Received: 10 February 2023 | Accepted: 25 June 2023

DOI: 10.1111/2041-210X.14191

Methods in Ecology and Evolution
BRITISH ECOLOGICAL SOCIETY

REVIEW

Positioning aquatic animals with acoustic transmitters

Robert J. Lennox[1,2,3] | Kim Aarestrup[4] | Josep Alós[5] | Robert Arlinghaus[6,7] | Eneko Aspillaga[5] | Michael G. Bertram[8,9,10] | Kim Birnie-Gauvin[4] | Tomas Brodin[8] | Steven J. Cooke[11] | Lotte S. Dahlmo[1,12] | Félicie Dhellemmes[6] | Karl Ø. Gjelland[13] | Gustav Hellström[8] | Henry Hershey[14] | Christopher Holbrook[15] | Thomas Klefoth[16] | Susan Lowerre-Barbieri[17] | Christopher T. Monk[18] | Cecilie Iden Nilsen[1,12] | Ine Pauwels[19] | Renanel Pickholtz[20] | Marie Prchalová[21] | Jan Reubens[22] | Milan Říha[21] | David Villegas-Ríos[23] | Knut Wiik Vollset[1] | Samuel Westrelin[24] | Henrik Baktoft[2,4]

[1]NORCE Norwegian Research Centre, Laboratory for Freshwater Ecology and Inland Fisheries, Bergen, Norway; [2]Norwegian Institute for Nature Research (NINA), Trondheim, Norway; [3]Ocean Tracking Network, Department of Biology, Dalhousie University, Halifax, Nova Scotia, Canada; [4]Section for Freshwater Fisheries and Ecology, Technical University of Denmark, Silkeborg, Denmark; [5]Instituto Mediterráneo de Estudios Avanzados (IMEDEA, CSIC-UIB), Esporles, Spain; [6]Department of Fish Biology, Fisheries and Aquaculture, Leibniz Institute of Freshwater Ecology and Inland Fisheries, Berlin, Germany; [7]Division of Integrative Fisheries Management, Faculty of Life Sciences, Humboldt-Universität zu Berlin, Berlin, Germany; [8]Department of Wildlife, Fish, and Environmental Studies, Swedish University of Agricultural Sciences, Umeå, Sweden; [9]Department of Zoology, Stockholm University, Stockholm, Sweden; [10]School of Biological Sciences, Monash University, Melbourne, Victorian, Australia; [11]Department of Biology and Institute of Environmental and Interdisciplinary Science, Carleton University, Ottawa, Ontario, Canada; [12]Department of Biological Sciences, University of Bergen, Bergen, Norway; [13]Norwegian Institute for Nature Research, Fram Centre, Tromsø, Norway; [14]School of Fisheries Aquaculture and Aquatic Sciences, Auburn University, Auburn, Alabama, USA; [15]U.S. Geological Survey, Great Lakes Science Center, Hammond Bay Biological Station, Millersburg, Michigan, USA; [16]Ecology and Conservation, Faculty of Nature and Engineering, Hochschule Bremen, Bremen, Germany; [17]Fisheries and Aquatic Sciences Program, School of Forest, Fisheries, and Geomatic Sciences, University of Florida, Gainesville, Florida, USA; [18]Marine Evolutionary Ecology, GEOMAR Helmholtz Centre for Ocean Research Kiel, Kiel, Germany; [19]Research Institute for Nature and Forest, Brussels, Belgium; [20]School of Zoology, George S. Wise Faculty of Life Sciences, Tel Aviv University, Tel Aviv, Israel; [21]Biology Centre of Czech Academy of Sciences, Institute of Hydrobiology, Ceske Budejovice, Czech Republic; [22]Flanders Marine Institute, Oostende, Belgium; [23]Instituto de Investigaciones Marinas, CSIC, Vigo, Spain and [24]INRAE, Aix Marseille Université, Pôle RandD ECLA, RECOVER, Aix-en-Provence Cedex 5, France

Correspondence
Robert J. Lennox
Email: lennox@dal.ca

Funding information
ALTER-NET; The European Aquatic Animal Tracking Network COST-Action, Grant/Award Number: CA18102; The Danish Rod and Net Licence Funds; EU Horizon 2020 Project STRAITS, Grant/Award Number: 101094649; Norwegian Research Council, Grant/Award Number: LOST 325840 and LaKES 320726; Research Foundation Flanders (FWO); European Maritime Fisheries Fund, Grant/Award Number: B730117000069 and MV-I.18-LM-004; Poul Due Jensens Fond

Handling Editor: Gavin Simpson

Abstract

1. Geolocating aquatic animals with acoustic tags has been ongoing for decades, relying on the detection of acoustic signals at multiple receivers with known positions to calculate a 2D or 3D position, and ultimately recreate the path of an aquatic animal from detections at fixed stations.
2. This method of underwater geolocation is evolving with new software and hardware options available to help investigators design studies and calculate positions using solvers based predominantly on time-difference-of-arrival and time-of-arrival.
3. We provide an overview of the considerations necessary to implement positioning in aquatic acoustic telemetry studies, including how to design arrays of receivers, test performance, synchronize receiver clocks and calculate positions from the detection data. We additionally present some common positioning algorithms,

including both the free open-source solvers and the 'black-box' methods provided by some manufacturers for calculating positions.

4. This paper is the first to provide a comprehensive overview of methods and considerations for designing and implementing better positioning studies that will support users, and encourage further knowledge advances in aquatic systems.

KEYWORDS
geolocation, multilateration, positioning solver, reverse-GPS, synchronization, telemetry

1 | INTRODUCTION

The study of aquatic animal movement ecology has emerged as a major research field with implications for understanding life on the planet, and how it can most effectively be managed and conserved against human interference (Nathan et al., 2008). However, the study of movement depends on efficient tools for animal observation and resolving where, when and how animals are moving. Importantly, movement is a fractal process (Turchin, 1996); therefore, the scale (both space and time) at which movement is observed will directly influence the outcome of the observations. High-frequency positions yield greater power to detect diverse behaviours, and continuous time series with fixed interval positions are important to yield consistent and comparable estimates of movement (Brown et al., 2012; Nathan et al., 2022). The most common way to position an object on land is with global navigation satellite systems (GNSS), which connect to orbiting satellites. Animal tags designed for movement ecology in terrestrial environments will link to these satellites and log positions at fixed intervals, providing a series of positions that can be leveraged to understand individual behaviours and ecologies (Kays et al., 2015). However, radio signals attenuate quickly in water (especially saltwater), and therefore limit the capacity with which scientists can obtain the locations of aquatic animals with GNSS, unless signals can be transmitted from the surface (e.g. by buoys). The efficient transmission of sound through water, coupled with the use of sensitive hydrophones to monitor and record sound has, however, provided new frontiers for underwater communications (Taraldsen et al., 2011). In aquatic environments, acoustic telemetry transmits the identities of tagged animals to logging stations (i.e. receivers or hydrophones) as well as additional data about the animal's behaviour and physiology or the surrounding environment depending on sensor integration in the tag (Hellström et al., 2022; Hussey et al., 2015).

Acoustic telemetry does not inherently provide accurate estimates of animal positions; detection of a tagged individual by a passive data-logging hydrophone confirms its presence within a detection polyhedron (i.e. dynamic, but typically within 200–1000 m; Kessel et al., 2014). Gridded receiver deployments have been used to calculate centres of activity based on the number of detections within a given time slot as pseudo-positions (Simpfendorfer et al., 2002; Winton et al., 2018). However, for precise 2D positioning, one signal must be detected by a minimum of two or three receivers (depending on the positioning methodology), and the clock drift inherent among independent stations must be accounted for to yield more precise calculation of positions based on time-difference-of-arrival (TDOA: Smith, 2013) and time-of-arrival (TOA; Baktoft et al., 2017; Nathan et al., 2022; Figure 1). In addition, for 3D positioning, receivers either have to be distributed across the tridimensional space for TDOA/TOA-based positioning, or tags need a depth sensor.

Since the first research on acoustic positioning (Kuroki et al., 1971), there have been major advances in the field and remarkable applications of the technology to achieve a better understanding of animal ecologies (Krause et al., 2013; Nathan et al., 2022; Orrell & Hussey, 2022; Box 1). Positioning data have proven valuable for testing fundamental ecological hypotheses about movement ecology and the underlying variables determining the extent and periodicity of movement, as well as developing applied strategies for protecting species and critical habitats, managing invasive species and developing fisheries management tools (Box 1). However, there is currently no overview of positioning in acoustic telemetry, including the development and availability of positioning methods and how the methods are being used. Furthermore, users lack a comprehensive guide to better understand how to conceive, design, implement and improve positioning studies using open, accessible and interoperable infrastructure and digital analytical tools. There is therefore a need to identify the present state-of-the-art in aquatic positioning and forecast the needs of the community to enhance the applicability, and grow the use of these valuable methods. In this paper, we consider the past, present and future of aquatic acoustic positioning for ecology. The paper is intended to provide an overview of the methods and best practices, standardize terminology (Table 1) and identify research avenues perceived by the tracking community that will continue to help advance the field by making it more accessible, user-friendly and open to new developments and innovations.

2 | PAST—HISTORY OF POSITIONING TECHNOLOGY

Positioning of telemetry transmitters began with triangulating positions by obtaining directional position fixes using yagi radio antennas (Heezen & Tester, 1967) or directional hydrophones (McCleave, 1978). Arrays of fixed telemetry receivers can also be used to position fish, predominantly using acoustic telemetry. The

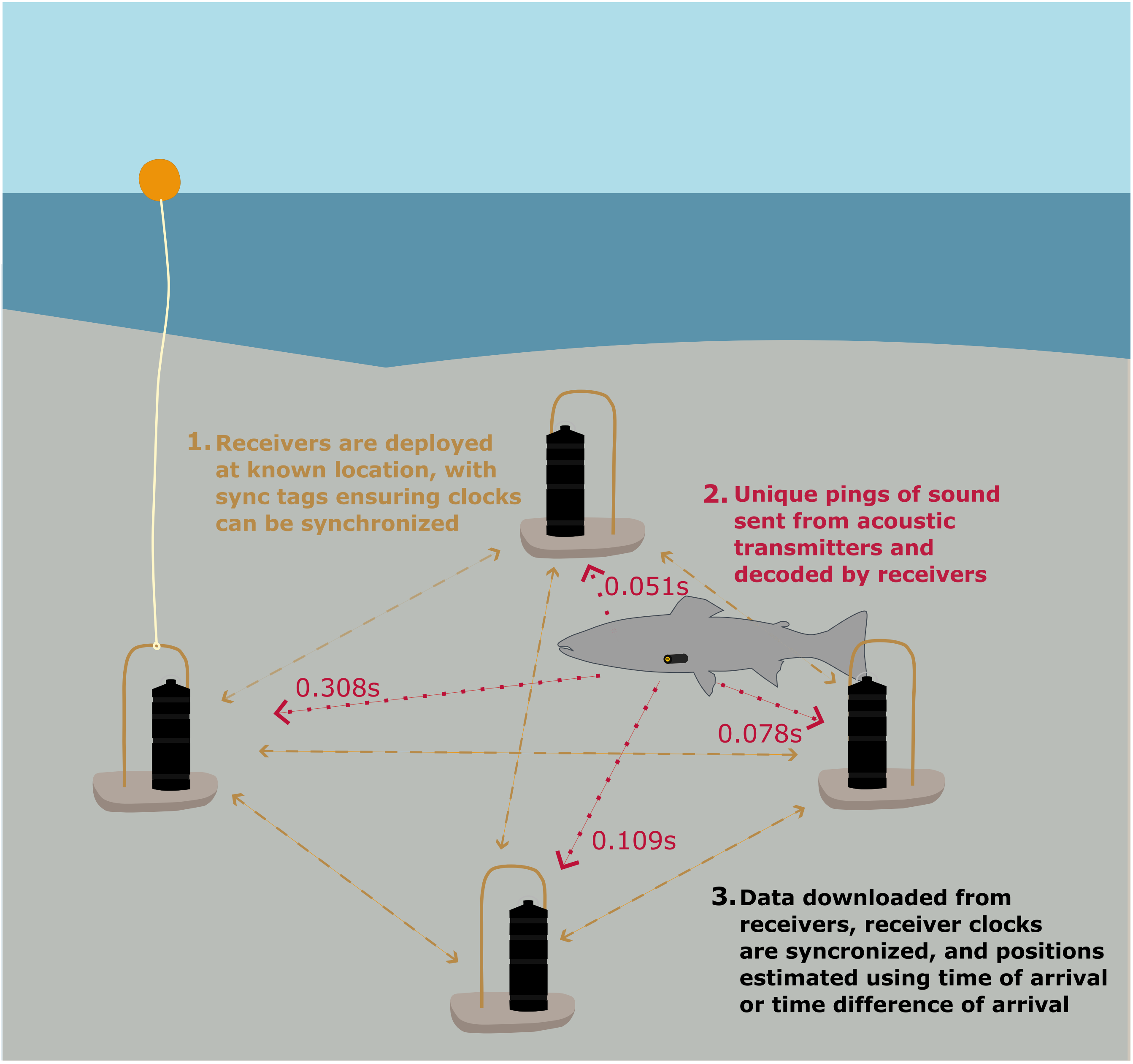

FIGURE 1 Illustration of the process of positioning acoustic transmitters within an array of receivers. Receivers must be deployed at fixed locations measured with high precision (i.e. differential global positioning system [GPS] from above water). Deployment of synchronization tags that are detected across the array is necessary for the user to later adjust the clocks of each independent hydrophone, unless they are cabled and set to a common clock. Data downloaded from the receivers are then fit to a positioning solver to calculate the position. After, users may interpolate missing positions using random walk or state-space models to infer missing positions and generate paths.

earliest paper we are aware of that used fixed acoustic telemetry stations to generate fish position solutions, presents tracking of crescent sweetlips (*Plectorhinchus cinctus*) and rainbow trout (*Oncorhynchus mykiss*) in both fresh- and saltwater (Lake Okutama and Sagami Bay, Japan; Kuroki Kuroki et al., 1971). Interestingly, in addition to the horizontal position estimation, the transponders (transmitters allowing two-way communication) relayed information about fish swimming depth and water temperature. A triplet of receivers moved by boat was used to detect signals from the transponders and an elaborate apparatus allowed real-time estimation and plotting (on paper) of the horizontal track and swimming depth of the tagged fish. Almost concurrently, Young et al. (1972) were soonafter tracking brown trout (*Salmo trutta*) in a loch in Scotland using directional acoustic receivers that could be controlled automatically. Fish were tracked and positioned for as long as 24h. The system was somewhat cumbersome and yielded only modest accuracy. This system was not widely adopted or commercialized but, nonetheless, is a fascinating example of early efforts to generate fine-scale positions for fish using autonomous acoustic apparatus reminiscent of what is conducted today.

BOX 1 Examples of positioning studies that highlight the various uses of acoustic positioning. Note that the positioning method shown is the method reported in each respective reference.

Species and location	Finding	Method	Reference
European perch (*Perca fluviatilis*), European catfish (*Silurus glanis*), common carp (*Cyprinus carpio*), tench (*Tinca tinca*), Germany	Strong seasonal and species-specific variation in behaviour, personality variation increasing with temperature, limited connectivity among species, benthivorous species use feeding sites and avoid future capture, selection on behavioural types	Lotek BFSK MAP 200kHz; 2D positions calculated using Lotek ALPS and corrected with a Kalman Filter (TDOA), Baktoft et al. (2015)	Monk et al. (2021), Monk and Arlinghaus (2017), Nakayama et al. (2016, 2017, 2018) and Vanovac et al. (2021)
European perch (*Perca fluviatilis*), Gosmer Lake, Denmark	Metabolism is not a strong determinant of activity in the wild	Intermittent flow respirometry; Lotek BFSK MAP 200kHz; 2D positions calculated using Lotek BioMap (TDOA)	Baktoft et al. (2016)
European eel (*Anguilla anguilla*), Bois Joli dam, Frémur River, France	Eels prefer to migrate via spillways but take longer to do so than by using a compensation flow pipe	Thelma Biotel PPM 69kHz; 3D positions estimated based on TDOA	Trancart et al. (2020)
Pearly razorfish (*Xyrichtys novacula*), Bay of Palma Marine Reserve, Balearic Islands, Spain	Pearly razorfish form a harem-like social structure; agonistic behaviour between males, and stronger association between males and females	Social network analysis; JSATS BPSK 416.7kHz; 2D Positions calculated using UMAP software from Lotek Wireless, Inc., based on TDOA	Aspillaga, Arlinghaus, Martorell-Barceló, Barcelo-Serra, and Alós (2021)
White shark (*Carcharodon carcharias*), Carpinteria, California, United States	Cruising speeds of aggregated juveniles likely reflect a behavioural strategy to optimize bioenergetic efficiency	Field routine metabolic rates; Innovasea PPM 69kHz; 2D Positions calculated by manufacturer using proprietary Vemco Positioning System (VPS) from Innovasea, based on TDOA	Anderson et al. (2022)
Roach (*Rutilus rutilus*), perch (*Perca fluviatilis*) and northern pike (*Esox lucius*), Lake Gosmer, Denmark	Species respond differently to boat noise with roach and perch showing increased swim speeds whereas pike were not affected by the disturbance	Lotek BPSK MAP 200kHz; 2D Positions calculated using proprietary BioMap software from Lotek Wireless, Inc., based on TDOA	Jacobsen et al. (2014)
Northern pike (*Esox lucius*), Lakes Milada and Most, Czech Republic	Pike display increased activity, space use, growth and spend more time in open water in a lake with low structural complexity than a in a lake with high complexity	Stable isotope analysis; Lotek BFSK MAP 76kHz; Positions calculated using UMAP from Lotek Wireless, Inc., based on TDOA	Říha et al. (2021)
Atlantic salmon (*Salmo salar*), Svorkmo hydropower plant, River Orkla, Norway	The degree of energy depletion in kelts induced by negotiating a hydropower plant can amount to 5% of remaining energy content, and reduce post-spawning survival	Lotek BFSK MAP 76kHz; 3D Positions estimated using Yet Another Positioning Solver (YAPS)	Baktoft et al. (2020)
Atlantic salmon (*Salmo salar*), Laudal and Svorkmo hydropower plants, Rivers Mandalselva and Orkla (respectively), Norway	Understanding of behavioural response of salmon smolts to various hydraulic conditions allows modelling of mitigation measures	Hydraulic 3D models; Lotek BFSK MAP 76 and 200 kHzs; 2D and 3D Positions estimated using YAPS	Szabo-Meszaros et al. (2021) and Silva et al. (2020)
Atlantic cod (*Gadus morhua*), offshore wind farm, Belgium	Seismic survey impacts the movement behaviour of cod at an offshore wind farm	Innovasea PPM 69kHz; 2D Positions calculated using Fathom web interface ('VPS lab') from Innovasea, based on TDOA	van der Knapp et al. (2021)
Chinook Salmon (*Oncorhynchus tshawytscha*), San Joaquin River and Old River, California, USA	Combined smolt swimming behaviour and a hydrodynamic model	JSATS BPSK MAP 416.7kHz; tags from ATS, receivers from Teknologics, positions estimated using YAPS	Holleman et al. (2022)

The next major innovation occurred in the mid-1970s, when Hawkins et al. (1974) deployed omni-directional acoustic telemetry receivers to position Atlantic cod (*Gadus morhua*) swimming freely in a Scottish sea loch. The researchers used differences in TOA of acoustic pulses on three to five receivers to estimate fish positions. In this study, the hydrophones were wired together and linked

TABLE 1 Glossary of key terms related to acoustic positioning.

Term	Acronym	Definition
Array		The deployment configuration of a group of receivers
Binary frequency shift keying	BFSK	Binary ID coding in one pulse with 0 and 1's indicated by signal frequency shift
Binary phase shift keying	BPSK	Binary ID coding in one pulse with 0 and 1's indicated by signal phase shift
Code collision		When multiple signals are received simultaneously by a receiver, and not decoded or incorrectly decoded due to signal corruption
Code-division multiple access	CDMA	Signal technology to enable multiple signals to be received simultaneously in a frequency band
Ghost/shadow location		In some circumstances, positioning algorithms may reveal two position solutions. One is (presumably close to) the truth, the other is the 'ghost' location
Hydrophone		A microphone that detects sound waves underwater
Managed acoustic positioning	MAP	A term used by Lotek for some products related to acoustic positioning
Multipath		A sound wave taking multiple paths to the receiver, for example, one direct and one bouncing off a hard surface nearby
Pulse		A sound burst made by a transducer
Pulse position modulation	PPM	ID code is defined by the composition of the time intervals between each pulse in pulse train of a fixed-frequency signal
Receiver		A unit with an integrated hydrophone and electronics to process and store acoustic signals from transmitters. Typically distinguished by its serial number
Reference tag, sentinel tag		A stationary transmitter deployed within an array for verification or evaluation of positioning error (i.e. to compare estimated and true positions)
Signal (coded or non-coded)		One or more pulses intended to be interpreted as one detection by the receiver
Station		Location where a receiver is deployed
Sync tag, beacon tag		A stationary transmitter deployed within an array to aid the receiver time synchronization during post-processing
Time-of-arrival	TOA	Signal arrival time at the receiver
Time-difference-of-arrival	TDOA	Difference in signal arrival times between pairs of receivers

back to a central processing station that synchronized the clocks. This basic method served as the basis for modern fine-scale positioning studies. The next iteration in positioning involved the use of radio-linked omni-directional fixed telemetry buoys by the company Vemco (now Innovasea, Bedford, Nova Scotia, Canada; O'Dor et al., 1998). The radio-links served to allow time synchronization and data transmission back to a base station. This system was used to study a variety of aquatic taxa (reviewed in O'Dor et al., 2001), but was also somewhat cumbersome and required that stations had access to the water surface to enable radio transmission of signals. To overcome clock drift on receivers, cabled arrays were the norm in early days (e.g. Juell & Westerberg, 1993) and it was not until Lotek Wireless (Newmarket, Ontario, Canada) developed a cabled acoustic telemetry system using code-division multiple access (CDMA) technology that it was possible to conduct high resolution tracking (with <1 m accuracy) of many individuals in a small area (glossary in Table 1; Baktoft et al., 2015; Cooke et al., 2005; Cote et al., 1998). CDMA emerged from the cell phone industry and was adapted by Lotek for fish tracking. The Lotek CDMA technology minimized code collisions, allowing signals from multiple transmitters to be detected at the same receiver in a short duration, and enabled studies of both marine (Cote et al., 1998) and freshwater (Baktoft et al., 2012; Hanson et al., 2007; Nakayama et al., 2018) fishes. This technology is still commercially available using non-cabled battery powered units. Similar technology (also cabled) was developed by Hydroacoustic Technology Inc. (HTI; now part of InnovaSea) and was applied to the tracking of smolts (*Salmonidae*) in rivers (Steig, 1999) and Atlantic cod in aquaculture net pens (Rillahan et al., 2009). Nielsen et al. (2012) created a towed array system that could be used to position acoustically tagged fish in 2D providing opportunities for tracking fish without fixed infrastructure. There may be future opportunities using remote uncrewed vehicles as well (Masmitja et al., 2020).

Methods for positioning acoustic transmitters were later developed for independent fixed receivers (e.g. Baktoft et al., 2017; Klimley et al., 1998; McMichael et al., 2010). The problem of clock drift was overcome by adding high-powered beacon transmitters placed at known locations that served to synchronize clocks (or more specifically, allow for the correction of clock drift) on receivers, such that accurate position solutions could be resolved. This approach works with any omni-directional hydrophone system (e.g. JSATS, Lotek Wireless, Innovasea, Sonotronics, Thelma Biotel, Advanced Telemetry Systems, and others; Aspillaga, Arlinghaus, Martorell-Barceló, Follana-Berná, et al., 2021). Perhaps the InnovaSea system has been most widely embraced and has been well described in a number of studies, but there are several manufacturers that provide technology (see Espinoza et al., 2011; Orrell

& Hussey, 2022; Table 2). Fine-scale positioning studies can now cover tens of square kilometres with extensive receiver arrays (e.g. Binder et al., 2018).

It is easy to forget that the fine-scale telemetry studies of today and tomorrow are not all that different from what was accomplished by the pioneering studies in the 1970s. What differs is that the tools for doing so are now commercially available, smaller, more versatile and cheaper; thus, more widely embraced. There is now potential for a golden age of fish positioning to generate big data sets (Nathan et al., 2022), but it is key to acknowledge and appreciate the historical work that has led us to this state.

3 | PRESENT—BEST PRACTICES IN ACOUSTIC POSITIONING

3.1 | Tag and receiver specification

3.1.1 | Tags and ID code systems

To position tags, and by extension the animals carrying tags, depend on the physics of underwater sound. The acoustic transmitter used in these studies consists of a sound transmitting element (transducer), electronics to control the signal emission, a battery providing power, sensors (optional) and a protective housing. The transmission interval (s) and power output (dB re 1 uPa at 1 m) are determined by the programming and electromagnetic properties but limited by the battery. Lower frequency (e.g. 69 kHz) demands a larger transducer and more battery power than higher frequency alternatives (i.e. >=180 kHz). Although higher frequency tags are comparatively smaller than lower frequency tags, the detection range is shorter at higher frequencies and performance may differ more by temperature and conductivity of the water (Pincock & Johnston, 2012).

There are two different main code categories widely in use, based on how the code is constructed. These are Pulse Position Modulation (PPM) codes and the aforementioned CDMA codes (Table 2). The PPM codes consist of unmodulated fixed-frequency pulses emitted in a 'pulse train', with the code information being defined by the composition of the time intervals between each pulse in the pulse train across several seconds of transmission (Ehrenberg & Steig, 2003). With CDMA, however, the full ID may be encoded within a single, short pulse by modulation of the pulse (Ehrenberg & Steig, 2003). There are two main categories used for such modulation in acoustic telemetry; binary frequency shift keying (BFSK), and binary phase shift keying (BPSK). The unique code ID is binary (0 and 1), and the shift between 0 and 1 is made either by a small frequency shift (BFSK) or by a phase shift (BPSK) in the signal (e.g. McMichael et al., 2010). Common to these categories is that the pulses consist of an initializing part (aka Barker), a part that constitutes the transmitter ID, and a trailing part for signal verification/error detection. For a sensor tag, a part containing the sensor value may either be included in the pulse coding for the ID, or sent as a separate pulse immediately after. The number of pulses depends on the desired number of unique IDs, and if the signal should include sensor data transmitted along with the ID but the full signal code generally consists of one to three pulses emitted within a very short time (<1 ms to a few ms). Sensor tags therefore generally have longer codes and hence shorter battery life than non-sensor tags for a given burst interval, though this can to some extent be mitigated by reducing the number of unique IDs. There have been quite a few different code spaces developed for PPM codes, but a code typically consists of 7–12 pulses emitted within 3–5 s (Reubens et al., 2021). The long code duration and the fixed frequency make PPM-based systems vulnerable to code collisions, and also to multipath (the signal code is corrupted due to reflection by surface, bottom, thermocline or some object of the signal from the same transmitter). To avoid repetitive code collisions, PPM-based tags are programmed to transmit with a random burst interval (time between signal transmissions) within a lower and upper limit (e.g. 40 and 80 s, with mean 60 s). Thelma Biotel (Trondheim. Norway) has developed a PPM-based receiver system that listens to more than one frequency, thus allowing tags at different frequencies (e.g. 67, 69, 71 and 73 kHz) to be detected, thereby reducing the potential for code collisions and thus increasing the number of tagged fish it is possible to track simultaneously.

Of the two types of CDMA coding, the BFSK coding has been used in Lotek systems at 76 and 200 kHz (e.g. Říha et al., 2022; Szabo-Meszaros et al., 2021) and BPSK codes are used by the Juvenile Salmon Acoustic Telemetry System at 416.7 kHz (JSATS, a non-proprietary system developed by the US Army Corps of Engineers, see McMichael et al., 2010) and by the Innovasea HR2 system at 180 kHz (e.g. Leander et al., 2020). The coded pulse and short signal duration of CDMA technology enables many tags with short burst intervals to be monitored simultaneously without code collisions being a problem (Cooke et al., 2005; Ehrenberg & Steig, 2003, 2009; Niezgoda et al., 2002). Whereas PPM code detection efficiency is often reduced by code collisions and/or noisy environments, false detections (i.e. registering a signal code that was not transmitted) are infrequent for newer code sets. On the other hand, CDMA systems may suffer more from frequent false detections. Removal of false detections can partly be done automatically during logging, but it should always be considered to do this during post-processing to avoid missing true positives. A different coding category from PPM and CDMA has been used by HTI, where the code ID is based on the exact interval between consecutive pulses. Each ID has a small difference in burst interval (Ehrenberg & Steig, 2003, 2009). Theoretically, this code system may work better than BPSK with a lower signal-to-noise ratio, however the system requires large efforts for code deciphering when multiple tags are present, and in particular where multipath signals are an issue. Identifying tags from code sequences can be facilitated using artificial intelligence (Medisetty et al., 2021). This coding system cannot be used for sensor data requiring many sensor levels.

TABLE 2 Overview of available acoustic transmitters for each of the brands.

Manufacturer	Location	Code sets	Frequencies (kHz)	Manufacturer offers position calculations	Sensors	Other relevant features (multi-channel, cabled, remote offloading, etc.)	Output range (dB re 1 μPa @ 1 m)	Transmission technology
Lotek	Newmarket, Canada	*OPi*, *OPs*, *R64K*, *S256*, Lotek MAP, *JSATS*	69, 76, 200, 416.7	Yes	Pressure, temperature, motion	Dual transmission system; combined technology (acoustic-radio); stable burst interval (CDMA)	144–160	PPM, BFSK, BPSK
Thelma Biotel	Trondheim Norway	*OPi*, *OPs*, *R64K*, *S256*, *S64K*, *R04K*, *R256*, R01M, HS256, DS256	63–77	Yes	Activity, pressure temperature, tilt, salinity, conductivity, mortality	Multiple frequencies simultaneously; acoustic release; LoRa link; burst interval sequences are reconstructable	139–158	PPM
Sonotronics	Tuscon, USA	*OPi*, *OPs*, *R64K*, *S256*, *R04K*, ACT	30, 32, 34–41, 69–83	Yes	Acceleration, pressure, temperature, tilt	Underwater diver receiver; equipment marking transmitter	135–165	PPM
ATS (Advanced Telemetry Systems)	Isanti, USA	*JSATS*	416.7	No	Pressure	Combined technology (acoustic-radio); cabled and autonomous receivers	156	BPSK
Innovasea (previously Vemco)[a]	Bedford, Canada	*R64K*, *S256*, *R04K*, *R256*, A69-9001, A69-9002, A69-9004, A69-9006, A69-9007, A69-1601, A69-1602, A69-1604, A69-1605, A69-1303, A180-1701, A180-1702, H170-1802	69, 180, 307	Yes[b]	Acceleration, pressure, temperature, predation	Acoustic release; combined technology (acoustic-DST); dual transmission system	137–162	PPM, BPSK(HR), fixed pulse repetition interval (HTI)

[a]Codesets in italic have compatibility across brands. It should be noted that some of the codesets are no longer available at specific manufacturers.

[b]Requires manufacturer to process the data.

3.1.2 | Receivers

The receiver operating frequencies must match those of the tags to record detections and calculate positions. Over the years, several frequencies in the range from 30 to 416.7 kHz were used, with PPM-based systems working at 69 kHz being typical for larger regional and global networks (Reubens et al., 2021). Frequencies near 70 kHz have been chosen over others because of a good detection range in saltwater environments, and relatively small tags that can be used for many species capable of travelling far. It should be noted though, that this is inadequate for long-term large-scale monitoring of smaller specimens capable of travelling far, such as salmon smolts. Higher frequencies may give better time resolution and precision than lower frequencies, and also more precise positioning, but come with the cost of shorter ranges and potentially shorter battery life (Ehrenberg & Steig, 2009; Leander et al., 2020). Most high-precision positioning studies work on scales from <1 to several square kilometres, where higher frequency systems may be feasible. Receiver configurations are increasingly important to specify for conducting a successful positioning study, as marketed options are increasing. Whereas most receivers listen to a single frequency, others may incorporate additional features such as listening to multiple frequencies and/or code sets, enabling a higher number of tags in the system, and even a combination of different signal systems.

There are two main categories of acoustic receivers: cabled receivers and autonomous receivers. Cabled receivers, where all hydrophones are coupled to the same receiver unit, enable all detections to be recorded and stored based on the same clock that is synchronized using the physical connection among receivers. Cabled systems are limited by cable length, and will typically not cover more than a few 100 m. Autonomous independent receivers, which operate without any cabling, have an internal quartz clock, and their measurement of time is affected by precision of the quartz oscillator and temperature-dependent time drift. This time drift must be corrected for by clock synchronization during post-processing, before positioning algorithms can be applied (see the Section 3.2). This may be assisted by using linear interpolation on each receiver prior to running the synchronization model, if the time drift is recorded. Synchronization signals from fixed beacon tags are necessary to aid in such time synchronization. Autonomous receivers containing built-in beacon tags are becoming more common to support 2D and 3D telemetry. Onboard temperature sensors are increasingly common on receivers, and may be important for positioning as the speed of sound changes with temperature (Simpfendorfer et al., 2008). Other sensors that are available for some receiver models are ambient noise, pressure and tilt, factors that may affect detection range (Kessel et al., 2014). Some receiver models are offered with acoustic release mechanisms, increasing efficiency of retrieval, removing the need for a surface buoy or grapple lines, and allowing deployment in deep waters or challenging environments (e.g. entanglement risk to marine mammals). Other features also include online retrieval of data, allowing near-live updates of positioning data by the use of a surface data modem (Baktoft et al., 2017; Manicacci et al., 2022). Such features may be relevant for event driven manipulation studies, active management of fishways or other installations where seasonal choices of activity can be made.

3.2 | Position calculations

3.2.1 | Synchronization

Modern acoustic receivers are typically autonomous battery-operated units that allow for modular and flexible receiver array configurations and deployments. Receivers are usually independent but may be cabled to an on-shore station for data collection and clock synchronization. For independent units, each autonomous receiver contains a quartz crystal-based internal clock. Because position estimation is based on extremely small differences in time of detection of an acoustic signal at multiple locations, these internal clocks need to be synchronized so that timestamps of detections are accurate to the milli-second or better to achieve sub-metre spatial precision (Figure 1). When receiver units are modular and operate independently of each other, this poses a challenge because each clock drifts as much as 1 s per day, depending on temperature experience and unique characteristics of each clock crystal.

Synchronization of independent receivers is typically based on internal or external beacon transmitters/sync tags colocated with all/several receivers (Baktoft et al., 2017; Smith, 2013; Table 1). In the simplest case where the exact position of receivers is known, receivers remain stationary throughout the study, and all receivers continuously detect the same beacon transmitter, correcting the clock drift is relatively uncomplicated. In this case, between-receiver distances are fixed and equivalent to signal travel time between pairs of beacon transmitters and receivers when accounting for the effect of water temperature on speed of sound. Field studies using acoustic telemetry often entail more complexity as receiver location might be uncertain (e.g. if deployed near the bottom in deep water) and receivers might move during the study period (e.g. wave-induced drift or being moved inadvertently by nets or anchors). Such complexity can be accounted for during the synchronization, if the model used allows for estimation of receiver positions. Additionally, areas of interest and thus receiver arrays, can be relatively large and of complex geography, and it is often impossible for all receivers to detect the same beacon transmitter. In such cases, synchronization can be done sequentially (which entails propagation of uncertainty), or using a more complex model allowing synchronization of the entire array at once.

3.2.2 | Positioning models

Positions in acoustic arrays are estimated from multilateration of detections on multiple receivers at known locations and with synchronized clocks. Regardless of the underlying positioning model and assumptions (see Table 3), position estimation is ultimately

Positioning method\service	Provider	Method? (e.g. TDOA, etc.)	Functions with less than three receivers overlapping?	Code available and transparent
Yet Another Positioning Solver (YAPS)	Open source	TOA	Yes	Yes
Vemco Positioning System (VPS)	Innovasea	TDOA	No	No
UMAP	Lotek	TDOA	No	No
Pinpoint	Thelma Biotel	TDOA	No	No

TABLE 3 Overview of acoustic positioning solvers. We note the service provider and the method used for positioning. Openly available code is also noted. TDOA, time-difference-of-arrival; TOA, time-of-arrival.

based on the principle that the distance between transmitters and receivers is directly proportional to the time it takes for the signal produced by the transmitter to travel to each receiver, which are at known locations. The precise time of a signal transmission is generally unknown, and position solvers have frequently been built on pairwise differences in TOA to estimate transmitter position for when the signal was sent. This TDOA method relies on solving sets of hyperbolic equations to determine the position (Juell & Westerberg, 1993). However, this method requires that the signal is detected on at least three receivers. Whereas current TDOA methods often rely on estimation of independent locations, it is possible to apply a more holistic approach and estimate coherent tracks, thereby utilizing all available information to inform the estimation model. Furthermore, a track-based approach allows estimation of the time of signal transmission and thereby allows position estimation based on TOA, which is more robust to suboptimal receiver array configuration and tagged animals being outside the receiver array footprint. Additionally, basing the track estimation on TOA and using all collected data, makes it possible to estimate tracks of tagged animals in cases where the number of receivers detecting each signal is less than three (Table 3). It is also possible to implement more complex error structures in the positioning model (e.g. mixture of Gaussian and *t* distributions) allowing for better handling of multipath propagated detections and noise with TOA. Such track-based estimation based on TOA was introduced by Yet Another Positioning Solver (YAPS, or yaps package in R; Baktoft et al., 2017) in 2017.

3.2.3 | Post-processing

Acoustic telemetry positioning systems generate vast amounts of location data that often require a thorough post-processing workflow. Many statistical methods used in the field of movement ecology, such as Hidden Markov Models (HMMs, Krause et al., 2013; Langrock et al., 2012) and Step Selection Functions (SSFs, Potts et al., 2014), rely on regularly sampled trajectories with negligible positioning error, requirements that are rarely satisfied by the raw positioned data from acoustic telemetry. A series of positions for each individual will be combined to form a track, but positioning methods are liable to generate outliers, positions that are improbable given the remainder of the data, which result in misleading calculations of swimming speeds, space use and habitat selection.

Filtering positions requires a method to flag and remove outlier positions (Aspillaga, Arlinghaus, Martorell-Barceló, Follana-Berná, et al., 2021; Baktoft et al., 2015; Leander et al., 2020). Different positioning algorithms provide different measures of uncertainty that can help with the process. The Vemco Positioning System (Table 3) provides an estimate of expected positional error at the estimated location for each pair of coordinates (e.g. horizontal positioning error [HPE] or dilution of precision [DOP]). HPE is calculated based on the geometry of the receiver network and users have in the past used HPE values to remove positions that exceed a threshold (Meckley et al., 2014). However, filtering on HPE can potentially introduce a spatial bias in the data. Previous studies in highly reflective environments (e.g. concrete walls or sheer rock faces) indicated the absence of a relationship between HPE and a real error measure in metres obtained through fixed reference tags for which the actual position was known, highlighting the limits of this filtering method (Vergeynst et al., 2020). There are no standard alternatives to HPE that are publicly available, meaning that position filtering with the Vemco Positioning System can benefit from validations in each study system. Other positioning solvers such as YAPS (Table 3) output estimated standard deviation of both coordinates for each position analogous to the familiar standard errors from other statistical models, but less rigorous validations have been conducted to test the reliability of these measurements for filtering. Regardless of the error measurement used to validate positions calculated by solvers, data quality will depend on validations of the array using tow tracks or sentinel tags to understand how position quality is related to the error metrics provided.

Irregularity of data over time is another common problem in acoustic telemetry due to the random emission intervals of some transmitters (notably with pulse-position modulation, see Table 1). When the underlying random interval sequence is not known, it can be difficult or impossible to predict the timing or number of missed detections. Despite the availability of simple methods to estimate positions at non-observed time stamps (e.g. linear interpolation and smoothing, McLean & Skowron Volponi, 2018), the application of movement models such as the Continuous Time Correlated Random Walk (CTCRW, Johnson et al., 2008) are used to predict plausible and regularly spaced trajectories that maintain the general characteristics of original data provided by positioning. Moreover, CTCRW models can also account for the uncertainty of positions in a state-space model approach (e.g. Alós et al., 2016), further improving the precision of the pre-processed trajectories (e.g. Aspillaga, Arlinghaus, Martorell-Barceló, Follana-Berná, et al., 2021). CTCRW models are already implemented in several libraries for analysing animal movement data (i.e. CRAWL package, Johnson & London, 2018; momentuHMM package, McClintock & Michelot, 2018).

3.3 | Project design—Optimizing application

3.3.1 | Tag and attachment choice

In cases where the species is highly resident, or a specific aspect of the movement of the individual is of interest (e.g. nesting black basses *Micropterus* spp., coastal wrasse species *Labrus* spp.), PPM-based systems may be a poor choice. The long code trains and code collision risk associated with PPM-based systems will limit minimum burst interval to higher values than desired, so CDMA-based systems may be preferred or needed. A PPM-based system will be strongly limited in the number of tags that can be in the study area simultaneously due to the potential for code collisions. It is possible to simulate the yield of the whole system in different configurations (burst interval vs. number of tagged animals vs. detection range). The risk of code collisions can be reduced by increasing the mean burst interval, and reducing signal power, but doing so will also decrease the positioning rate, and thereby reduce the tracking performance. PPM-based transmitters that also have sensors will have longer code trains that are more vulnerable to collisions and are overall more challenging to consistently calculate positions for. Although PPM systems may have a larger detection radius than CDMA, the latter will have higher positioning rates while within detection range due to the shorter burst intervals (Leander et al., 2020).

Acoustic tags without sensors may be sufficient in some situations, but in other cases, a sensor may be important for interpreting the animal behaviour in relation to the research objectives. For example, it may be very difficult to discern if the transmitter signals come from the animal that was tagged, or a predator that has ingested the tagged animal. In such cases, predation event data can be very useful, using temperature or predation sensors (Hanssen et al., 2022; Klinard & Matley, 2020; Lennox et al., 2023). If the prey and the predator exhibit different behaviours, information from a pressure or acceleration sensor may allow the identification of predation events (e.g. Halttunen et al., 2018). Temperature sensors could also detect predation by mammals who have higher internal temperatures than fish. A pressure sensor, accelerometer or a mortality sensor (a sensor that registers if movement has stopped or if the carrier has lost the ability to maintain orientation for more than a defined period) can also aid in determining if the animal is not moving at all (presumably dead), or if it is moving just very little (alive). Moreover, a decision key should be used to probabilistically assess the fate of tagged individuals based on objective, repeatable criteria (e.g. Halttunen et al., 2018; Lennox et al., 2023). The timing of the fate event (e.g. predation) is important to assess, to separate tagged animal behaviour from other data in the subsequent analyses.

Methods for tagging have been extensively covered elsewhere and do not bear repeating here (Brown et al., 2011; Jepsen et al., 2015), except for specific notes relevant to positioning. External tags are likely to have a larger detection radius (Dance et al., 2016), particularly for animals with thick abdominal walls that will more significantly attenuate the signal, but internal tagging should be considered if external transmitter attachment poses extra drag to the animal, increases the visibility of the tagged animal to predators, increases the potential for entanglement, or moves too freely around the animal and comlicates positioning. The internal transmitter may have negligible effects on growth if the tag: animal size ratio is not too large (e.g. but see Hühn et al., 2014), but what this critical ratio will be is likely to depend on species and its size. The current smallest available acoustic transmitter is the ELAT (Eel-Lamprey Acoustic Tag), made for the JSAT system measuring only 2×12 mm, and may be used for fish as small as 70–80 mm (Mueller et al., 2019). However, smaller tags are liable to have lower power and will be harder to design arrays upon which a single transmission will be detected at multiple points.

3.4 | Array design and testing

3.4.1 | Mooring design, biofouling and retrieval

Currents, unstable substrate and human interference can all shift a mooring's location during the study period (Goossens et al., 2020). Many of these problems can be mitigated by simply adding more weight and using denser materials. Depending on water temperature and salinity, and the density of the mix, concrete typically weighs 40% less under water than in air. Steel-reinforced moorings may therefore be more appropriate. For large moorings (>1 m^3), hydrodynamic shapes like pyramids may mitigate the effect of currents on drift. If currents occur in a prevalent direction (as in a river or dam tailrace), use of an upstream anchor may provide enhanced stability. On bedrock or other smooth, hard substrates, a wider mooring base may provide enough friction to mitigate sliding along the bottom. On sandy or soft bottoms, auger anchors screwed into the substrate are one of the most efficient systems to maintain acoustic receivers at fixed locations.

Biofouling can also significantly affect positioning system performance. Biofouling is the growth of organisms on the hydrophone structure, such as algae and macroinvertebrates that settle and can occlude sound signals from being detected. Different treatments can be used to prevent or mitigate it, but few studies have tested their performance (see Heupel et al., 2008). Preventative measures (e.g. anti-fouling paint) can vary in their efficacy, and regular cleaning or equipment replacement may not guarantee an increase in performance (Mathies et al., 2014). More work is required to test the effects of biofouling and the efficacy of various treatments.

How receivers are deployed and retrieved can affect positioning performance simply in that difficult retrieval may increase receiver loss and subsequently array coverage. Upon deployment, investigators should also strive to minimize the lag time between deployment of the receivers to minimize clock drift associated with differential temperature experience. Depending on the conditions in the study area (i.e. current, depth, noise, etc.) and the array geometry and mooring weight, several solutions may be practical. Certified professional SCUBA divers can safely and consistently recover receivers at shallow depths. Acoustic releases (which are available as integrated within receiver hull, or as a separate unit) allow for remote retrieval when diving or grappling is impossible or too dangerous, but re-deployment may be challenging without a rope canister to maintain a connection with the mooring (Goossens et al., 2020). In some cases, a new mooring may need to be deployed each time the receivers are downloaded. Furthermore, acoustic releases may malfunction in noisy waters, making retrieval impossible and breaking an acoustic array; investigators may need to design their arrays with redundancies as a contingency against loss so that one missing unit does not compromise an entire study area, with considerable cost ramifications. Finally, remote data offloading is now possible with wireless technology, which can mitigate retrieval problems, though receiver battery life still limits the duration of a single receiver deployment event.

The way receivers are attached to the mooring can affect positioning accuracy. For instance, one of the most popular methods of receiver deployment is to attach the receiver to a rope that is fixed to a mooring weight on the bottom and a surface or subsurface buoy (Figure 1). Depending on the rope length and current velocities, the receiver, in these situations, can oscillate around the mooring point up to several metres. Movement of receivers deviates the receiver's listening position from the original coordinates, affecting the grid geometry and the ability of positioning algorithms to estimate an accurate position due to varying distances between receivers detecting an acoustic signal.

3.4.2 | Array geometry

The distance between gridded receivers has to be selected according to the detection range at that location, which in turn, will depend on the power output, sound attenuation and working frequency of the transmitters. The habitat characteristics, such as bottom topography, determine the possibility for direct signal travel between transmitter and receiver. More dynamic factors such as biological (Payne et al., 2010) and industrial noise (Ingraham et al., 2014; Simpfendorfer et al., 2008), macrophytes, biofouling, temperature gradients, wind, wave action and tide will cause detection range to vary over time (Gjelland & Hedger, 2013; Huveneers et al., 2016; Winter et al., 2021). Tags can even be overpowered in the vicinity of reflective surfaces (hard substrates), in which case reflections or echoes (multipath) self-destructively collide, reducing detection range at short distances but not at long distances (Kessel et al., 2015).

Independent of other factors, a positioning array's geometry greatly determines the positioning precision (e.g. Kraus et al., 2018; Welsh et al., 2012), especially when applying hyperbolic multilateration positioning algorithms. The decrease in the accuracy of the positioning can be estimated by calculating the dilution of precision (DOP, including the HPE), which depends on the relative location of the transmitter and the receivers that detected the signal (Niezgoda et al., 2002). Overall, signals detected from contrasting angles (e.g. a signal detected by three or four surrounding receivers) produce better position estimates than signals detected from similar angles (e.g. receivers placed in a row at 180 degrees). The acoustic range and the DOP can be incorporated into computer simulations to compare the efficiency of different grid designs. In these simulations, the positioning efficiency of different configurations can be tested by simulating trajectories based on a movement model (e.g. random walks) and then estimating the positioning efficiency (i.e. percentage of signals detected by at least three receivers) and accuracy (estimating DOP), to select the optimal design that adapts to the specific experimental conditions (Aspillaga, Arlinghaus, Martorell-Barceló, Follana-Berná, et al., 2021; Kraus et al., 2018). Developing open-source tools and packages to facilitate these tests for researchers will be helpful to support decision-making. Lastly, knowledge on the bathymetry of the study site and the bottom substrate can be crucial to prevent violation of the direct line of sight between receivers. In the case where tags are not in direct line of sight (i.e. there is an underwater hill or corner), but transmissions are detected by the hydrophones, the calculated position will deviate from the true position.

Another key aspect that may affect the estimation of animal positions is the error associated with the positions recorded for the different acoustic stations within the array. In this regard, there are at least two important aspects to consider: the ability to record precise and accurate receiver positions, and the potential movement of the acoustic receivers during the study period. The position of the acoustic receivers is typically recorded at the start of the study by means of a handheld GNSS, and should ideally be supplemented with an additional position at the end of the study for comparison. However, conventional GNSS has a positioning error of ±2–3 m in good weather conditions, but shows much higher error distances on rainy days (Yeh et al., 2009). A better alternative is the use of differential GPS (dGPS) that records positions with a <1 m error. To date, however, no systematic experiment has evaluated the increase in positioning accuracy derived from using dGPS to record receiver locations and calculate positions. Even with a dGPS, it can be challenging to obtain accurate coordinates from a receiver deployed on the bottom or close to it when measuring from a boat at the surface, especially in deep waters or when flows are rapid. Some positioning methods can estimate the position of errant receivers (e.g. VPS will re-estimate receiver positions prior to fitting, YAPS can re-estimate receiver positions if individual receivers have moved; Table 3), but it is best if the majority of receivers remain at a fixed and accurately measured position. Once the coordinates of the receivers are recorded, they should ideally remain fixed over the course of the study. Locations should be measured at the beginning and end of deployments to verify.

3.4.3 | Performance of the experimental setup

Once the receivers' geometry has been established, the next important step is to evaluate its positioning performance in terms of accuracy, precision and expected frequency of positioning (Baktoft et al., 2015). It is strongly recommended to perform detection range assessments in the full range of environmental conditions the experimental site could face (e.g. strong dominant winds, winter/summer, the presence of macrophytes in some periods that hinder the acoustic signal propagation; Thiemer et al., 2022), before and after the deployment of the final array of receivers to ensure proper positioning, regardless of the positioning system used. Given that whole-track TOA-based methods can calculate positions without detections on three receivers (Baktoft et al., 2017), they may be more robust than single-point TDOA-based methods to fluctuating asymmetry in detection distances.

Over the life of the experiment, several fixed tags whose positions (and measurement errors) are known should be deployed in the study area, synchronizing tags should be tied to (at least some) receivers, and reference tags, similar to those used for tagging animals, should be spread at different known locations in the experimental setup, separately from receivers to ground truth position estimates on an ongoing basis. Both these tags, whose positions can be estimated by the positioning algorithm as well, inform on how the setup performs, can detect potential anomalies (Binder et al., 2016; Huveneers et al., 2016; Winter et al., 2021), and inform development of filter criteria (Meckley et al., 2014).

In addition to these fixed sentinels, moving tests should be performed, ideally simulating similar movement patterns to those expected from the study species. Best practice is to tow a transmitter whose position is continuously recorded by dGPS through the array, and then to compare the dGPS positions with those estimated by the positioning algorithm (e.g. Aspillaga, Arlinghaus, Martorell-Barceló, Follana-Berná, et al., 2021; Baktoft et al., 2015; Baktoft et al., 2017; Leander et al., 2020; Roy et al., 2014). Ideally, the test should be performed at different depths and across different habitats, representing what is expected from the targeted species (e.g. benthic/pelagic). Importantly, and especially for species known to prefer nearshore habitats, it is recommended to perform tests inside and outside the array, as performances can vary between both (e.g. Roy et al., 2014). The speed and turning angles of the towed tags should also be in agreement with the movement characteristics of the targeted species.

4 | FUTURE—NEW HORIZONS AND OPPORTUNITIES FOR AQUATIC POSITIONING SYSTEMS

Positioning acoustic tags was one of the most significant developments in aquatic movement ecology, because it allows the generation of high-throughput underwater tracking data (Nathan et al., 2022). Overcoming the challenges of the water-air boundary to acquire knowledge of where and when animals are present in aquatic ecosystems has allowed major advances in the field (Box 1). However, an obvious limitation has been the reliance on stationary receiver array grids, which need to be relatively closely spaced and thus occupy a finite space limited by detection range and number of receivers. Near real-time positioning faces additional limitations of data transmission rates between mobile receivers and a central computer. As ambitions for studying animals scale up to major lakes or marine areas, such innovations will greatly expand the applicability of positioning beyond what has been possible to date.

Computing power needed to calculate positions is a clear limitation to scaling up positioning studies. Running synchronization models and positioning algorithms on these large datasets is time consuming, computationally expensive, and may be inaccessible to smaller research groups without access to servers or centralized computing. How to store, analyse, use and transform these massive amounts of movement data into useful knowledge is already a challenge for many acoustic positioning studies. Positioning is unlikely to become simpler in the future and open-source solutions are complex. Investment in community-centralized computing resources may be a solution to reduce the burden on research groups using positioning. This challenge could be addressed by changing the paradigm from a traditional model-driven approximation towards a more data-driven oriented approach to transform the large amount of positions into real knowledge. The integration of artificial intelligence, and deep learning in particular, in aquatic high-throughput movement is a good candidate to bridge this gap, but is still in its infancy (Maekawa et al., 2020). In addition to computing power, improved connectivity between receivers and computers that run positioning algorithms could improve the quality of positional telemetry data by allowing feedback in near real time. In most contemporary positioning studies, positions are only derived after the conclusion of a study, preventing opportunities to identify and address performance issues as they arise.

Synchronizing clocks on independent receivers is one of the most challenging steps to overcome in acoustic positioning. Cabled receivers eliminate this challenge but limit coverage area and impose significant logistical constraints, so independent receivers are more common. Use of more accurate timepieces (e.g. alternatives to quartz crystals) or other methods to synchronize clocks in near real time (e.g. a periodic correction from a GPS clock) would represent a significant advancement.

Accurate positioning of large numbers of individuals offers the opportunity to create genuine wild laboratories to measure responses of aquatic animals to abiotic factors. The combination of acoustic positioning with continuous collection of fine-scale hydrodynamic and meteorological factors can provide new avenues for testing hypotheses about external drivers of movement. Such information is highly valuable for managers, for instance in their ambitions to better guide migratory fish around barriers and reduce entrainment in hydropower facilities through improved passage design. Understanding how individuals respond to environmental variables can also help predict the effect of future climate scenarios on fish populations, especially using smaller systems such as whole-lake studies. Furthermore, knowledge on the relations between hydrodynamics and meteorological factors (among others) could also improve operations of infrastructure through predictions of fish behaviour based on continuously monitored environmental factors. Hence, humans can better adapt operations of infrastructure (e.g. water level management in reservoirs through hydropower operations) to fish movement, migration and habitat use (Koster et al., 2018; Westrelin et al., 2018).

Positioning algorithms are common throughout modern technology, from use in cell networks to wifi networks to GNSS-based tracking to pinpoint positions in space, and provide a coordinate that can be mapped for a large variety of use cases. The field of underwater movement ecology must closely follow and borrow from new advancements in positioning solutions from other related fields to fully capitalize on the potential of acoustic telemetry. For example, the use of CDMA technology in radio signal communications such as mobile phones and WLAN have essentially eliminated the problem of signal collisions, while also reducing the battery power required for transmissions due to the shorter transmission time required. In addition to borrowing new signal encoding methods, opportunities exist for developing improved signal detection methods within receivers, with respect to detecting quiet signals at further ranges, picking out transmission from noisy environments and sorting true detections from false multipath generated signals. Acoustic positioning has matured to be a widely used method of underwater geolocation, but we believe the present state-of-the-art is now at a plateau, short of its potential peak of performance. The next decade will hopefully bring new modes of synchronizing receiver clocks, better methods of measuring receiver positions, improvements to open-source positioning algorithms, and better ways of archiving and sharing positioning data within the community for meta-analyses and comparative research. Many of these developments will rely on engineering and cross-fertilization of the technology with other fields of communications.

There is a clear need for more bottom-up development in positioning. Open-source tools have been important to ecology and development of open hardware and software can help advance the field towards open science and reproducibility. Tools that support different parts of designing positioning studies, such as: simulations that help investigators choose the right number of tags or receivers, tools that help synchronize receivers and tools that help calculate positions are key to increase accessibility of positioning to new users. Moreover, open and accessible tools maintain a high level of reproducibility, which has repeatedly been emphasized as important to ecology (Powers & Hampton, 2019). Development of open tools for positioning requires investment and interdisciplinary work with data scientists and statisticians to optimize code and expand on the existing tools. The acoustic telemetry field is already benefiting from such tools, which have been developed for assisting users with designing experiments and interpreting their data including glatos (Holbrook et al., 2021) for study design and data management and YAPS (Baktoft et al., 2017) for receiver synchronization and position calculation. Supporting new open tools and advances in the field will be key to increased uptake of positioning and higher relevance of this tool for aquatic ecologists.

5 | CONCLUSIONS

The aquatic realm is mysterious and studying the movement of animals underwater at biologically relevant resolution and scale has been a challenge for centuries. Acoustic telemetry positioning systems increasingly enable us to do just that. The basic concepts behind positioning animals underwater using acoustic telemetry have remained fundamentally the same since the early experiments of Kuroki et al. (1971), Young et al. (1972) and Hawkins et al. (1974). However, the collective experience, including successes and failures, of the scientific community involved in positioning aquatic animals now leaves us with the knowledge necessary to routinely plan and execute successful fine-scale tracking projects across a range of aquatic environments (from inland rivers and lakes to coastal marine waters) according to best practices, generating rich datasets of animal movement.

Advances in computing power, battery life, clock synchronization techniques, positioning solvers, signal encoding methods (CDMA-variants) and array design knowledge have been key contributors towards reaching the high data yields currently achievable. Fish can now be positioned with remarkable accuracy and precision, provided that care is taken in the development of tracking systems and the interpretation of findings. Future improvements towards signal detection across longer ranges, accuracy measuring receiver locations, and incorporation of environmental variability (e.g. flow, currents) into positioning methods will enable large gains in spatial accuracy and consequently our understanding of the behaviour of underwater organisms, with corresponding improvements in the ability to draw inferences about the movement ecology of aquatic animals in high resolution and in relation to their environment.

AUTHOR CONTRIBUTIONS

Concept: Robert J. Lennox conceived the manuscript with input from all authors on manuscript structure and narrative. Writing: All authors contributed to writing. Visualization: Lotte S. Dahlmo and Cecilie Iden Nilsen conceived and illustrated Figure 1. Editing: All authors contributed to editing and approved the final version.

ACKNOWLEDGEMENTS

We acknowledge support from the project "Multi-lake research of fish ecology and management using high-resolution 3D telemetry systems", funded by ALTER-NET within the MultiSite Research Initiative. This work is supported by The European Aquatic Animal Tracking Network COST-Action (CA18102)—a project supported by COST (European Cooperation in Science and Technology) as part of the Horizon Europe program, ALTER-NET (Through the Lake Fish Telemetry Workshop), The Danish Rod and Net Licence Funds, and the EU Horizon 2020 Project STRAITS (grant no. 101094649). Lennox and Cooke are members of Ocean Tracking Network, supported by the Canada Foundation for Innovation. Vollset, Nilsen and Dahlmo were supported by the Norwegian Research Council (projects LaKES 320726 and LOST 325840). Reubens acknowledges support by the Research Foundation Flanders (FWO) as part of the Belgian contribution to LifeWatch. The contribution by Arlinghaus was made possible through a grant from the European Maritime Fisheries Fund and the State of MV (Grant/Award numbers MV-I.18-LM-004 and B730117000069; BODDENHECHT). Contribution by Baktoft was made possible through Poul Due Jensens Fond. Contribution by Gjelland was supported by the Norwegian Research Council (project Hydrocen) and NINA internal funding). The text was checked for technical accuracy in its final iteration by Frank Smith (InnovaSea), by Eivind Brandsæter Hvam (Thelma Biotel), and by Dave Gambin (Lotek Wireless).

CONFLICT OF INTEREST STATEMENT

The authors have no interests in competition with the work presented here. References to specific manufacturers are intended to be representative of the market and not an endorsement of their products. Any use of trade, product or firm names is for descriptive purposes only and does not imply endorsement by the US Government.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/2041-210X.14191.

DATA AVAILABILITY STATEMENT

No data.

ORCID

Robert J. Lennox https://orcid.org/0000-0003-1010-0577
Kim Aarestrup https://orcid.org/0000-0001-8521-6270
Josep Alós https://orcid.org/0000-0003-4385-9539
Robert Arlinghaus https://orcid.org/0000-0003-2861-527X
Kim Birnie-Gauvin https://orcid.org/0000-0001-9242-0560
Steven J. Cooke https://orcid.org/0000-0002-5407-0659
Karl Ø. Gjelland https://orcid.org/0000-0003-4036-4207
Christopher T. Monk https://orcid.org/0000-0002-1647-4740
Milan Říha https://orcid.org/0000-0002-3930-420X
David Villegas-Ríos https://orcid.org/0000-0001-5660-5322
Knut Wiik Vollset https://orcid.org/0000-0003-0210-4316
Henrik Baktoft https://orcid.org/0000-0002-3644-4960

REFERENCES

Alós, J., Palmer, M., Balle, S., & Arlinghaus, R. (2016). Bayesian state-space modelling of conventional acoustic tracking provides accurate descriptors of home range behavior in a small-bodied coastal fish species. *PLoS ONE*, *11*(4), e0154089.

Anderson, J. M., Spurgeon, E., Stirling, B. S., May, J., III, Rex, P. T., Hyla, B., McCullough, S., Thompson, M., & Lowe, C. G. (2022). High resolution acoustic telemetry reveals swim speeds and inferred field metabolic rates in juvenile white sharks (*Carcharodon carcharias*). *PLoS ONE*, *17*(6), e0268914.

Aspillaga, E., Arlinghaus, R., Martorell-Barceló, M., Barcelo-Serra, M., & Alós, J. (2021). High-throughput tracking of social networks in marine fish populations. *Frontiers in Marine Science*, *8*, 688010.

Aspillaga, E., Arlinghaus, R., Martorell-Barceló, M., Follana-Berná, G., Lana, A., Campos-Candela, A., & Alós, J. (2021). Performance of a novel system for high-resolution tracking of marine fish societies. *Animal Biotelemetry*, *9*(1), 1.

Baktoft, H., Aarestrup, K., Berg, S., Boel, M., Jacobsen, L., Jepsen, N., Koed, A., Svenden, J. C., & Skov, C. (2012). Seasonal and diel effects on the activity of northern pike studied by high-resolution positional telemetry. *Ecology of Freshwater Fish*, *21*(3), 386–394.

Baktoft, H., Gjelland, K. Ø., Økland, F., & Thygesen, U. H. (2017). Positioning of aquatic animals based on time-of-arrival and random walk models using YAPS (yet another positioning solver). *Scientific Reports*, *7*(1), 1–10.

Baktoft, H., Gjelland, K. Ø., Szabo-Meszaros, M., Silva, A. T., Riha, M., Økland, F., Alfredsen, K., & Forseth, T. (2020). Can energy depletion of wild Atlantic salmon kelts negotiating hydropower facilities lead to reduced survival? *Sustainability*, *12*(18), 7341.

Baktoft, H., Jacobsen, L., Skov, C., Koed, A., Jepsen, N., Berg, S., Boel, M., Aarestrup, K., & Svendsen, J. C. (2016). Phenotypic variation in metabolism and morphology correlating with animal swimming activity in the wild: Relevance for the OCLTT (oxygen-and capacity-limitation of thermal tolerance), allocation and performance models. *Conservation Physiology*, *4*(1), cov055.

Baktoft, H., Zajicek, P., Klefoth, T., Svendsen, J. C., Jacobsen, L., Pedersen, M. W., Morla, D. M., Skov, C., Nakayama, S., & Arlinghaus, R. (2015). Performance assessment of two whole-lake acoustic positional telemetry systems is reality mining of free ranging aquatic animals technologically possible? *PLoS ONE*, *10*(5), e0126534.

Binder, T. R., Farha, S. A., Thompson, H. T., Holbrook, C. M., Bergstedt, R. A., Riley, S. C., Bronte, C. R., & Krueger, C. C. (2018). Fine-scale acoustic telemetry reveals unexpected lake trout, *Salvelinus namaycush*, spawning habitats in northern Lake Huron, North America. *Ecology of Freshwater Fish*, *27*(2), 594–605.

Binder, T. R., Holbrook, C. M., Hayden, T. A., & Krueger, C. C. (2016). Spatial and temporal variation in positioning probability of acoustic telemetry arrays: Fine-scale variability and complex interactions. *Animal Biotelemetry*, *4*(1), 1–15.

Brown, D. D., LaPoint, S., Kays, R., Heidrich, W., Kümmeth, F., & Wikelski, M. (2012). Accelerometer-informed GPS telemetry: Reducing the trade-off between resolution and longevity. *Wildlife Society Bulletin*, *36*(1), 139–146.

Brown, R. S., Eppard, M. B., Murchie, K. J., Nielsen, J. L., & Cooke, S. J. (2011). An introduction to the practical and ethical perspectives on the need to advance and standardize the intracoelomic surgical implantation of electronic tags in fish. *Reviews in Fish Biology and Fisheries*, *21*, 1–9.

Cooke, S. J., Niezgoda, G. H., Hanson, K. C., Suski, C. D., Phelan, F. J., Tinline, R., & Philipp, D. P. (2005). Use of CDMA acoustic telemetry to document 3-D positions of fish: Relevance to the design and

monitoring of aquatic protected areas. *Marine Technology Society Journal*, *39*(1), 31–41.
Cote, D., Scruton, D. A., Niezgoda, G. H., & McKinley, R. S. (1998). A coded acoustic telemetry system for high precision monitoring of fish location and movement: Application to the study of nearshore nursery habitat of juvenile Atlantic cod (*Gadus morhua*). *Marine Technology Society Journal*, *32*(1), 54.
Dance, M. A., Moulton, D. L., Furey, N. B., & Rooker, J. R. (2016). Does transmitter placement or species affect detection efficiency of tagged animals in biotelemetry research? *Fisheries Research*, *183*, 80–85.
Ehrenberg, J. E., & Steig, T. W. (2003). Improved techniques for studying the temporal and spatial behavior of fish in a fixed location. *ICES Journal of Marine Science*, *60*(3), 700–706.
Ehrenberg, J. E., & Steig, T. W. (2009). A study of the relationship between tag-signal characteristics and achievable performances in acoustic fish-tag studies. *ICES Journal of Marine Science*, *66*(6), 1278–1283.
Espinoza, M., Farrugia, T. J., Webber, D. M., Smith, F., & Lowe, C. G. (2011). Testing a new acoustic telemetry technique to quantify long-term, fine-scale movements of aquatic animals. *Fisheries Research*, *108*(2–3), 364–371.
Gjelland, K. Ø., & Hedger, R. D. (2013). Environmental influence on transmitter detection probability in biotelemetry: Developing a general model of acoustic transmission. *Methods in Ecology and Evolution*, *4*(7), 665–674.
Goossens, J., T'Jampens, M., Deneudt, K., & Reubens, J. (2020). Mooring scientific instruments on the seabed—Design, deployment protocol and performance of a recoverable frame for acoustic receivers. *Methods in Ecology and Evolution*, *11*(8), 974–979.
Halttunen, E., Gjelland, K.-Ø., Hamel, R.-M., Serra-Llinares, R.-M., Nilsen, R., Arechavala-Lopez, P., Skarðhamar, J., Johnsen, I. A., Asplin, L., Karlsen, Ø., Bjørn, P.-A., & Finstad, B. (2018). Sea trout adapt their migratory behaviour in response to high salmon lice concentrations. *Journal of Fish Diseases*, *41*(6), 953–967.
Hanson, K. C., Cooke, S. J., Suski, C. D., Niezgoda, G., Phelan, F. J. S., Tinline, R., & Philipp, D. P. (2007). Assessment of largemouth bass (*Micropterus salmoides*) behaviour and activity at multiple spatial and temporal scales utilizing a whole-lake telemetry array. In *Developments in fish telemetry* (pp. 243–256). Springer.
Hanssen, E. M., Vollset, K. W., Salvanes, A. G. V., Barlaup, B., Whoriskey, K., Isaksen, T. E., Normann, E. S., Hulbak, M., & Lennox, R. J. (2022). Acoustic telemetry predation sensors reveal the tribulations of Atlantic salmon (*Salmo salar*) smolts migrating through lakes. *Ecology of Freshwater Fish*, *31*(2), 424–437.
Hawkins, A. D., MacLennan, D. N., Urquhart, G. G., & Robb, C. (1974). Tracking cod *Gadus morhua* L. in a Scottish Sea loch. *Journal of Fish Biology*, *6*(3), 225–236.
Heezen, K. L., & Tester, J. R. (1967). Evaluation of radio-tracking by triangulation with special reference to deer movements. *The Journal of Wildlife Management*, *31*, 124–141.
Hellström, G., Lennox, R. J., Bertram, M. G., & Brodin, T. (2022). Acoustic telemetry. *Current Biology*, *32*(16), R863–R865.
Heupel, M. R., Reiss, K. L., Yeiser, B. G., & Simpfendorfer, C. A. (2008). Effects of biofouling on performance of moored data logging acoustic receivers. *Limnology and Oceanography: Methods*, *6*(7), 327–335.
Holbrook, C., Hayden, T., Binder, T., & Pye, J. (2021). glatos: A package for the great lakes acoustic telemetry observation system. R package version 0.5.1. https://gitlab.oceantrack.org/GreatLakes/glatos
Holleman, R. C., Gross, E. S., Thomas, M. J., Rypel, A. L., & Fangue, N. A. (2022). Swimming behavior of emigrating Chinook Salmon smolts. *PLoS ONE*, *17*(3), e0263972.
Hühn, D., Klefoth, T., Pagel, T., Zajicek, P., & Arlinghaus, R. (2014). Impacts of external and surgery-based tagging techniques on small northern pike under field conditions. *North American Journal of Fisheries Management*, *34*, 322–334.
Hussey, N. E., Kessel, S. T., Aarestrup, K., Cooke, S. J., Cowley, P. D., Fisk, A. T., Harcourt, R. G., Holland, K. M., Iverson, S. J., & Whoriskey, F. G. (2015). Aquatic animal telemetry: A panoramic window into the underwater world. *Science*, *348*(6240), 1255642.
Huveneers, C., Simpfendorfer, C. A., Kim, S., Semmens, J. M., Hobday, A. J., Pederson, H., Stieglitz, T., Vallee, R., Webber, D., Heupel, M. R., Peddemors, V., & Harcourt, R. G. (2016). The influence of environmental parameters on the performance and detection range of acoustic receivers. *Methods in Ecology and Evolution*, *7*, 825–835.
Ingraham, J. M., Deng, Z. D., Martinez, J. J., Trumbo, B. A., Mueller, R. P., & Weiland, M. A. (2014). Feasibility of tracking fish with acoustic transmitters in the Ice Harbor Dam tailrace. *Scientific Reports*, *4*(1), 1–8.
Jacobsen, L., Baktoft, H., Jepsen, N., Aarestrup, K., Berg, S., & Skov, C. (2014). Effect of boat noise and angling on lake fish behaviour. *Journal of Fish Biology*, *84*(6), 1768–1780.
Jepsen, N., Thorstad, E. B., Havn, T., & Lucas, M. C. (2015). The use of external electronic tags on fish: An evaluation of tag retention and tagging effects. *Animal Biotelemetry*, *3*(1), 1–23.
Johnson, D. S., & London, J. M. (2018). crawl: An R package for fitting continuous-time correlated random walk models to animal movement data.
Johnson, D. S., London, J. M., Lea, M. A., & Durban, J. W. (2008). Continuous-time correlated random walk model for animal telemetry data. *Ecology*, *89*(5), 1208–1215.
Juell, J. E., & Westerberg, H. (1993). An ultrasonic telemetric system for automatic positioning of individual fish used to track Atlantic salmon (*Salmo salar* L.) in a sea cage. *Aquacultural Engineering*, *12*(1), 1–18.
Kays, R., Crofoot, M. C., Jetz, W., & Wikelski, M. (2015). Terrestrial animal tracking as an eye on life and planet. *Science*, *348*(6240), aaa2478.
Kessel, S. T., Cooke, S. J., Heupel, M. R., Hussey, N. E., Simpfendorfer, C. A., Vagle, S., & Fisk, A. T. (2014). A review of detection range testing in aquatic passive acoustic telemetry studies. *Reviews in Fish Biology and Fisheries*, *24*, 199–218.
Kessel, S. T., Hussey, N. E., Webber, D. M., Gruber, S. H., Young, J. M., Smale, M. J., & Fisk, A. T. (2015). Close proximity detection interference with acoustic telemetry: The importance of considering tag power output in low ambient noise environments. *Animal Biotelemetry*, *3*(1), 1–14.
Klimley, A. P., Voegeli, F., Beavers, S. C., & Le Boeuf, B. J. (1998). Automated listening stations for tagged marine fishes. *Marine Technology Society Journal*, *32*(1), 94–101.
Klinard, N. V., & Matley, J. K. (2020). Living until proven dead: Addressing mortality in acoustic telemetry research. *Reviews in Fish Biology and Fisheries*, *30*(3), 485–499.
Koster, W. M., Crook, D. A., Dawson, D. R., Gaskill, S., & Morrongiello, J. R. (2018). Predicting the influence of streamflow on migration and spawning of a threatened diadromous fish, the Australian grayling Prototroctes maraena. *Environmental Management*, *61*, 443–453.
Kraus, R. T., Holbrook, C. M., Vandergoot, C. S., Stewart, T. R., Faust, M. D., Watkinson, D. A., Charles, C., Pegg, M., Enders, E. C., & Krueger, C. C. (2018). Evaluation of acoustic telemetry grids for determining aquatic animal movement and survival. *Methods in Ecology and Evolution*, *9*(6), 1489–1502.
Krause, J., Krause, S., Arlinghaus, R., Psorakis, I., Roberts, S., & Rutz, C. (2013). Reality mining of animal social systems. *Trends in Ecology & Evolution*, *28*(9), 541–551.
Kuroki, T., Kawaguchi, K., Sakamoto, W., & Watanabe, H. (1971). A new telemetric apparatus to detect fish location and its surrounding water temperature. *Nippon Suisan Gakkaishi*, *37*, 964–972.
Langrock, R., King, R., Matthiopoulos, J., Thomas, L., Fortin, D., & Morales, J. M. (2012). Flexible and practical modeling of animal telemetry data: Hidden Markov models and extensions. *Ecology*, *93*(11), 2336–2342.

Leander, J., Klaminder, J., Jonsson, M., Brodin, T., Leonardsson, K., & Hellström, G. (2020). The old and the new: Evaluating performance of acoustic telemetry systems in tracking migrating Atlantic salmon (Salmo salar) smolt and European eel (*Anguilla anguilla*) around hydropower facilities. *Canadian Journal of Fisheries and Aquatic Sciences*, *77*(1), 177–187.

Lennox, R. J., Dahlmo, L. S., Ford, A. T., Sortland, L. K., Vogel, E. F., & Vollset, K. W. (2023). Predation research with electronic tagging. *Wildlife Biology*, *2023*(1), e01045.

Maekawa, T., Ohara, K., Zhang, Y., Fukutomi, M., Matsumoto, S., Matsumura, K., Shidara, H., Yamazaki, S. J., Fujisawa, R., Ide, K., Nagaya, N., Yamazaki, K., Koike, S., Miyatake, T., Kumura, K. D., Ogawa, H., Takahashi, S., & Yoda, K. (2020). Deep learning-assisted comparative analysis of animal trajectories with DeepHL. *Nature Communications*, *11*(1), 5316.

Manicacci, F. M., Mourier, J., Babatounde, C., Garcia, J., Broutta, M., Gualtieri, J. S., & Aiello, A. (2022). A wireless autonomous real-time underwater acoustic positioning system. *Sensors*, *22*(21), 8208.

Masmitja, I., Navarro, J., Gomaríz, S., Aguzzi, J., Kieft, B., O'Reilly, T., Katija, K., Bouvet, P. J., FannJiang, C., Vigo, M., Puig, P., Alcocer, A., Vallicrosa, G., Palomeras, N., Carreras, M., Del Rio, J., & Company, J. B. (2020). Mobile robotic platforms for the acoustic tracking of deep-sea demersal fishery resources. *Science. Robotics*, *5*(48), eabc3701.

Mathies, N. H., Ogburn, M. B., McFall, G., & Fangman, S. (2014). Environmental interference factors affecting detection range in acoustic telemetry studies using fixed receiver arrays. *Marine Ecology Progress Series*, *495*, 27–38.

McCleave, J. D. (1978). Telemetric techniques for studying fish behaviour in the field. *Aquaculture Research*, *9*(4), 114–115.

McClintock, B. T., & Michelot, T. (2018). momentuHMM: R package for generalized hidden Markov models of animal movement. *Methods in Ecology and Evolution*, *9*, 1518–1530.

McLean, D. J., & Skowron Volponi, M. A. (2018). trajr: An R package for characterisation of animal trajectories. *Ethology*, *124*, 440–448.

McMichael, G. A., Eppard, M. B., Carlson, T. J., Carter, J. A., Ebberts, B. D., Brown, R. S., Weiland, M., Ploskey, G. R., Harnish, R. A., & Deng, Z. D. (2010). The juvenile salmon acoustic telemetry system: A new tool. *Fisheries*, *35*(1), 9–22.

Meckley, T. D., Holbrook, C. M., Wagner, C. M., & Binder, T. R. (2014). An approach for filtering hyperbolically positioned underwater acoustic telemetry data with position precision estimates. *Animal Biotelemetry*, *2*(1), 1–13.

Medisetty, S., Ouellette, D., Smith, F., Richard, M., Johnston, S., Quirion, J., Newport, J., Whidden, C., & Kirsebom, O. (2021). Identification of periodic fish tags with deep learning. *Journal of Ocean Technology*, *16*(3), 139–149.

Monk, C. T., & Arlinghaus, R. (2017). Encountering a bait is necessary but insufficient to explain individual variability in vulnerability to angling in two freshwater benthivorous fish in the wild. *PLoS ONE*, *12*(3), e0173989.

Monk, C. T., Bekkevold, D., Klefoth, T., Pagel, T., Palmer, M., & Arlinghaus, R. (2021). The battle between harvest and natural selection creates small and shy fish. *Proceedings of the National Academy of Sciences of the United States of America*, *118*(9), e2009451118.

Mueller, R., Liss, S., & Deng, Z. D. (2019). Implantation of a new micro acoustic tag in juvenile pacific lamprey and American eel. *Journal of Visualized Experiments*, *145*, e59274.

Nakayama, S., Doering-Arjes, P., Linzmaier, S., Briege, J., Klefoth, T., Pieterek, T., & Arlinghaus, R. (2018). Fine-scale movement ecology of a freshwater top predator, Eurasian perch (*Perca fluviatilis*), in response to the abiotic environment over the course of a year. *Ecology of Freshwater Fish*, *27*, 798–812.

Nakayama, S., Laskowski, K. L., Klefoth, T., & Arlinghaus, R. (2016). Between-and within-individual variation in activity increases with water temperature in wild perch. *Behavioral Ecology*, *27*, arw090.

Nakayama, S., Rapp, T., & Arlinghaus, R. (2017). Fast–slow life history is correlated with individual differences in movements and prey selection in an aquatic predator in the wild. *Journal of Animal Ecology*, *86*(2), 192–201.

Nathan, R., Monk, C. T., Arlinghaus, R., Adam, T., Alós, J., Assaf, M., Baktoft, H., Beardswoth, C. E., Bertram, M. G., Bijeveld, A. I., Brodin, T., Brooks, J. L., Campos-Candela, A., Cooke, S. J., Gjelland, K.-Ø., Gupte, P. R., Harel, R., Hellstrom, G., Jeltsch, F., … Jaric, I. Big-data approaches lead to an increased understanding of the ecology of animal movement. *Science*, *375*(6582), eabg1780.

Nathan, R., Monk, C. T., Arlinghaus, R., Adam, T., Alós, J., Assaf, M., Baktoft, H., BJarić, I. (2022). Big-data approaches lead to an increased understanding of the ecology of animal movement. *Science*, *375*(6582), eabg1780.

Nielsen, J. K., Niezgoda, G., Taggart, S. J., Cooke, S. J., Anson, P., Hasler, C. T., Hanson, K. C., & Carl, G. (2012). Mobile positioning of tagged aquatic animals using acoustic telemetry with a synthetic hydrophone array (SYNAPS: Synthetic aperture positioning system). *American Fisheries Society Symposium*, *76*, 233–250.

Niezgoda, G., Benfield, M., Sisak, M., & Anson, P. (2002). Tracking acoustic transmitters by code division multiple access (CDMA)-based telemetry. In *Aquatic Telemetry* (pp. 275–286). Springer.

O'Dor, R. K., Aitken, J. P., Babcock, R. C., Bolden, S. K., Seino, S., Zeller, D. C., & Jackson, G. D. (2001). Using radio-acoustic positioning and telemetry (RAPT) to define and assess marine protected areas (MPAs). In *Electronic tagging and tracking in marine fisheries: Proceedings of the symposium on tagging and tracking marine fish with electronic devices*, February 7–11, 2000, East-West Center, University of Hawaii (pp. 147–166). Springer Netherlands.

O'Dor, R. K., Andrade, Y., Webber, D. M., Sauer, W. H. H., Roberts, M. J., Smale, M. J., & Voegeli, F. M. (1998). Applications and performance of radio-acoustic positioning and telemetry (RAPT) systems. In *Advances in invertebrates and fish telemetry* (pp. 1–8). Springer.

Orrell, D. L., & Hussey, N. E. (2022). Using the VEMCO positioning system (VPS) to explore fine-scale movements of aquatic species: Applications, analytical approaches and future directions. *Marine Ecology Progress Series*, *687*, 195–216.

Payne, N. L., Gillanders, B. M., Webber, D. M., & Semmens, J. M. (2010). Interpreting diel activity patterns from acoustic telemetry: The need for controls. *Marine Ecology Progress Series*, *419*, 295–301.

Pincock, D. G., & Johnston, S. V. (2012). Acoustic telemetry overview. In N. S. Adams, J. W. Beeman, & J. H. Eiler (Eds.), *Telemetry techniques: A user guide for fisheries research* (pp. 305–338). American Fisheries Society.

Potts, J. R., Bastille-Rousseau, G., Murray, D. L., Schaefer, J. A., & Lewis, M. A. (2014). Predicting local and non-local effects of resources on animal space use using a mechanistic step selection model. *Methods in Ecology and Evolution*, *5*, 253–262.

Powers, S. M., & Hampton, S. E. (2019). Open science, reproducibility, and transparency in ecology. *Ecological Applications*, *29*(1), e01822.

Reubens, J., Aarestrup, K., Meyer, C., Moore, A., Okland, F., & Afonso, P. (2021). Compatibility in acoustic telemetry. Animal. *Biotelemetry*, *9*(1), 1–6.

Říha, M., Gjelland, K. Ø., Děd, V., Eloranta, A. P., Rabaneda-Bueno, R., Baktoft, H., Vejřík, L., Vejříková, I., Draštík, V., Šmejkal, M., Holubová, M., Jůza, T., Rosten, C., Sajdlová, Z., Økland, F., & Peterka, J. (2021). Contrasting structural complexity differentiate hunting strategy in an ambush apex predator. *Scientific Reports*, *11*(1), 17472.

Říha, M., Rabaneda-Bueno, R., Jarić, I., Souza, A. T., Vejřík, L., Draštík, V., Smejkal, M., Holubova, M., Juza, T., Rosten, C., Økland, F., & Peterka, J. (2022). Seasonal habitat use of three predatory fishes in a freshwater ecosystem. *Hydrobiologia*, *849*(15), 3351–3371.

Rillahan, C., Chambers, M., Howell, W. H., & Watson, W. H., III. (2009). A self-contained system for observing and quantifying the behavior of Atlantic cod, Gadus morhua, in an offshore aquaculture cage. *Aquaculture*, *293*(1–2), 49–56.

Roy, R., Beguin, J., Argillier, C., Tissot, L., Smith, F., Smedbol, S., & De-Oliveira, E. (2014). Testing the VEMCO positioning system: Spatial distribution of the probability of location and the positioning error in a reservoir. *Animal Biotelemetry*, *2*(1), 1–7.

Silva, A. T., Bærum, K. M., Hedger, R. D., Baktoft, H., Fjeldstad, H. P., Gjelland, K. Ø., Økland, F., & Forseth, T. (2020). The effects of hydrodynamics on the three-dimensional downstream migratory movement of Atlantic salmon. *Science of the Total Environment*, *705*, 135773.

Simpfendorfer, C. A., Heupel, M. R., & Collins, A. B. (2008). Variation in the performance of acoustic receivers and its implication for positioning algorithms in a riverine setting. *Canadian Journal of Fisheries and Aquatic Sciences*, *65*(3), 482–492.

Simpfendorfer, C. A., Heupel, M. R., & Hueter, R. E. (2002). Estimation of short-term centers of activity from an array of omnidirectional hydrophones and its use in studying animal movements. *Canadian Journal of Fisheries and Aquatic Sciences*, *59*(1), 23–32.

Smith, F. (2013). Understanding HPE in the VEMCO positioning system (VPS). Retrieved from http://vemco.com/wp-content/uploads/2013/09/understanding-hpe-vps.pdf

Steig, T. W. (1999, May). The use of acoustic tags to monitor the movement of juvenile salmonids approaching a dam on the Columbia River. In *Proceedings of the 15th International Symposium on Biotelemetry, Juneau, Alaska* (pp. 9–14).

Szabo-Meszaros, M., Silva, A. T., Bærum, K. M., Baktoft, H., Alfredsen, K., Hedger, R. D., Økland, F., Gjelland, K.-Ø., Fjeldstad, H.-P., Calles, O., & Forseth, T. (2021). Validation of a swimming direction model for the downstream migration of Atlantic Salmon Smolts. *Water*, *13*(9), 1230.

Taraldsen, G., Reinen, T. A., & Berg, T. (2011). The underwater GPS problem. In *OCEANS 2011 IEEE-Spain* (pp. 1–8). IEEE.

Thiemer, K., Lennox, R. J., & Haugen, T. O. (2022). Influence of dense macrophyte vegetation and total gas saturation on the performance of acoustic telemetry. *Animal Biotelemetry*, *10*(1), 4.

Trancart, T., Carpentier, A., Acou, A., Danet, V., Elliott, S., & Feunteun, E. (2020). Behaviour of endangered European eels in proximity to a dam during downstream migration: Novel insights using high accuracy 3D acoustic telemetry. *Ecology of Freshwater Fish*, *29*(2), 266–279.

Turchin, P. (1996). Fractal analyses of animal movement: A critique. *Ecology*, *77*(7), 2086–2090.

van der Knapp, I., Reubens, J., Thomas, L., Ainslie, M. A., Winter, H. V., Hubert, J., Martin, B., & Slabbekoorn, H. (2021). Effects of a seismic survey on movement of free-ranging Atlantic cod. *Current Biology*, *31*(7), 1555–1562.

Vanovac, S., Howard, D., Monk, C. T., Arlinghaus, R., & Giabbanelli, P. J. (2021). Network analysis of intra-and interspecific freshwater fish interactions using year-around tracking. *Journal of the Royal Society Interface*, *18*(183), 20210445.

Vergeynst, J., Vanwyck, T., Baeyens, R., De Mulder, T., Nopens, I., Mouton, A., & Pauwels, I. (2020). Acoustic positioning in a reflective environment: Going beyond point-by-point algorithms. *Animal Biotelemetry*, *8*(1), 1–17.

Welsh, J. Q., Fox, R. J., Webber, D. M., & Bellwood, D. R. (2012). Performance of remote acoustic receivers within a coral reef habitat: Implications for array design. *Coral Reefs*, *31*, 693–702.

Westrelin, S., Roy, R., Tissot-Rey, L., Bergès, L., & Argillier, C. (2018). Habitat use and preference of adult perch (*Perca fluviatilis* L.) in a deep reservoir: Variations with seasons, water levels and individuals. *Hydrobiologia*, *809*, 121–139.

Winter, E. R., Hindes, A. M., Lane, S., & Britton, J. R. (2021). Detection range and efficiency of acoustic telemetry receivers in a connected wetland system. *Hydrobiologia*, *848*, 1825–1836.

Winton, M. V., Kneebone, J., Zemeckis, D. R., & Fay, G. (2018). A spatial point process model to estimate individual centres of activity from passive acoustic telemetry data. *Methods in Ecology and Evolution*, *9*(11), 2262–2272.

Yeh, S. C., Hsu, W. H., Su, M. Y., Chen, C. H., & Liu, K. H. (2009). A study on outdoor positioning technology using GPS and WiFi networks. In *2009 International Conference on Networking, Sensing and Control* (pp. 597–601). IEEE.

Young, A. H., Tytler, P., Holliday, F. G. T., & MacFarlane, A. (1972). A small sonic tag for measurement of locomotor behaviour in fish. *Journal of Fish Biology*, *4*(1), 57–65.

How to cite this article: Lennox, R. J., Aarestrup, K., Alós, J., Arlinghaus, R., Aspillaga, E., Bertram, M. G., Birnie-Gauvin, K., Brodin, T., Cooke, S. J., Dahlmo, L. S., Dhellemmes, F., Gjelland, K. Ø., Hellström, G., Hershey, H., Holbrook, C., Klefoth, T., Lowerre-Barbieri, S., Monk, C. T., Nilsen, C. I. … Baktoft, H. (2023). Positioning aquatic animals with acoustic transmitters. *Methods in Ecology and Evolution*, *14*, 2514–2530. https://doi.org/10.1111/2041-210X.14191