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Review

Global trends in aquatic animal tracking with acoustic telemetry

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Acoustic telemetry (AT) is a rapidly evolving technique used to track the movements of aquatic animals. As the capacity of AT research expands it is important to optimize its relevance to management while still pursuing key ecological questions. A global review of AT literature revealed region-specific research priorities underscoring the breadth of how AT is applied, but collectively demonstrated a lack of management-driven objectives, particularly relating to fisheries, climate change, and protection of species. In addition to the need for more research with direct pertinence to management, AT research should prioritize ongoing efforts to create collaborative opportunities, establish long-term and ecosystem-based monitoring, and utilize technological advancements to bolster aquatic policy and ecological understanding worldwide.

Highlights

Animal tracking provides integral spatiotemporal information that contributes to the growing field of movement ecology.

AT is one of the main approaches to track the movements of aquatic animals.

The proliferation of AT research and technological innovation have increased the ability to explore ecological and management-related questions.

Effective integration of AT data at relevant scales to inform management is still limited by a disconnect between management goals and research objectives, as well as global challenges such as equipment compatibility.

A comprehensive global overview of existing AT research identifying the knowledge gaps across regions of the world is necessary to ensure that future research advances aquatic animal science and governance.

The revolution of aquatic animal tracking

Movements of aquatic animals shape ecosystems by structuring interactions in space and time with other animals and humans that depend on them for economic, social, and cultural reasons. Advancements in technology have enabled **animal tracking** (see Glossary) in environments that would otherwise be difficult or impossible to monitor, providing novel insight into the growing field of **movement ecology** [1,2]. **Acoustic telemetry** (**AT**) is a primary method used worldwide to track the movement and behaviour of submerged aquatic animals in systems ranging from inland lakes and rivers to the high seas, and from polar regions to the tropics [1,3]. While the specific equipment and sampling protocols differ across studies, AT broadly consists of stationary or mobile receivers detecting the presence and location of animals via encoded acoustic signals originating from transmitters (i.e., tags) that have been internally or externally attached to animals. The diverse questions that AT can address [4–6], in addition to continued technological innovation [7], have yielded results revolutionizing our understanding of the aquatic realm. A few examples include gaining insight into the complex migratory movements of anadromous fishes [8–10], postrelease behaviour and survival of bycatch species [11,12], predator–prey interactions [13,14], and demographic parameters for fisheries management [15–17]. Furthermore, the spatial (e.g., meters to 1000s of kilometers) and temporal (e.g., days to years) dimensions that comprise animal tracking create a powerful tool to understand organismal responses and ecosystem consequences of human disturbances such as invasive species, habitat degradation, migration impediments, and climate change [2]. Similarly, AT holds significant potential to increase the effectiveness of conservation efforts and fishery practices by identifying areas and periods that are important for animal populations. Government agencies, now more than ever, are incorporating AT into regulatory initiatives such as fishing quotas, transboundary movements, and **aquatic protected areas** (**APAs**) [6].

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Despite the widespread ecological and management value of AT, historical trends relating to how research priorities have changed over time are not known. Similarly, identification of recent and emerging trends that indicate how AT studies are shaped by regional management, species of interest, or other ecosystem initiatives remains elusive. Here we synthesize historical (1965–2019) and emerging (2010–2019) AT research trends (see the supplemental information online for review methods) across 26 global regions – Food and Agriculture Organization **(FAO) major fishing areas** – to identify current management gaps and establish priorities for future work.

Global history and evolution of AT research

The 1834 AT studies published between 1969 and 2019 primarily focused on describing or quantifying spatial patterns of animals, termed 'ecology' here (n = 1442 studies; Figure 1A,B). The remaining types of studies included tagging effects (117), methodology (90), review (77), technology (74), and range testing (34) (Figure 1C; see the supplemental information online for definitions). We focus on ecological studies because they provide explicit spatial and behavioural information pertinent to ecosystems.

The marine FAO areas where animal movements were studied the most were the Northeast (n = 184 studies) and Northwest (179) Atlantic, followed by the Western Central Atlantic (166) (Figure 1A). North America (166) and Europe (69) represented the most studies in inland FAO areas. These areas encompass important fisheries within North America and Europe (e.g., Salmonidae, Anguillidae) as well as the Gulf of Mexico and the Caribbean (e.g., Serranidae, Lutjanidae). Several **AT networks** have also been established in these regions to support infrastructure for research [18–21]. Although AT networks are relatively new (most were founded in 2010 or after), they have had a significant impact on the already existing interest in AT and have expanded the diverse ecological topics that can be addressed. Not surprisingly, AT is mostly used in FAO areas (and countries) where funding and institutional (i.e., government, academic, etc.) support for research exists, and often poorly reflects where fisheries production is highest. For example, Asia and Africa have the highest inland fisheries production globally [22] but conduct limited AT or other types of telemetry (e.g., **radio telemetry**) research [23].

Bony fish (hereafter referred to as ‘fish’; n = 1361 studies) and **elasmobranchs** (301) were the most common animal groups studied using AT (Figure 2A). At least 20 other animal groups have been studied, the most prominent being crustaceans (e.g., crab, lobster, prawn – 62 studies) and turtles (27 studies) (Figure 2B). Within the past 10 years, fish have become increasingly more targeted than elasmobranchs, including more individuals being tagged (Figure 2C,D). Salmonid fisheries and aquaculture constitute the largest export revenue of all species groups worldwide [22], especially in North America and Europe; therefore, it is unsurprising that research has followed suit. Due to life history traits that lead to predictable migrations through confined riverine systems, salmon are typically studied using smaller AT tags, which are more cost effective [9], potentially enabling greater research output (187 967 tagged individuals) compared to other fishes (43 630) or elasmobranchs (8656; Figure 2D). **Satellite telemetry** is often used to track larger and more mobile species, namely sharks, billfishes, and tunas [24] accounting, in part, for some discrepancy when comparing across animal groups.

Emerging regional trends relating to management

The utility of AT research to directly inform managers (e.g., government agencies) by providing accessible spatiotemporal behavioural information has led to changes in regulations (e.g., fishery closures, fishing quotas, APA designation) in freshwater and marine environments [6,25]. For example, acoustic tagging of permit (*Trachinotus falcatus*) in Florida revealed the timing of spawning aggregations, which was rapidly incorporated into recreational policy to prevent overfishing [26].

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Similarly, AT monitoring and community engagement within an Indigenous Greenland halibut (*Reinhardtius hippoglossoides*) fishery in the Canadian Arctic indicated that an existing management boundary was ineffective, leading to its relocation and potential to develop an additional open-water fishery [27]. Despite these examples, there is still a paucity of readily accessible information explicitly demonstrating the impact that AT research has in guiding or supplementing management directives [28,29]. Consequently, we quantified the association between AT research and predefined management topics and identified which topics require greater attention to effectively progress AT research (Figure 3; also see the supplemental information online).

General movement

Acoustic telemetry studies investigated general movement more frequently than any other management category (Figure 3A,B) although it was listed as a moderately pressing issue for AT to address in most regions (Figure 3C). Examples of studies include estimating home range or other spatial metrics [30], quantifying diel and seasonal differences in spatial patterns [31], and incorporating telemetered sensors (e.g., depth, temperature, acceleration) to explore drivers of behaviour [32]. Much of this research is driven by the need for basic ecological understanding, for example, elasmobranchs often have different research priorities than commonly studied fish because they are not necessarily targeted for food consumption. Instead, knowledge of general movements, such as environmental drivers and habitat selection, provide a foundation to support threatened species management or other initiatives [33]. Indeed, 56% of elasmobranch species studied using AT that have been evaluated by the International Union for Conservation of Nature (IUCN) are listed as Vulnerable, Endangered, or Critically Endangered compared to 24% of fish species (Figure 4).

Migration

Migration is a complex biological undertaking to amass fitness benefits that is widespread in the animal kingdom [34]. Understanding pathways and mechanisms that facilitate animal migrations is important for management because of shifting contributions across resource pools (e.g., freshwater and marine), varying vulnerability to exploitation, and transboundary movements with jurisdictional implications [35]. Acoustic telemetry is widely used across FAO areas to track aquatic animals along predictable or confined freshwater, estuarine, or marine routes [36,37] and migration is one of the main categories where research effort has been allocated proportionally to ongoing AT needs (Figure 3A,C). In particular, the proliferation of salmon (Salmonidae) fisheries and eel (Anguillidae) conservation along the west coast of North America and in freshwater European systems, respectively (Figure 3B), has necessitated a more comprehensive understanding of migration across different life stages. Not only has AT research identified key movement corridors [21] it has also been instrumental in estimating survival rates along different segments of migration routes, contributing to more adaptive resource planning [8,38].

Spawning/mating

Identifying the spatiotemporal characteristics of reproduction is essential to the management of aquatic animals as it helps to monitor vital locations and periods that contribute to population growth and enables greater protection for species at risk [39]. Spawning-related research using AT includes evaluating reproductive timing, identifying spawning/reproductive events, and locating spawning grounds [40,41]. Species such as groupers (Serranidae), walleye/perch (Percidae), and sturgeon (Acipenseridae) aggregate and spawn at recurring locations, creating valuable opportunities to study spatial aspects related to their biology (Figure 3B). As a result, AT has provided previously unknown insight about reproduction for highly targeted fishery species as well as for those with threatened status [42,43].

Glossary

Acoustic telemetry (AT): remote transmission of data through water, typically using low-frequency (63–417 kHz) sound waves from electronic tags attached to aquatic animals. We use the term here to refer specifically to the measurement of spatial data although it otherwise may also encompass physiological data transmitted via sound. AT may also be termed acoustic tracking, ultrasonic telemetry, or ultrasonic tracking.

Animal tracking: gathering information on an animal's location over time.

Aquatic protected area (APA): the geographic area in marine, estuarine, or freshwater environments where extractive (e.g., fishing) or other activities are regulated for the purpose of provisioning for enhanced biodiversity, conservation, animal population sustainability or recruitment, or other reasons. They may be closed year-round or seasonally with different levels of regulations both in space and time. The term APA incorporates both marine (MPA) and freshwater (FPA) protected areas.

AT network: a collaborative organization that connects telemetry projects and researchers with each other to facilitate equipment and data sharing at regional, national, and international scales. Networks frequently feature a semipermanent deployment of a series of acoustic receiver arrays. Networks mentioned in the text include: the Ocean Tracking Network (OTN), European Tracking Network (ETN), Florida Atlantic Coast Telemetry Network (FACT), Integrated Tracking of Aquatic Animals in the Gulf of Mexico (iTAG), Integrated Marine Observing System (IMOS), Acoustic Tracking Array Platform (ATAP), Great Lakes Acoustic Telemetry Observation System (GLATOS), California Fish Tracking Consortium (CFTC), Southern California Acoustic Telemetry Tracking Network (SCATTN), Pacific Ocean Shelf Tracking (POST), and MigraMar.

Bony fish: a taxonomic group (Osteichthyes) of fish that have skeletons primarily composed of bone. It consists of the majority of fish across the world.

Elasmobranch: a taxonomic group (Elasmobranchii) of fish that is part of the Chondrichthyes class, known for having cartilaginous skeletons and includes sharks, rays, skates, and sawfish.

Passage, impediments, or construction

Human alteration of aquatic environments is increasingly relevant to management because of the detrimental effects it can have on aquatic animals and their access to resources [44,45]. In European inland waters, for example, the effects of human-built barriers (e.g., hydroelectric dams) on fish migration and survival are prioritized by researchers and managers alike (Figure 3A,C) due to the rapid development of infrastructure and legislation for renewable resources, as well as the scale of river fragmentation [46]. Other human-built structures within the Western Indian Ocean, such as fish aggregating devices (FADs), contribute to pelagic fisheries by attracting highly mobile species (e.g., tuna, mackerel – Scombridae; Figure 3B) and are ideally suited for AT because finer-scale spatial resolution supplements other methods (e.g., satellite telemetry) to identify the presence of fisheries-targeted and bycatch species [47,48].

Protected areas or closures

Spatial and temporal closures to regulate human pressures on aquatic environments is an increasingly employed management strategy worldwide [49]. The range in spatial resolution possible with AT makes it particularly useful for evaluating the effectiveness of APAs by identifying patterns in space use, such as the geographic extent and duration that an animal is protected or not [50,51]. Using AT in conjunction with underwater video, Dwyer *et al*. [50] estimated the effectiveness of marine protected areas (MPAs) for coral reef sharks, providing novel management guidance about the relationship between MPA size and fishing vulnerability. Coral reefs are biodiversity hotspots facing severe risks from environmental perturbations (e.g., coral bleaching) and direct human activities (e.g., overfishing), requiring protection of critical coral reef habitat (e.g., Coral Triangle [52], Great Barrier Reef [53]). As a result, coral-reef-associated species (e.g., Lutjanidae, Carangidae, Carcharhinidae, Serranidae) are often focal in AT research associated with MPAs (Figure 3B). Although protected-area research using AT is conducted to some extent in FAO areas where it is a priority, additional effort is needed (Figure 3C).

Restoration or stocking

Restoration and stocking programmes provide the opportunity to enhance populations that have declined, typically due to human activities (e.g., overfishing, habitat degradation). Acoustic telemetry is well suited to evaluate rehabilitation efforts by monitoring behaviour and survival of target species. For example, the previously unknown postrelease movement and survival of stocked salmonids have recently been revealed using AT [54,55]. Salmonidae stocking along the west coast of North America has been a dominant contributor to AT research [56] (Figure 3B). In fact, the widely used Juvenile Salmonid Acoustic Telemetry System (JSATS) is a micro tag that was developed specifically to meet research needs for monitoring juvenile salmon in the Columbia River Basin [9].

Fisheries

Fisheries contribute to economic growth and stability and support human nutrition worldwide (e.g., 17% of animal protein consumed [22]), yet the application of AT to quantitatively inform fisheries practice is relatively limited despite its potential and urgency (Figure 3A,C). Examples of AT being implemented to guide fisheries include determining the effects of angling on fish behaviour [57], quantifying incidental or illegal captures [58], estimating fishing mortality [59], and identifying interactions between fishers and fish [60]. The ability of AT to act as a mark–recapture platform, while also providing key metrics associated with survival, space use, and activity across different life stages and seasons, makes it intrinsically applicable to fisheries management.

Other categories

Several management objectives were not readily pursued with AT, yet they all encompass important emerging ecological issues throughout FAO areas worldwide [44,61]. Invasive species,

FAO major fishing area: internationally established marine and inland boundaries created by the Food and Agriculture Organization of the United Nations for statistical purposes.
Movement ecology: a field of ecology dedicated to understanding the internal and external drivers of animal movement and the consequences of movement for individuals, populations, communities, and ecosystems.
Radio telemetry: remote transmission of data through radio signals (150–180 MHz) to locate electronic tags attached to animals of interest. In aquatic environments, this method is mainly limited to riverine or constrained freshwater systems where signal transmission is optimal.
Satellite telemetry: remote transmission of data through radio signals (401 MHz) between electronic tags attached to animals of interest and satellites orbiting the Earth. In aquatic environments, satellite telemetry is typically used for large individuals that undergo broad-scale movements.

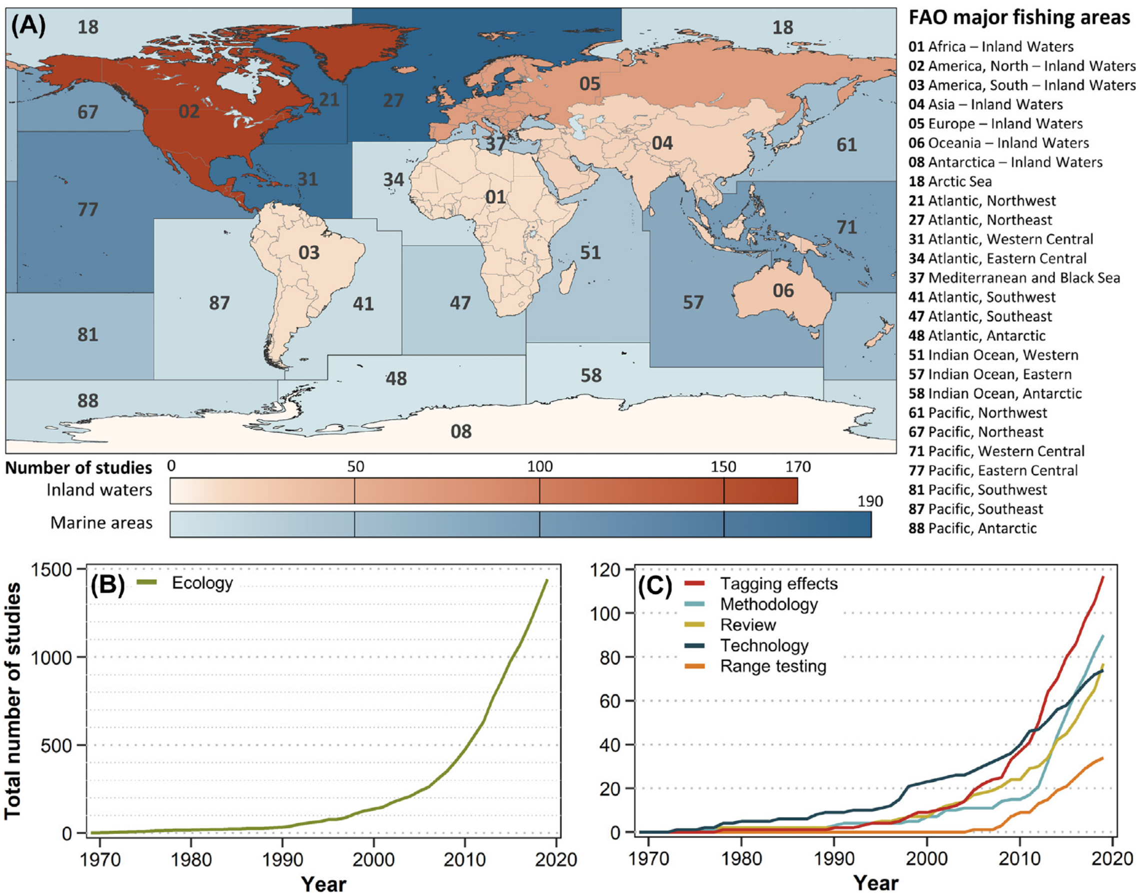

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Figure 1. Global distribution and types of acoustic telemetry studies. (A) Total number of ecology studies across FAO major fishing areas. (B) Cumulative number of ecology studies per year from 1969 to 2019. (C) Cumulative number of tagging effects, methodology, review, technology, and range-testing studies per year from 1969 to 2019. See the supplemental information online for study type definitions. Abbreviation: FAO, Food and Agriculture Organization.

aquaculture, water quality/pollution, climate change, and tourism (Figure 3A) all have direct relevance to resource management and are topics which AT has the ability to effectively address. Of these categories, climate change was identified as a leading priority yet has received minimal focus in studies (Figure 3C).

Global research gaps and future directions

Despite incredible advancements in the use of AT to understand the movement ecology of aquatic animals, many opportunities still exist to optimize its application for management and broaden ecological knowledge. We identified current AT research trends at regional scales, synthesized the current gaps within the context of management themes, and highlighted potential trajectories to ensure that future research is more relevant to aquatic governance (Figures 3 and 4 and Table 1). Still, clear steps are needed from a global perspective to elucidate how AT practices worldwide can be adapted to better support policy decisions. In addition to focusing AT research on management application, we identified five other overarching global directives that will continue to move AT forward (Table 1 and Figure 3A,C). These included: optimizing spatiotemporal tracking coverage, incorporating technological advancements, shifting towards ecosystem-based objectives, integrating AT across political boundaries, and supporting AT in developing nations.

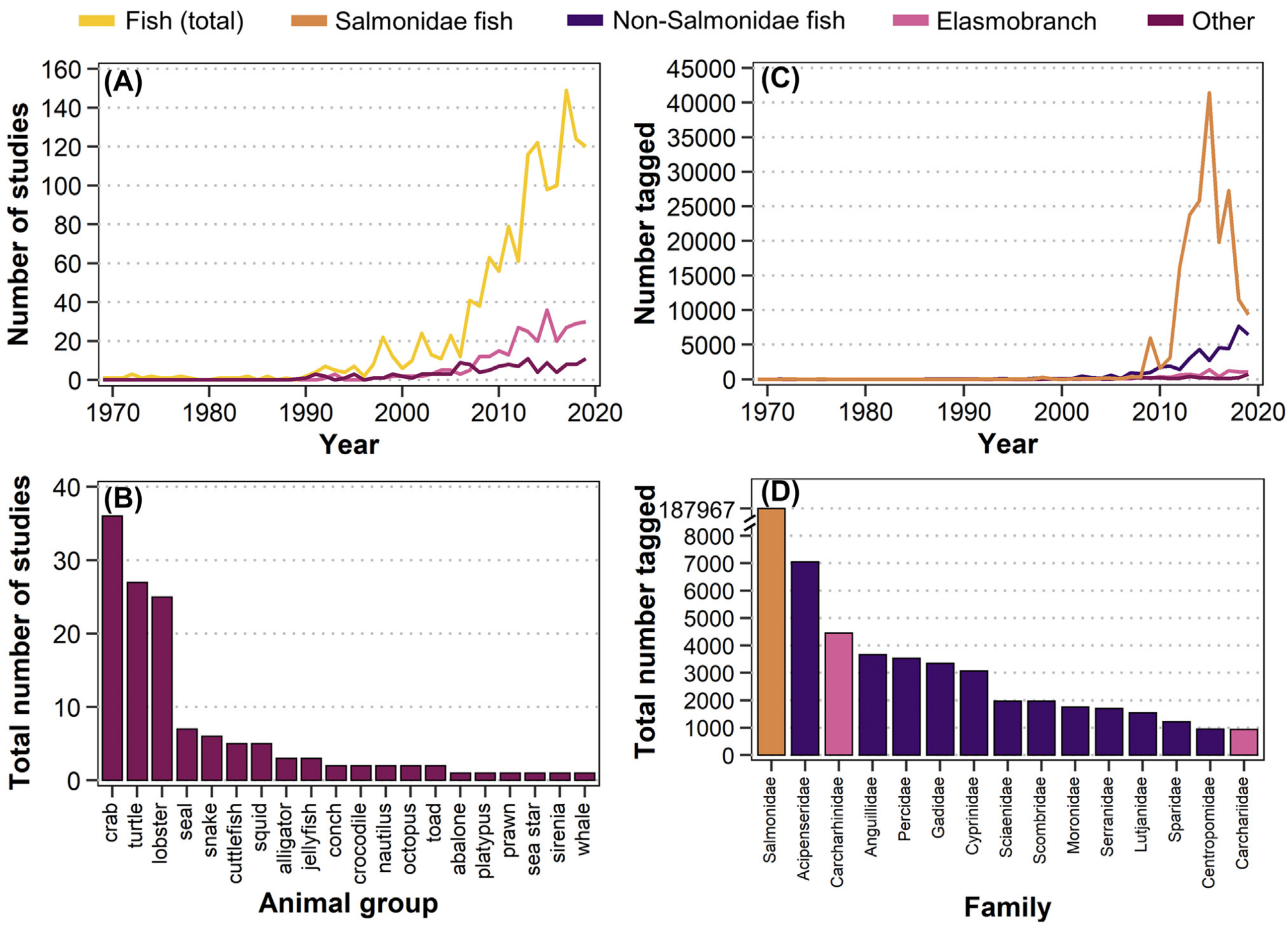

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Figure 2. Historical trends of the animals tagged in acoustic telemetry studies. (A) Yearly number of ecology studies for fish, elasmobranch, and other animal categories from 1969 to 2019. (B) Total number of studies across all years for each animal group comprising the 'other' category in (A). (C) Yearly number of individuals tagged in ecology studies for Salmonidae, non-Salmonidae fish, elasmobranch, and other animal categories from 1969 to 2019. The 'fish' category in (A) was divided into 'Salmonidae' and 'non-Salmonidae fish' to better illustrate the types of fish tagged. (D) Total number of individuals tagged across all years for the 15 most commonly tagged families among all animal categories.

Management application

It was apparent that an overwhelming number of studies were not designed to explicitly address management-related issues but rather built upon existing knowledge, or provided new knowledge, of general patterns of movement and behaviour. Regardless of location and species, studies should be designed with forethought to how applicable and accessible the findings are to contribute to policy and governance. The lack of studies directly associated with fisheries, in combination with its high research priority need (Figure 3C), was noteworthy since fisheries production (i.e., fishing and aquaculture) is one of the main sources of human and animal nutrition worldwide [22] and supports additional activities that are economically valuable (e.g., recreational or charter fishing). As a result, we advise that AT be increasingly used to gather empirical data that can be readily utilized by management, such as traditional fishery science metrics (e.g., mortality rates, fishery discard, by-catch, depredation, geographic distribution, immigration/emigration rates, and predation pressures). Evaluating these metrics with AT will further support fisheries models [16], especially for data-poor species, and contribute to the increasing global push for ecosystem-based management [62]. Research (and decision making) is also

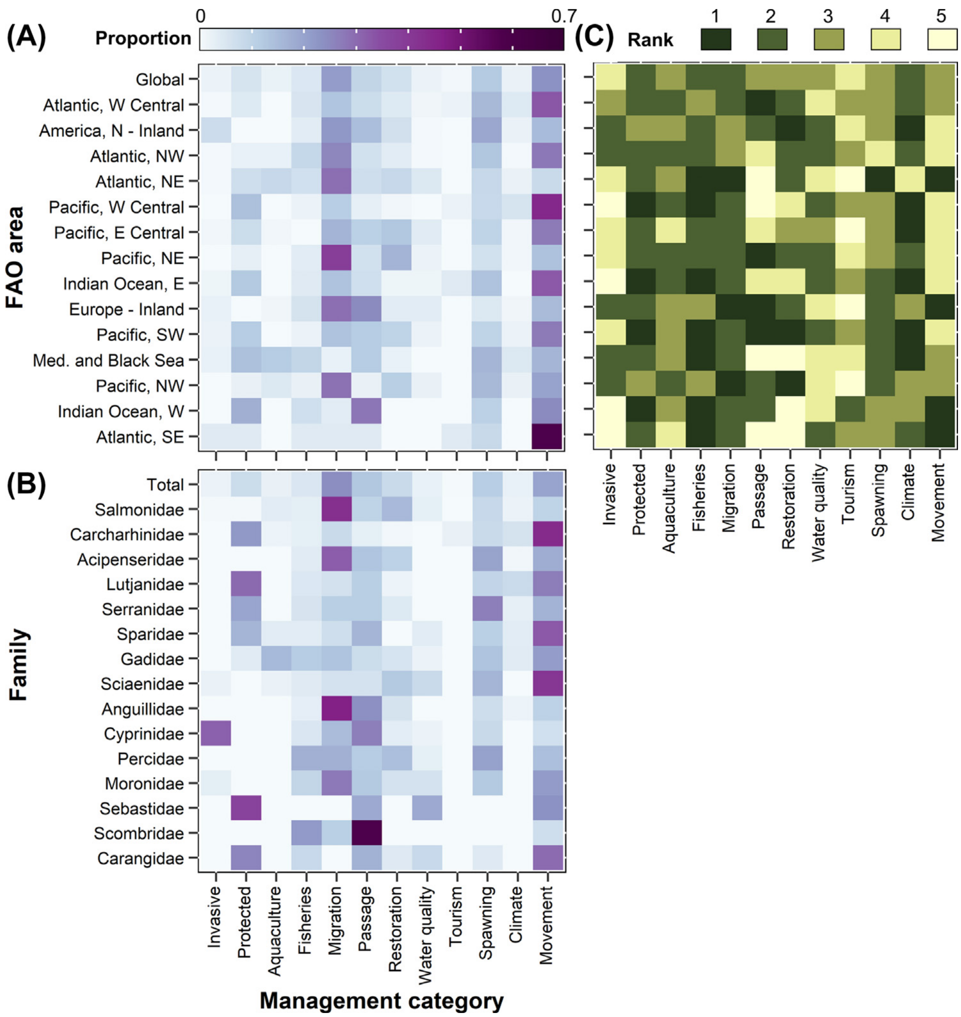

Figure 3. Management-related objectives for ecology studies. (A) Proportional total of objectives addressed for FAO areas with >20 studies. (B) Proportional total of objectives for the 15 most studied families. FAO areas in (A) and families in (B) are ordered from the highest number of studies (top) to lowest (bottom), and proportions are calculated within each FAO area and family (within rows). (C) Prioritizion of management objectives needed to be addressed with acoustic telemetry at current or near future (~10 years) timelines ranked within each FAO area from 1 (most pressing) to 5 (least pressing). All subplots were based on emerging trends (2010–2019). Abbreviation: FAO, Food and Agriculture Organization.

conducted within the confines of organizations responsible for regulation and management and may be reported independently of primary literature, in languages other than English, sourced out privately (e.g., consultancy firms), or not reported at all. As a result, collaboration and consultation with management entities throughout study design, implementation, and dissemination is an effective way to ensure that relevant data are collected and the impact of AT is maximized.

Spatiotemporal tracking coverage

Strategic deployment of monitoring equipment is key to optimizing tracking coverage in space and time and requires ongoing evaluation and commitment of resources [63,64]. Investigating how animal movements are influenced by environmental variables is commonplace in AT research [65]; however, the duration of studies is typically limited to months or a few years. Climate change emerged as one of the most under-utilized management categories in this review (Figure 3A,C) despite its continuing impact on aquatic ecosystems throughout the world [66]. Evaluation of climate change effects often requires monitoring over representative periods. Investment in long-term AT arrays and environmental sampling at strategic locations is an ongoing need to monitor species as they face numerous environmental stressors, often caused by human activities. Furthermore, methodical study design that targets aquatic locations with ecological or management relevance such as APAs, platforms of opportunity (e.g., navigational markers,

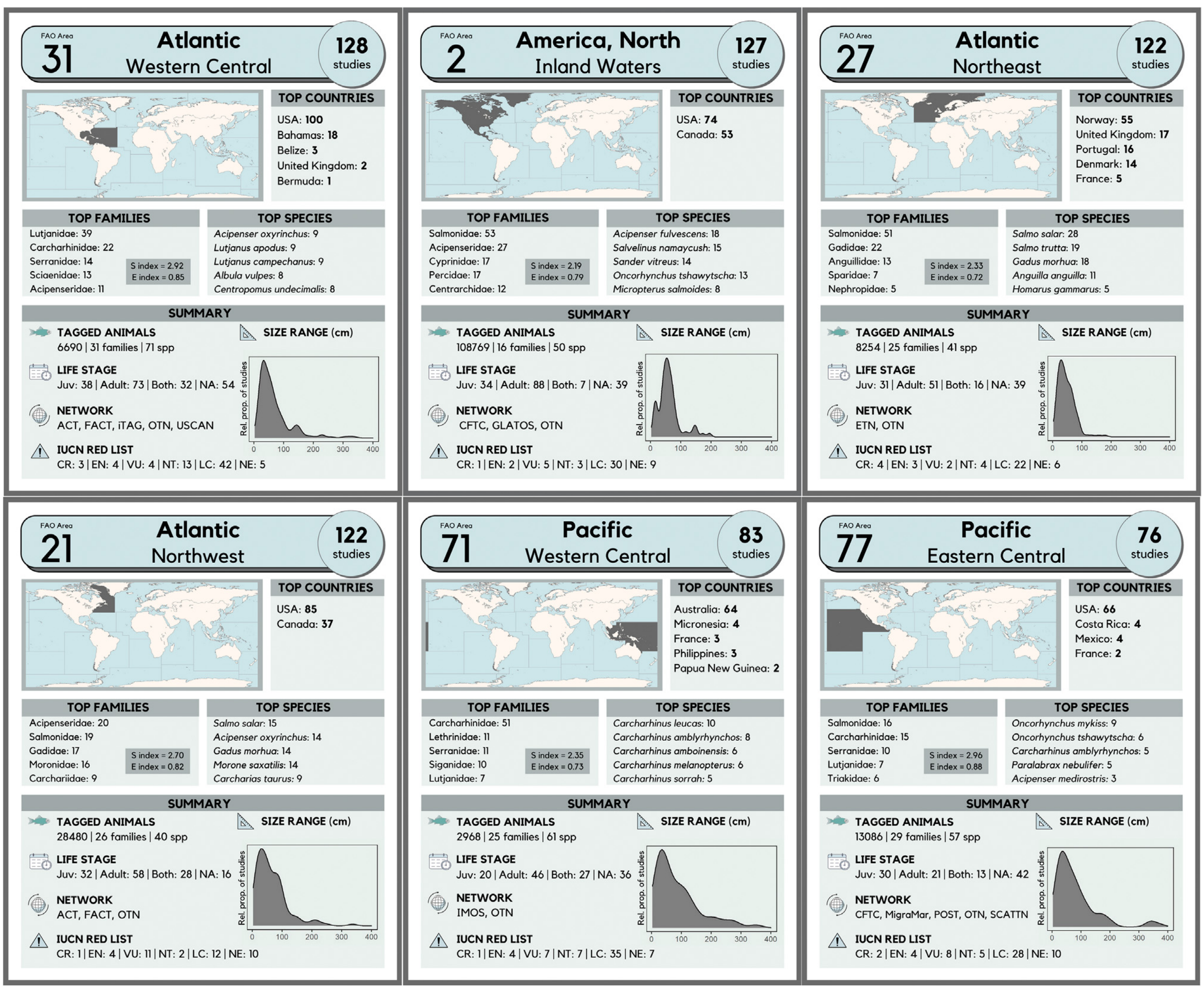

Figure 4. Acoustic telemetry (AT) study statistics for FAO major fishing areas. Summaries of study and species information are listed for each FAO area (n = 14) with more than 20 studies conducted between 2010 and 2019. All values were based on emerging trends (2010–2019) from ecology studies only. Shannon-Weaver diversity (S index) and evenness (E index) indices are based on the number of families studied and provide additional context into the composition of different focal families in AT studies. 'Tagged animals' refers to the total number of tagged individuals, families, and species inclusive of all animal groups. Life stage represents the number of studies that tagged juveniles, adults, both juveniles and adults, or it was not indicated. Where life stage was not identified in a study, it was estimated, if possible, based on the size range in the study relative to size at maturity stated on Fishbase or Sealifebase. Network terms (see Glossary) indicate established AT networks that exist (or have existed) in that area. International Union for Conservation of Nature (IUCN) Red List values represent the number of species in each designation (https://www.iucnredlist.org/). Size range illustrates the distribution of the mean size of individuals tagged in each study, where stated, shown as a relative proportion of all studies in the region. Abbreviation: FAO, Food and Agriculture Organization.

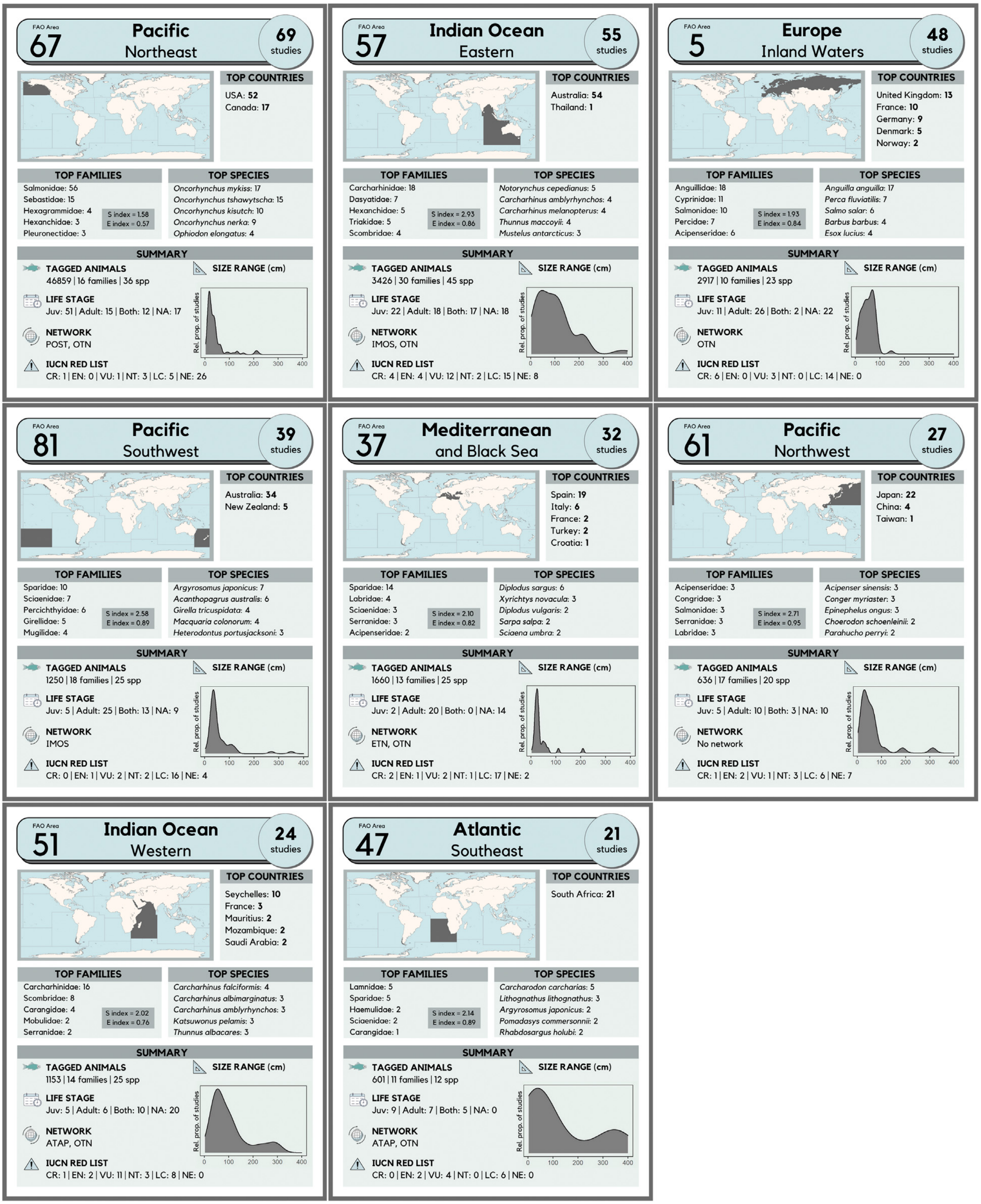

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Figure 4 (*continued*).

Table 1. Current gaps and future directions for AT research. Synthesis of current gaps and future directions for FAO areas (n = 14) are based on regional expertise from contributing authors with extensive AT background. Current gaps consist of three selected knowledge gaps affiliated with a management category (in square brackets) as well as an additional biological (or other) disparity derived from Figure 4. Only FAO areas with more than 20 studies conducted between 2010 and 2019 were included

Current gaps	Future directions	Refs
Atlantic, Western Central (128 studies)		
• [Migration/Passage] Riverine portion of diadromous migrations and affiliated impacts from human alteration (e.g., dams) • [Tourism] Interaction between movements and tourism in Gulf of Mexico and Caribbean • [Water quality] Scale-dependent effects of pollution and algal blooms • [Biological/Other] Relative diversity of species sampled	• Impacts of multispecies movements on ecosystem functionality and predator–prey linkages • Environmental stressors (e.g., red tide) that continue to impact species of fisheries value • Long-term monitoring via AT networks to evaluate the impacts of severe weather events (e.g., hurricanes) and ongoing human development (e.g., oil extraction) • Impact of coral reef health on fish and elasmobranch movements	[89,90]
America, North – Inland Waters (127 studies)		
• [Water quality/Climate] Current and historical issues related to industrial pollution and agriculture runoff • [Fisheries] Impacts of movements on fisheries given economic output of recreational fisheries in the US valued over 100 billion USD • [Restoration/Passage] Effects of rapidly growing human development and habitat degradation on Great Lakes fish populations • [Biological/Other] Arctic and subarctic areas given enormous surface area, rapid climate change, and economic and cultural importance to local Indigenous communities	• Long-term spatial responses to increasing human-induced environmental changes (e.g., harmful algal blooms, ice cover) • Large-scale environmental effects via collaboration with limnologists • Greater suite of species including juvenile life stages • Evaluate habitat restoration as landlocked systems become more developed	[44,91,92]
Atlantic, Northeast (122 studies)		
• [Climate/Passage] Coastal marine species and habitats under threat from human activities • [Migration] Open ocean migrations of diadromous and marine species • [Fisheries/Aquaculture] Impact of important commercial fisheries and aquaculture operations • [Biological/Other] Smaller and less resilient fish (to tagging), particularly commercial species	• Expansion of geographic and species coverage, particularly within highly diverse coastal ecosystems and for commercial fishery species • Amalgamation of AT with marine fisheries science (e.g., survival modelling) • Global open standard for compatibility among AT equipment to facilitate collaboration	[18,93,94]
Atlantic, Northwest (122 studies)		
• [Fisheries] Stock structure of small fishes of importance to commercial fisheries (e.g., Atlantic herring) and Indigenous peoples (e.g., tomcod) • [Movement] Critical habitats and temporal distributions of species of interest • [Migration] Off-shelf oceanic movement of small (e.g., Atlantic mackerel) and large (e.g., Atlantic sharpnose shark) migratory species • [Biological/Other] Northern region (e.g., Arctic) which incorporates Indigenous communities and critical animal migratory routes	• Sampling of small commercial species as technology advances • Mobile tracking platforms to increase geographic coverage • Deep ocean (>500 m) animal tracking • Use of large animals as mobile tracking units • Effectiveness of MPAs • Wider investment in AT by regulators of commercial species	[20,95]
Pacific, Western Central (83 studies)		
• [Fisheries] Species that comprise the extensive recreational, commercial, and subsistence fisheries • [Climate] Behavioural responses of fish and elasmobranchs to coral bleaching • [Movement] Movement of continental slope species • [Biological/Other] Small island nations with cultural, economic and food security reliance on marine species	• Effects of climate change on coral reef species • Connectivity of species between nations prioritized to help inform joint management • Increased collaboration between developed and developing nations to fill gaps within biodiversity hotspots (e.g., Coral Triangle)	[51,96]

Table 1. (continued)

Current gaps	Future directions	Refs
Pacific, Eastern Central (76 studies)		
• [Invasive/Fisheries] Economically important endemic deepwater and invasive shallow water Lutjanidae and Serranidae • [Climate] El Niño Southern Oscillation (ENSO) events and range shifts • [Protected] Fish movements associated with MPAs • [Biological/Other] Connectivity among oceanic islands and archipelagos that serve as hotspots for pelagic and reef fishes	• Use of MPAs across ecosystems • Support for AT network enhancement and connectivity, as well as longer-term monitoring • Multispecies impetus across size classes • Mobile AT platforms for monitoring offshore species and examining oceanic/neritic coupling	[97]
Pacific, Northeast (69 studies)		
• [Passage/Climate] Longer-term monitoring to determine human impacts such as wind/wave energy generation, mining, and climate change • [Movement] Intra- and inter-specific behavioural interactions as well as offshore and deep-water habitat use • [Fisheries] Validation of off-shore fish-environment models used to calculate growth and survival • [Biological/Other] Diversity of species studied (e.g., non-salmonid)	• Impacts of climate change related events (e.g., dead zones, marine heat waves) on species distributions and physiology • Stock models of species impacted by benthic trawling • Movements of apex predatory elasmobranchs (e.g., Pacific sleeper shark, salmon shark) • Use of platforms of opportunity and complementary tracking technologies • Predator–prey interactions between marine mammals and fish • Real-time tracking systems that enable adaptive management of socioeconomically important salmonid populations	[20]
Indian Ocean, Eastern (55 studies)		
• [Fisheries] Fish species targeted in commercial and recreational fisheries • [Climate] Effects of marine heatwaves throughout species extent • [Tourism] Impact of tourism on space use of key species (e.g., whale shark, manta rays) • [Biological/Other] Populated countries in Southeast Asia (e.g., India, Indonesia) that rely heavily on aquatic resources for food and economic security	• Diadromous fish migrations in Southeast Asia given high level of fishing pressure • Effects of intensive fisheries on fish and elasmobranch populations in Southeast Asia • Collaboration between developed and developing nations to facilitate sustainable commercial and subsistence fisheries	[22,98]
Europe – Inland Waters (48 studies)		
• [Migration] Riverine portion of potadromous and anadromous migrations and affiliated impacts from anthropogenic alteration (e.g., dams and weirs) • [Passage] Impact and function of different types of fish passage technology • [Invasive] Spread and impact of invasive species • [Biological/Other] Collaboration barriers (e.g., lack of AT networks) between regions and within water bodies	• Large-scale studies that incorporate transboundary movements and are suitable for large lakes • Impact of migration barriers to provide better scientific advice to managers • Life history, migration patterns, and habitat use of potamodromous and semianadromous species (e.g., grayling, whitefish, vimba bream, asp, nase)	[18,99]
Pacific, Southwest (39 studies)		
• [Fisheries] Oceanic species subject to fisheries exploitation (e.g., Scombridae, Carangidae) • [Restoration] Response of fish species to management interventions (e.g., habitat repair) • [Climate] Longer term (5–10 year) studies examining influence of environmental variability • [Biological/Other] Juvenile life stages of fish species	• Influence of changes in the oceanography of the southwestern Pacific Ocean on species distribution, phenology and migration • Meta-analyses of long-distance movements of fish and elasmobranch species throughout integrated coastal arrays (e.g., IMOS) • Application of AT to examine ecological function of restored habitats for fishes (e.g., oyster reefs, reflooded coastal wetlands)	

(continued on next page)

Table 1. (continued)

Current gaps	Future directions	Refs
Mediterranean and Black Sea (32 studies)		
• [Migration] Large mobile or migratory species (e.g., Atlantic bluefin tuna, sharks, sea turtles) • [Climate/Invasive] Long-term studies given rate of climate change and biological invasions • [Fisheries] Species of interest for commercial and recreational fisheries and species generating spawning aggregations • [Biological/Other] African coast of the Mediterranean Sea and the Black Sea	• International network initiatives within the European Tracking Network (ETN) and transboundary receiver arrays • International AT collaboration at sites critical to multispecies migrations (e.g., Straits of Gibraltar, Messina, Bosphorus) • Collaboration between European and African countries to expand tracking networks to poorly studied areas	[18]
Pacific, Northwest (27 studies)		
• [Migration] Highly migratory oceanic species (e.g., Scombridae) and offshore migrations of diadromous fish (e.g., Anguillidae, Salmonidae) • [Movement] Intra- and inter-specific behavioural interactions in estuarine, coastal, and offshore areas • [Fisheries] Fishery-targeted invertebrates (e.g., crab, lobster, sea cucumber) • [Biological/Other] AT networks among related countries	• Collaboration between countries to study highly migratory oceanic and deep-water species long term (>5 years) • Development and application of AT platforms to better understand population and community dynamics • Effects of human activity (e.g., fishing, artificial reef construction) on movements of aquatic animals, particularly threatened species • Use of miniature AT tags to investigate stock enhancement objectives	[100]
Indian Ocean, Western (24 studies)		
• [Fisheries] Exploited species important to artisanal and recreational fishing in coastal biodiversity hotspots • [Water quality/Passage] Impact of habitat destruction, increased pollution and general environmental degradation on fish populations • [Climate] Long-term response of fish and elasmobranchs to coral bleaching events • [Biological/Other] Species/families resident to localized areas	• Collaboration and data sharing between established AT networks throughout the region • Transboundary movements and migrations for improved conservation and regional management efforts • Support research of high-value recreational fisheries to provide economic opportunities throughout the region	[101]
Atlantic, Southeast (21 studies)		
• [Climate] Long-term studies on the influence of environmental variability on marine animal movements • [Fisheries] Overexploited commercial fishery and oceanic species • [Migration] Long-term studies on migrations and distribution patterns • [Biological/Other] Research capacity in several areas	• Expansion of the ATAP receiver network along the west coast of southern Africa • Long-term monitoring given potential impacts of intense industrialized fishing and oil extraction • Contribute to management and conservation efforts of developing nations • Optimize tracking of endemic fish (e.g., Sparidae) and elasmobranchs (e.g., Scyliorhinidae) in biodiversity hotspots • Predator–prey interactions of the annual 'sardine run' – the largest marine animal migration on the planet	[70]

ocean drilling rigs) [67], multispecies high-use areas (e.g., migration and connectivity corridors), foraging hotspots, and spawning habitats, is also advised [18,68,69]. The implementation of collaborative AT networks [19,70,71] is the most promising pathway to effectively address these existing spatiotemporal constraints because they pool regional resources and possess the infrastructure to maintain equipment and databases. The establishment of AT networks also creates opportunities for a wider variety of species to be studied (e.g., threatened and non-exploited species) with relatively minimal financial investment. However, the lack of open standards for AT equipment compatibility is a major hurdle restricting the development of collaborative networks, particularly within Europe and between the rest of the world. Widespread integration of AT networks to generate new types of knowledge can be achieved through global partnership to unify opinions on data sharing, garner equipment compatibility across manufacturers, and secure long-term financial support [18,20,72,73].

Technological advancements

The continued application and development of new technology has been instrumental to the success of AT research [3]. For example, technological innovation has facilitated autonomous monitoring [5,74], miniaturization of tags, biological and physical sensors, and high-resolution spatial tracking [75], all of which have catalysed the proliferation and significance of AT. We encourage researchers to take advantage of new technologies that will, where applicable, broaden the scope of research, such as real-time monitoring [76,77], high-residence positioning systems [78,79], and novel tag sensors (e.g., predation) [80]. Nevertheless, balancing equipment costs relative to study goals is paramount and can be supplemented through collaboration, equipment sharing, and AT networks.

Ecosystem-based objectives

Obtaining a holistic understanding of an ecosystem's structure and function is increasingly important as ecosystem-based management approaches are implemented to combat the cumulative effects of multiple stressors [62]. With strategic development of tracking coverage and advances in technology there is greater opportunity to transition away from single-species focus in AT research towards incorporating a greater diversity of interconnected species. The onus should then fall upon researchers to develop studies that address the role and interactions of multiple species within an ecosystem, ensuring interoperability of data across repositories and analyses [81,82]. A greater shift towards ecosystem-level study design would enable researchers to address common gaps that persist at regional levels, such as predator–prey interactions, the role of biodiversity hotspots, and variability across animal sizes and life history stages.

Transboundary movements

Many pelagic or migratory species are exposed to distinct regulations or threats as they move across regional and national boundaries [83]. For example, in Lake Erie, which consists of Canadian and US waters, migratory walleye (*Sander vitreus*) are targeted by different fisheries (US: recreational, Canada: commercial) depending on which side of the border they are caught [59]. An outcome of increased spatial tracking coverage (e.g., through AT networks) is the ability to monitor movements beyond local or regional jurisdictions [18,20,84]. Consequently, there are increasing opportunities to integrate AT with spatial management planning across jurisdictional or geographic boundaries for species that have wide distributions or migrate for reproductive, environmental, foraging, or other reasons [85]. Although migration research appears to be conducted at commensurate levels to its global relevance (Figure 3A,C), often only small portions of migratory routes are monitored, resulting in segmented understanding across life history stages and size classes. Building connections with other researchers within AT networks, particularly across different political jurisdictions, is a potential first step to facilitate transboundary research. Furthermore, researchers need to engage with regulatory agencies to convey the value of AT with the goal of establishing cooperative relationships across all parties.

Developing nations

Developing nations, like those in South America and West Africa, are important diversity hotspots [86,87] with productive fishing grounds [22], yet there has been relatively limited use of AT in these freshwater and marine systems [23]. Similarly, locations that are remote or experience extreme environmental conditions (e.g., the Arctic) are under-represented despite their ecological and economic value [88]. The participation of, and engagement with, local stakeholders from lesser-studied areas should be prioritized when conducting research to incorporate their invaluable input [1]. Increasing funding availability, institutional support, opportunities for capacity building, and collaborative relationships between developed and underdeveloped nations are essential goals to work towards expanding the use of AT and enhancing its potential as a tool for global assessments of aquatic animal movement ecology.

Concluding remarks

AT has transformed our ability to track animal movements, leading to a greater understanding of aquatic ecosystems and their relationship with humans. Differences among research priorities and infrastructure, financial opportunities, technologies used, collaborative agreements, logistical constraints, geography/habitat, and composition of species were some of the main topics that influence how AT research is conducted across different regions. Yet, the broad applicability of AT identified in this review (e.g., full range of species and sizes, multiscale tracking resolution, collaborative databases, etc.) reinforces it as one of the most promising technologies for studying ecological and management questions worldwide. As the scope and scale of questions that can be addressed by AT continue to expand (see Outstanding questions), it is increasingly important to direct research to maximize its potential. Prospective ideas include developing studies with management-driven objectives such as greater focus on fisheries-specific and threatened species integration; continued progression towards optimizing multispecies tracking through collaborative networks and technological innovation; emphasis on long-term monitoring to effectively characterize human- and climate-driven impacts; use of AT to better inform transboundary or interjurisdictional management; and cultivating greater support for, and collaboration with, developing nations that often heavily rely on aquatic resources for nutrition and economic stability. Incorporating these topics into future research will help to garner more management-driven findings to help prioritize and address conservation and resource use concerns.

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Declaration of interests

There are no interests to declare.

Supplemental information

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Outstanding questions

Will the development of analytical tools be rapid enough to effectively process the influx of AT and other data being produced? The widespread use of autonomous tracking, biologging, and environmental sampling creates immense data repositories. Employing effective and statistically valid analytical techniques that encompass such large spatiotemporal datasets is a growing problem.

Can researchers implement a universal standardized approach for data management, quality control, and analysis? Different procedures in data handling and processing used across individuals and groups (e.g., AT networks) can shroud findings and cause incongruity between studies.

Can an open standard for compatibility of AT equipment be utilized worldwide to promote regional and global collaboration, the development of networks, and sharing of data? Manufacturers utilize unique programming and technology when developing their products, which hampers compatibility between systems, resulting in fragmented coverage of animal-tracking data.

How can developed nations further support or increase collaborations with underdeveloped nations?

Given the often-limited funding cycles (e.g., a few years), is there enough long-term financial support and stability to maintain monitoring arrays at climate-change scales?

How can projects led independently by management bodies (i.e., government agencies) and academic institutions (i.e., universities) be better integrated to effectively communicate and achieve common AT goals? Organizations often have similar research objectives but function independently of each other, leading to redundancy or suboptimal use of resources.

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