiency during a study might also reveal redundancy within the array design

(Gabriel et al., 2021) that once identified, might free up a proportion of valuable receivers to monitor new locations.

Advances in transmitter and receiver design and data processing techniques provide increasing capability to achieve high accuracy and precision from both cabled and non-cabled arrays. For example, more sophisticated transmitter programming has reduced data loss from transmission collision when multiple transmitters are present and increased detection probability and positioning accuracy (Cooke et al., 2005), even in acoustically noisy environments (Bergé et al., 2012; Leander et al., 2019; Weiland et al., 2011). Fine-scale positioning studies typically require substantial post-processing to derive 2D or 3D positions from detection data, but the continual refinement of positioning methods is improving accuracy and reducing data omission during this process. For example, by employing a time-of-arrival rather than time-difference-of-arrival algorithm and incorporating a random walk movement model, the YAPS (Yet Another Positioning Solver) approach developed by Baktoft, Gjelland, Økland, & Thygesen (2017) out-performed comparable methods in terms of both accuracy and number of positions resolved, a method that has been successfully applied to acoustically reflective environments (Vergeynst et al., 2020). On a broader scale, where receivers may be dispersed over a wide area, model simulations that predict each receiver's theoretical detection range based on site-specific architecture, environmental variables and target species characteristics can be useful at the design stage (Gjelland & Hedger, 2013; Hobday & Pincock, 2011). Subsequent parametrisation with empirical environmental datasets and detection range tests collected within the study, enables calibration of live animal detection data post-collection. Brownscombe, Griffin, et al. (2019) developed an approach that uses variation in the detection efficiency of fixed reference transmitters collected at a subset of representative 'sentinel receivers' as a proxy measure for detection range across the whole array. Application of the detection range correction factors they generated to an Atlantic tarpon (*Megalops atlanticus*) dataset from the Florida Keys, showed substantial departure from the raw data (up to 127%) with most difference in the space use patterns associated with habitat and diel differences (Brownscombe, Griffin, et al., 2019).

Conclusions

Meeting the needs required of our rapidly changing aquatic environments, and doing so in ways that are fair, equitable, sustainable and responsive, is not trivial. In 2017, Lennox et al., (2017) set out a vision for how multiplatform tracking systems will be utilised in the future to monitor simultaneously the position, physiology and activity of aquatic animals and their environment. They highlight the four pillars of progress required to achieve this as "(1) technological and infrastructural innovations; (2) transdisciplinary integration of collected data and new methods of analysis; (3) emergent applications for telemetry data in fisheries, ecosystems, and the global management of aquatic animals; and (4) looking forward to solving challenges that currently inhibit progress in telemetry research" (Lennox et al., 2017). Since then, there have been advances in AT technology, data integration, analyses and application, many of which we have tried to cover in this review, but all of which have significantly progressed research within the key themes discussed.

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

Acknowledgements

Funding for this project to DMPJ was provided by the Bertarelli Foundation and contributed to the Bertarelli Programme in Marine Science and also by Research England. ATP was funded by Research England.

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