



# Conducting and interpreting fish telemetry studies: considerations for researchers and resource managers

Jacob W. Brownscombe · Elodie J. I. Lédée · Graham D. Raby · Daniel P. Struthers · Lee F. G. Gutowsky · Vivian M. Nguyen · Nathan Young · Michael J. W. Stokesbury · Christopher M. Holbrook · Travis O. Brenden · Christopher S. Vandergoot · Karen J. Murchie · Kim Whoriskey · Joanna Mills Flemming · Steven T. Kessel · Charles C. Krueger · Steven J. Cooke

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**Abstract** Telemetry is an increasingly common tool for studying the ecology of wild fish, with great potential to provide valuable information for management and conservation. For researchers to conduct a robust telemetry study, many essential considerations exist related to selecting the appropriate tag type, fish capture and tagging methods, tracking protocol, data processing and analyses, and interpretation of findings. For telemetry-derived knowledge to be relevant to managers and policy makers, the research approach

must consider management information needs for decision-making, while end users require an understanding of telemetry technology (capabilities and limitations), its application to fisheries research and monitoring (study design), and proper interpretation of results and conclusions (considering the potential for biases and proper recognition of associated uncertainties). To help bridge this gap, we provide a set of considerations and a checklist for researchers to guide them in conducting reliable and management-relevant

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J. W. Brownscombe (✉) · E. J. I. Lédée · V. M. Nguyen · S. J. Cooke  
Fish Ecology and Conservation Physiology Laboratory, Department of Biology and Institute of Environmental and Interdisciplinary Science, Carleton University, 1125 Colonel By Dr., Ottawa, ON K1S 5B6, Canada  
e-mail: jakebrownscombe@gmail.com

J. W. Brownscombe  
Department of Biology, Dalhousie University, 1355 Oxford Street, Halifax, NS B4H 4R2, Canada

G. D. Raby  
Great Lakes Institute for Environmental Research, University of Windsor, 2601 Union St., Windsor, ON N9B 3P4, Canada

D. P. Struthers  
Parks Canada, Banff National Park, Box 900, Banff, AB T1L 1K2, Canada

L. F. G. Gutowsky  
Aquatic Research and Monitoring Section, Ontario Ministry of Natural Resources and Forestry, Trent University, 2140 East Bank Drive, Peterborough, ON K9L 1Z8, Canada

N. Young  
Department of Sociology and Anthropology, University of Ottawa, Ottawa, ON K1N 6N5, Canada

M. J. W. Stokesbury  
Department of Biology, Acadia University, 33 Westwood Ave., Wolfville, NS B4P 2R6, Canada

C. M. Holbrook  
U.S. Geological Survey, Great Lakes Science Center, Hammond Bay Biological Station, 11188 Ray Rd., Millersburg, MI 49759, USA

T. O. Brenden  
Department of Fisheries and Wildlife, Michigan State University, East Lansing, MI 48824, USA

telemetry studies, and for managers to evaluate the reliability and relevance of telemetry studies so as to better integrate findings into management plans. These considerations include implicit assumptions, technical limitations, ethical and biological realities, analytical merits, and the relevance of study findings to decision-making processes.

**Keywords** Fishery management · Biotelemetry · Conservation · Uncertainty · Data interpretation

## Introduction

The availability of electronic tagging and tracking tools for the study of the ecology of wild fish has expanded dramatically during the last few decades. With present technologies, fish can be tracked in habitats ranging from small streams to oceans, and from polar to tropical regions. Although electronic tags were invented and first affixed to fish in the middle of the 20th century (reviewed in Hockersmith and Beeman 2012), it was not until the early 21st century that electronic tags moved from a niche technology to a routine part of modern fishery assessment and research (Cooke et al. 2013a, 2016a; Donaldson et al. 2014; Hussey et al. 2015). Many types of electronic tags exist, ranging from those that log data (i.e., biologgers; see Rutz and Hays 2009) to those that transmit data (i.e., telemetry). Here we focus on the latter—transmitters that use radio or acoustic propagation to transmit information to telemetry

receivers or to satellites (Mech 1983; Fancy et al. 1988; Cooke et al. 2004). Fish can be tracked manually by foot, from vehicles, from planes (for radio telemetry) or vessels, through use of autonomous fixed receivers, or remotely by satellites that continuously “listen” for tagged animals.

Tens to hundreds of thousands of transmitters (tags) are affixed to fish within projects around the globe every year (e.g., it is not uncommon for a single study in the Columbia River basin of the USA to involve 20,000 tagged salmon *Oncorhynchus* sp.). Because telemetry equipment is relatively expensive, studies that are poorly planned or lack clear research objectives and questions (i.e., studies that involve tagging animals simply for the sake of tagging) can result in a great deal of wasted effort and money as well as a burden on data bases (Kenward 2001; Koehn 2012). This problem is of particular concern in the conservation and management realm where financial resources are limited (McGowan et al. 2017). For the findings of a telemetry study to be reliable, numerous technical aspects must be considered such as whether the fish’s fate was accurately classified, the sample was representative of the population, and the data were appropriate for the research question. For telemetry studies to be impactful, their findings must be both relevant and interpretable by managers to integrate them into management plans (McGowan et al. 2017). To this end, many telemetry studies today are conducted by, or in partnership with government natural resource management agencies (e.g., Brooks et al. 2017a; Klimley et al. 2017). Telemetry can be used to answer questions that are superficially simple but have been traditionally difficult to address (e.g., what are the spatial–temporal distributions of populations, locations of key movement corridors, natural mortality rates?). For this reason, a growing number of examples exist in which telemetry has informed management and conservation of fish populations (Donaldson et al. 2014; Cooke et al. 2016a; Crossin et al. 2017; Brooks et al. 2018). Despite these successes, barriers still limit the application of telemetry findings to management and conservation in many instances. For example, social science studies revealed that managers of a Pacific salmon fishery on Canada’s west coast were sometimes unsure of how telemetry data could be harmonized with traditional data-collection methods and long-term databases (Young et al. 2016a). Concerns also exist about the

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C. S. Vandergoot  
U.S. Geological Survey, Great Lakes Science Center,  
Lake Erie Biological Station, 6100 Columbus Avenue,  
Sandusky, OH 44870, USA

K. J. Murchie · S. T. Kessel  
Daniel P. Haerther Center for Conservation and Research,  
John G. Shedd Aquarium, 1200 South Lake Shore Drive,  
Chicago, IL 60605, USA

K. Whoriskey · J. Mills Flemming  
Department of Mathematics and Statistics, Dalhousie  
University, Halifax, NS B3H 4R2, Canada

C. C. Krueger  
Department of Fisheries and Wildlife, Center for Systems  
Integration and Sustainability, Michigan State University,  
East Lansing, MI 48823, USA

ability of telemetry to answer management questions (McGowan et al. 2017), and the relevance and applicability of telemetry findings at management scales, which are often at the population, ecosystem, or landscape level (Nguyen et al. 2018). In addition, similar to other fisheries sampling methods, legitimate concerns exist about uncertainties and biases that can arise from analyses and conclusions from telemetry data.

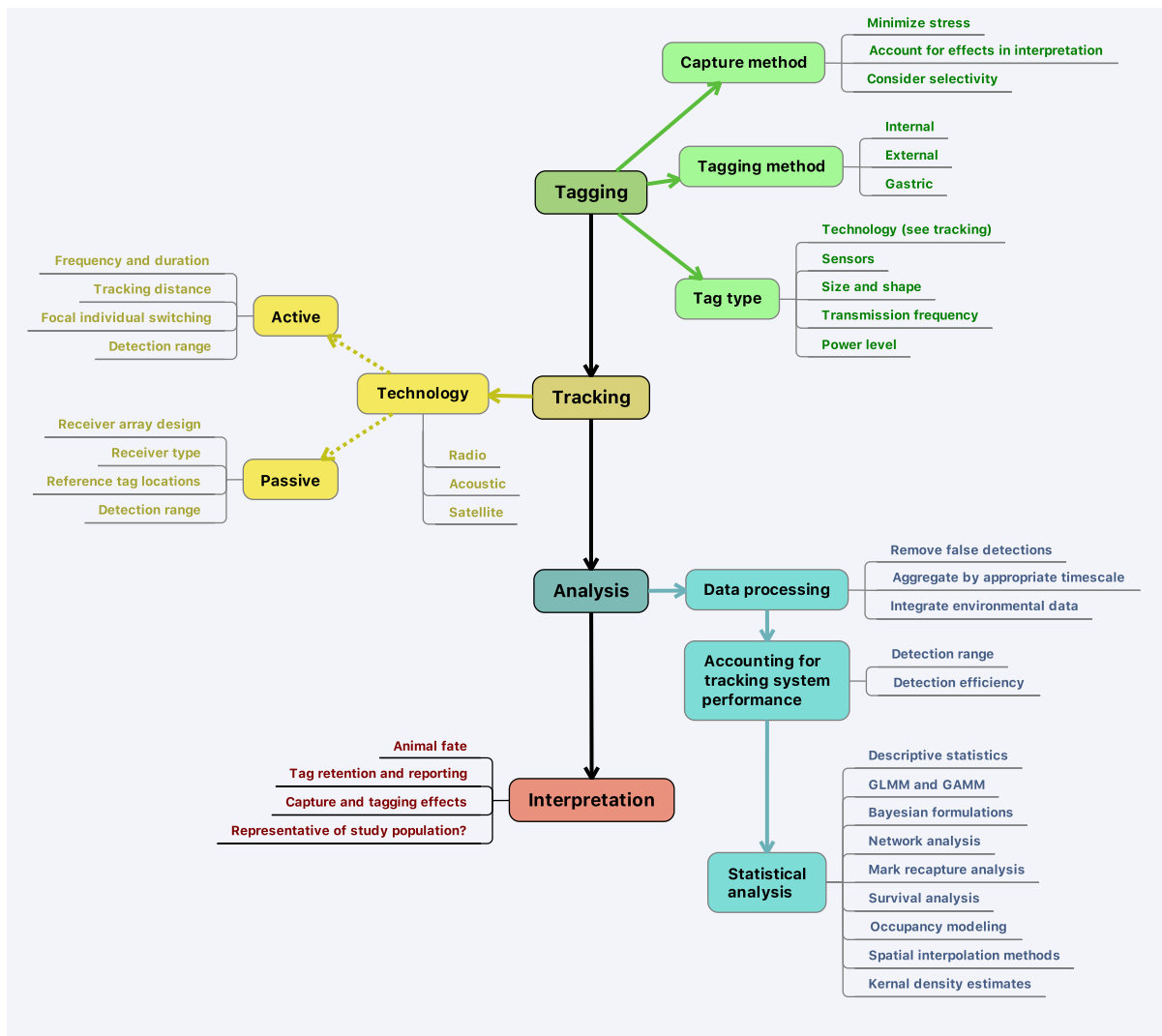
Although findings from biotelemetry studies have potential to be routinely applied to management and conservation issues, application requires (1) that researchers conducting telemetry studies consider aspects of study design, implementation, and analysis that maximize the likelihood that data generated will be of use to managers, and (2) that managers have a thorough understanding of telemetry technology (capabilities and limitations), its applicability to fisheries research and monitoring (study design), and the ability to properly interpret and use findings and conclusions. To help bridge this gap, we outline key considerations for implementing and interpreting telemetry studies that integrate technical limitations, implicit assumptions of tagging studies, ethical and biological realities, and analytic approaches. These considerations are organized under **Tagging, Tracking, Analysis, and Interpretation**, and are presented in a concept diagram (Fig. 1), as well as a checklist (Table 1). We focus on acoustic and radio telemetry (referred hereon as simply ‘telemetry’) because these are the technologies predominantly applied to quantify fish ecology, but we also glean insights from satellite telemetry studies when relevant to study design, analysis, and interpretation. Our aim is for these guidelines to also serve as a thorough primer for researchers and fishery managers with different levels of experience working with telemetry.

## Tagging

### Capture method

With diverse methods available for capturing fish for tagging in telemetry studies, consideration should be given to study objectives, capture efficacy, minimizing stress and injury to target and non-target organisms, as well as impacts on habitat integrity. Importantly, capture-related stressors can influence

the ability to address study objectives. For example, if short-term behaviour is of interest, methods that minimize fish stress and injury, such as rapid capture by angling or netting, may be the best approaches. Further, all fish capture methods have some level of selectivity in the fish they capture, related to fish species, size, morphology, behaviour, and physiology (Wardle 1986; Armstrong et al. 1990; MacLennan 1992), which is relevant for both designing and interpreting studies (see ***Were tagged fish representative of the study population?*** below). The efficacy of capture methods depends heavily on species and ecosystem characteristics. In shallow freshwater systems, electrofishing is often highly effective (Larimore 1961). Variables that influence capture efficiency with electrofishing are complex (Hense et al. 2010; Price and Peterson 2010), but generally this method is usually ineffective for fish species lacking a swim bladder, which do not float to the surface. Electrofishing can be used in estuaries (e.g., Lowe et al. 2009b), but is ineffective in marine environments because the conductivity of saltwater is greater than fish. With electrofishing, optimal settings should be used to minimize external or internal injuries, while also providing enough power to immobilize the fish for capture (Hollender and Carline 1994; Dalbey et al. 1996). Some species are also more sensitive to the effects of electrofishing than others (Snyder 2004). Trap, seine, or gill netting are effective capture methods in diverse aquatic ecosystems and across varied water depths (Hamley 1975; Hubert 1996). Optimal set times and mesh sizes are essential to ensure fish are captured effectively and experience minimal injuries and stress; an extensive body of literature exists that should provide insights into these choices (e.g., Hamley 1975; Hayes et al. 1996; Hubert 1996). In some cases, existing infrastructures such as weirs or fish counting fences can be used to capture fish for tagging. For less mobile species, hand netting is also a viable option in some cases (e.g., Akins et al. 2014). In situations where the above methods are not options, angling with rod and reel or longlines are often used with diverse gear configurations and bait types that can be optimized to minimize bycatch of non-target species and have minimal impacts on habitat integrity (Stoner 2004; Watson and Kerstetter 2006).



**Fig. 1** Concept diagram outlining the diverse considerations for implementing and interpreting telemetry studies

## Tag choice

Electronic tags are available with various types of technology, sensors, shapes, and sizes, all of which are important considerations in relation to species (see **Tag burden** below), ecosystem type, and study objectives. In shallow freshwater ecosystems (i.e., lakes and rivers < 8 m water depth), radio transmitters generally provide the greatest detection range, which enables optimal data collection by ensuring fish are detected when present (Lucas and Baras 2000). However, in deep freshwater systems and marine environments, acoustic transmitters perform better than radio transmitters (Cooke et al. 2004; Hussey

et al. 2015). Some tags also combine multiple technologies. For example, combined radio/acoustic transmitters are useful for studying fish movement through multiple ecosystems, from oceans or deep lakes into shallow rivers, as often occurs with migratory fish (Niezgoda et al. 1998). In large freshwater ecosystems (e.g., the Laurentian Great Lakes) and coastal marine ecosystems, many researchers are cooperatively maintaining large numbers of passive acoustic receivers, sharing animal detections through organized tracking networks, extending the potential for researchers to track fish movements over spatial and temporal scales previously impossible (see **Passive receiver arrays** for more details on these

**Table 1** To aid those interpreting results from a telemetry study we have generated a checklist for evaluating the extent to which a given proposal/study/report addresses issues that have the potential to influence the outcome and reliability of results. This checklist could also be used by researchers designing and executing telemetry studies such that the science that they generate will more likely be policy/management relevant. In

general, more checkmarks indicates a greater likelihood that the findings will be reliable. However, not all points are expected to have equal weighting. For example, if all aspects are considered yet the tag to body mass ratio is 25%, then all other points are not even worth consideration. Generally, a robust and telemetry study will have:

Telemetry study quality	Y/ N?
Consideration of tag burden in tag choice and specifications, study design, analysis and interpretation	
Clear description of the tagging methods used and their justification in the literature	
Computed pre-study simulations to inform optimal study design	
Clearly documented fish collection methods	
Completed a tagging validation study that examines the extent to which the presence of the tag and the tagging method influence behaviour and survival (or other relevant endpoints), or a reference was provided to a relevant validation study (noting the risks involved with using surrogates if applicable)	
A single tagger/surgeon or an analysis that controlled for the tagger/surgeon was used, along with a description of training/experience of the tagger(s)/surgeon(s)	
Provided reference to their animal care protocol (including number and institution)	
Tracking protocols (passive and/or active) that consider optimal design for detecting animals and addressing study questions	
Systematically filtered data to remove false detections	
Methods that account for variation in detection efficiency over space and time	
Methods that account for spatial and/or temporal autocorrelation in data and repeated measures of individuals	
Consideration of whether tagged fish are representative of the population	
Integration of managers and/or stakeholders in project planning	

networks). Importantly, to participate in these networks, specific technologies must be utilized to enable cooperative tracking efforts.

### Tag burden

An implicit assumption of most tagging studies (aside from those assessing tagging effects) is that transmitters do not significantly alter or impede behaviour, physiology, or survival of tagged individuals (Ross and McCormick 1981; Welch et al. 2007; Thompson et al. 2014). However, telemetry tags can constrain fish movement and incur energetic costs due to tag weight, size, shape, and attachment method. Ideally, for a telemetry study to be considered reliable, evidence should be available demonstrating that tags used do not impede the behaviour or survival of fish with similar characteristics (e.g., species, size range). Attaining comparative information from untagged fish in the wild is difficult but needed to determine whether or not tagged fish were impaired by telemetry

tags (e.g., behaved differently, grew slower, experienced higher mortality than untagged fish; Hellström et al. 2016; Hondorp et al. 2015). As such, precautionary measures must be applied to minimize burden (i.e., limiting tag size, volume, weight, and selecting a tag shape that conforms with fish locomotion) and evaluating endpoints (e.g., growth, incision healing, mortality; Cooke et al. 2011b) to reduce the risk of the tag affecting the fish.

One of the main considerations for tag burden is the tag weight relative to that of the fish (Jepsen et al. 2002; Brown et al. 2010). A 2% tag:fish-weight ratio (in water; hereafter 2% rule) is commonly used as the upper acceptable limit (Jepsen et al. 2002, 2005); however, lighter tags are generally preferred (Brown et al. 2010). The 2% rule may be a conservative or liberal measure depending on species or ontogeny of the study organism; this is an area of telemetry that is in need of further methodological study (Thiem et al. 2011). The 2% rule has been challenged by several researchers, and has been extensively evaluated for

juvenile salmonids (Jepsen et al. 2002). Research on the impacts of tag weight on the behaviour and survival of juvenile salmonids has considered buoyancy compensation (Perry et al. 2001), predation (Anglea et al. 2004), and movement rate for out-migrating smolts (Peake et al. 1997). In general, these studies have suggested that a 7–10% tag:fish-weight ratio is a more accurate threshold in this case. Ultimately, tag load should be selected according to species and ontogeny, and is a critical for evaluating the merits of research findings (Cooke et al. 2011b).

Tag burden is also influenced by tag placement, which can be internal, intragastric, or external. Internal tagging (typically in the coelomic cavity) causes little to no additional drag or tag biofouling issues, making it the ideal choice for most long-term tagging studies, but gastric insertion and external tagging are often used for shorter-term tagging studies due to their reduced short-term tagging effects compared to more invasive surgery required for internal implantation (Jepsen et al. 2002; Cooke et al. 2013a; Thorstad et al. 2013). Tag shape and volume should also be selected according to the body shape of the fish being tagged (Cooke et al. 2011b). For example, for fish with slender body shapes (i.e., anguilliform, compressiform), slenderer tags and those with less volume would be intuitively less likely to restrict movement. Because most fish rely on being hydrodynamically efficient, drag is a major consideration for external tags, which reduces swimming performance and increase energetic costs (Bridger and Booth 2003). External tags may also make tagged fish more visible and vulnerable to predators (Ross and McCormick 1981). Gastric insertion avoids issues associated with external tagging, but can cause perforations in the stomach and impede feeding (Keefer et al. 2004; Thorstad et al. 2013). Gastric insertion is therefore often the method of choice for migratory salmon studies because they cease feeding during this period (Thorstad et al. 2013).

#### Tag configuration and tracking reliability

Transmitters must be detected reliably by the tracking system in order for data to effectively address study objectives. Detection reliability is influenced by the interaction between transmitter specifications, tracking system design, and environmental conditions. Environmental parameters such as water temperature,

salinity, wind, anthropogenic noise, and flow turbulence can impede the detection efficiency of transmitters (See *Detection efficiency* below; Clements et al. 2005; Heupel et al. 2006; Cooke et al. 2013a; Stokesbury et al. 2016). For radio transmitters, water depth and salinity are key limiting variables for detection range (Thorstad et al. 2013).

Transmitter specifications can often be modified according to the environmental conditions and the biology of the species being investigated (How and De Lestang 2012). Generally, a trade-off exists amongst transmission delay (i.e., how often tagged fish may be potentially detected), power output (i.e., how far fish can be detected), and battery lifespan (i.e., how long can the fish be tracked). For example, tag transmission delay and life are critical for survival and migration studies that use gates or curtains of receivers to detect fish as they swim past. If the transmission delay is too long, then detections of a tagged fish could be missed by the receivers as they swim by (Melnichuk 2012). If too short, battery life can be expended and the tracking duration for individuals is limited unnecessarily. Fish movement speeds are therefore a key consideration for selecting tag transmission delays in such studies.

The type of telemetry technology being used is also relevant when selecting a transmission delay. With systems where transmitters function on unique wavelength frequencies (e.g., see Cooke et al. 2005b; Guzzo et al. 2018) many transmitters can be tracked by one receiver simultaneously. However, when all transmitters operate on the same frequency (e.g., Vemco VR2W acoustic receivers) and many tagged individuals are located in proximity to a receiver, code collisions cause detection failures and/or false detections (i.e., incorrect transmitter codes; See *Data pre-processing* below; Simpfendorfer et al. 2015). In the latter case, transmission delay should be selected based on the number of individuals being tagged and their projected residency patterns adjacent to acoustic receivers. In some cases, this may involve animals outside of the focal study that were tagged by other researchers working in the system.

Transmitters with integrated sensors can provide detailed ecological information on the species of interest, such as providing thermal selection, depth use, and locomotor activity (Wilson et al. 2015b). Sensor technology is continually advancing to improve the ability of investigators to understand ecological interactions. Integrated transmitting



sensors have some degree of observation error that causes imprecision in resulting data. For example, studies that require high precision depth data should consider field-calibrations of sensor tags beyond those provided by the manufacturer (e.g., Veilleux et al. 2016), particularly when working in conditions where extreme variation in environmental parameters (e.g., salinity, water temperature, flow rate) commonly occurs (e.g., estuaries, proximal to hydropower facilities). When interpreting results and conclusions from sensor data, managers should consider the accuracy and precision of sensors, and if they were used within an appropriate range of environmental conditions.

The method by which a transmitter is attached to a fish may influence its detectability by receivers. For example, coiling the antennae of radio tags in the fish's body can attenuate the transmission signal resulting in reduced detection range (Collins et al. 1999; Cooke and Bunt 2001). Internally-placed acoustic tags can also have a smaller detection range than externally-placed tags due to attenuation of the signal through the body (e.g., 2–sevenfold difference for red drum (*Sciaenops ocellatus*); Dance et al. 2016). However, the greater detectability of external transmitters may become compromised over time due to biofouling or damage from rubbing against structures in the aquatic environment (Jepsen et al. 2002). When attaching telemetry tags, researchers need to consider research objectives, fish morphology, and environmental conditions prior to determining the appropriate method of tag attachment to optimize tag detectability (Cooke and Bunt 2001).

### Tagging methods

Intracoelomic implantation is one of the most common approaches for tagging fish due to high tag retention rates (Bridger and Booth 2003; Brown et al. 2011), therefore most tagging guidelines focus on surgical procedures (e.g., Mulcahy 2011; Wargo Rub et al. 2014). However, best tagging practices have application to external or gastric tagging as well (Jepsen et al. 2015). A few methods for tagging fish without capture or handling exist that minimize effects from capture and handling, but they have specialized applications. For example, tags can be “hidden” in prey items and fed to fish. With Atlantic cod (*Gadus morhua*), this voluntary form of gastric tagging yielded longer durations of tag retention relative to fish that were

handled and had tags forced down their esophagus by the research team (Winger and Walsh 2001). For some projects, external tags may be attached to free-swimming fish using a tagging pole—this approach has been used for acoustic transmitters (Klimley et al. 1988; Stokesbury et al. 2005) and Pop-up Satellite Archival Tags (PSATs; Stokesbury et al. 2005) in marine systems. Aside from these specialized applications, in the majority of cases fish need to be captured and immobilized for tagging. Key considerations for choosing a method to immobilize fish should include animal care, logistics, and safety to the fish, tagger, and the public. Immobilization can be achieved through forced restraint, finess (e.g., tonic immobility), or chemical or electrical sedation. The immobilization method used should reflect the biology of the fish, study objectives, and tag to be used. Fish that reside in cool waters may take hours to metabolize anesthetics such that use of chemical anesthetics may be a poor choice. If the core research question focuses on the short-term behavioural consequences of a catch-and-release angling event, then anesthetic would likely affect post-release behaviour and confound study findings (Cooke et al. 2013b). Some fish species (based on their biology/morphology/anatomy) can be easily restrained such that use of sedatives would not be necessary for external or gastric tagging. For sharks and some other taxa (e.g., sturgeon), tonic immobility (a temporary state of motor inhibition) can be achieved by placing fish in a supine position (Kohler and Turner 2001; Kessel and Hussey 2015). Yet, in other cases, sedatives are needed for surgical implantation.

Considering the variety of ways to sedate a fish, consultation with regulatory agencies (often human health agencies) is important prior to adopting a particular sedation method. In general, sedatives work by either depressing (most chemicals) or overwhelming (electro-sedation methods) the central nervous system (Ross and Ross 2009; Vandergoot et al. 2011). Efforts to identify and develop a zero-withdrawal chemical sedative—one where no residue remains (Trushenski et al. 2013) are gaining momentum. Sometimes, an assumption is made that all fish need to be sedated for tagging no matter the technique or species. However, sedation itself can be stressful (Cooke et al. 2016b), and there is ongoing debate about whether fish have the capacity to feel pain (Rose et al. 2014). For most external and gastric tagging

methods, fish can be adequately restrained in a flow-through water-filled trough (see Cooke et al. 2005a,b for details). Fish should not be tagged in air whenever possible (whether sedated or not) and if a fish is sedated, it is important to ensure that the fish are vigorous prior to release in increase the probability of survival. Another consideration is whether to use other pharmaceuticals such as analgesics for “pain” relief, or antibiotics to reduce infections. Currently, these pharmaceuticals are generally not recommended for tagging studies because the pharmacokinetics of analgesics are not fully understood (Cooke et al. 2016). Releasing a fish that has had antibiotic treatment is also undesirable because antibiotics have the potential to kill essential helpful bacteria (e.g., those that reside on the surface of the fish and in the gut), which could influence their later condition and fate in wild fish (Mulcahy 2011). Overall, only in exceptional circumstances should analgesics and antibiotics be used and if so, their use should be adequately justified (not simply that the animal care committee demanded it).

The success of tagging procedures depends on the skill of the surgeon. The surgeon must be familiar with fish anatomy so as not to cut vital tissue and minimize the amount of tissue damage and surgery times (Murray 2002). Thus, surgeons need to be adequately trained and well-practiced (Mulcahy 2011; Wargo Rub et al. 2014). Cooke and Wagner (2004) provided a clear example of performance differences in novice and expert surgeons, with experts having greater fish survival, greater suture retention, and increased speed of the various aspects of the fish surgery practice. Training should involve a combination of lectures and hands-on practice with an experienced surgeon and veterinarian (Cooke et al. 2011a). Vagaries of field surgeries are best handled by experienced personnel (Fiorello et al. 2016).

Providing the surgeon with a quality portable surgical set-up in the field, with strategically placed holding and recovery tanks, table, and lighting is highly beneficial for successful tagging and fish survival. Surgeries may be conducted in a variety of locales ranging from a boat, to on shore or the back of a truck; regardless of surgery locale, stability and good lighting are key for fish and tagger well-being (Brown et al. 2010; Cooke et al. 2011a). Proper ergonomics of the surgical set-up will also reduce fatigue in the surgeon (Fiorello et al. 2016).

The use of aseptic techniques should be considered when designing the surgical set-up. Surprisingly, the Animal Welfare Act in the United States does not include aseptic surgery techniques on fish (Walker et al. 2014). Maintaining asepsis in an aquatic environment can be challenging (Wargo Rub et al. 2014) because aquatic environments are not pathogen free (Walker et al. 2014). However, most institutional animal care and use committees require that fish surgeries be as aseptic as possible (Walker et al. 2014). Wagner et al. (2011) encouraged the adoption of as many sterile practices as possible within the limitations of the environmental conditions and study species. Nickum et al. (2004) suggested using all precautionary methods available to help minimize bacterial contamination of the incision and body cavity. As outlined by Cooke et al. (2013b) aseptic surgical techniques require further research, and we encourage fishery managers and biologists to keep up to date on best practices. Comprehensive reviews of considerations for surgical implantation of electronic tags are available (e.g., Wargo Rub et al. 2014).

To perform surgical implantation of electronic tags in fish, surgical tools are required (e.g., scalpels, forceps, needle holders, and suture material; Wargo Rub et al. 2014). Because of the diversity of options within each of these types of surgical tools, researchers can choose tools that match the size of the fish. Intuitively, Brown et al. (2010) suggested small scalpel blades be used for small fish (e.g., microblades) and large blades (e.g., size 10 or the smaller 15) for large fish with thick body walls. Needle holders with built in scissors reduce the need for additional tools and increase the ease at which sutures are trimmed. Choosing high-grade materials such as carbon steel tools allows for a variety of sterilization techniques (Cooke et al. 2011a). Suturing material is recommended for closing incisions in fish, as opposed to surgical staples or surgical adhesives (see Petering and Johnson 1991; Lowartz et al. 1999; Mulcahy 2003). When choosing suture material, absorbable monofilament (PDS-II) has been shown to produce the least inflammation and the fastest healing (Gilliland 1994; Hurty et al. 2002). Needle size and diameter of suture material should take into consideration the size of the fish in an effort to minimize the hole left in the fish’s integument. Brown et al. (2010) recommended needles with a curvature of three-eighths of a circle be used as they required less hand movement during



suturing, and also suggest reverse-cutting needles or tapered needles to minimize tissue damage.

Specifics of the surgical procedures to be used (i.e., where to place the incision) are best evaluated on a species-by-species basis (Helfman et al. 2009). In general, a good rule of thumb is laying the transmitter on the ventral side of the fish to visualize where it will fit the best (see review by Wagner et al. 2011). Best tagging procedures and guidelines have been mostly developed with juvenile salmonids (e.g., Brown et al. 2010; Wagner et al. 2011; Deters et al. 2012). However, fish with other body forms also have been evaluated such as flatfishes (Loher and Rensmeyer 2011) and anguilliformes (Thorstad et al. 2013). Just as fish are a diverse taxon, the habitats they live in are also diverse, and best tagging practices can be habitat-specific (e.g., Murchie et al. 2012 outline considerations in tropical marine habitats). Most studies examining tagging effects of intracoelomic implantation have focused on freshwater species and typically in laboratories (Cooke et al. 2011b). Regardless of the species or location, all tagging methodologies must be clearly reported so that comparisons among studies can be made (Brown et al. 2010; Wagner et al. 2011; Thiem et al. 2011).

## Tracking

To detect the position of tagged fish over time, tracking protocols are generally categorized into either active (i.e., researchers following fish with a mobile receiver), or passive (i.e., placing receivers in the environment in set locations). Both have advantages and disadvantages, with specific applications depending on research questions and the study environment.

### Active tracking

Active tracking typically involves the researcher using a mobile receiver to follow tagged fish. The three major advantages to this technique are (1) the high rate at which animal positions can be determined (e.g., by following an animal equipped with tag transmitting every 3–5 s), (2) position estimates of the animal are not limited to areas in range of fixed receiver stations, meaning the animal can (theoretically) be tracked wherever it goes, and (3) relatively precise animal positions can be obtained. However, manual tracking

is labour intensive and restricts the sample size of any study compared to a passive tracking system because (1) typically, only one animal can be tracked at a time, and (2) the duration which animals can be tracked is usually limited to hours, days, or intermittent surveys (e.g., monthly) of a closed study area or transects of interest. The length of time that fish can be manually tracked depends on the movements of the fish and the size of the system. Ogura and Ishida (1992) manually tracked four coho salmon (*Oncorhynchus kisutch*) on the high seas with pressure-sensor acoustic transmitters, one fish at a time, beginning immediately after capture, tagging, and release, and for an average of 54 h each. This approach provided useful insight into the swimming depths and speeds of salmon in the open ocean, where no acoustic receiver coverage exists even today (i.e., far from any coastline, in international waters). Colotelo et al. (2013) spent weeks acquiring daily position estimates for radio-tagged northern pike (*Esox lucius*) in a small lake in Ontario, Canada, in an effort to assess survival of fish after being incidentally caught in commercial fishing nets. That effort was labour-intensive, resulted in a maximum of one position estimate per day per fish, and was only feasible because the fish were confined to a small area (787 ha). Similarly, Hightower et al. (2001) surveyed an entire reservoir (Virginia/North Carolina, USA) by boat every 4 weeks for ~ 2 years in an attempt to locate 51 striped bass equipped with acoustic transmitters to assess long-term survival. These examples illustrate that manual tracking may be the best (or only) option available in some instances and can, in some cases, provide information of interest to fishery managers. However, if tracking is only conducted short-term, such studies may be making inferences about fish behaviour while the animal is recovering from the acute stress of capture and tagging.

Although active tracking methods are labour intensive, novel mobile tracking techniques have been developed that use unoccupied vessels for acoustic receivers, which can be drifted with water currents in oceans or rivers, or autonomous rovers traverse programmed paths (Eiler et al. 2013; Holbrook et al. 2016; White et al. 2016). Another option is to affix receivers to large animals in the wild, with the added potential to explore ecological interactions between animals equipped with transmitters and those carrying the receivers (Hayes et al. 2013). These mobile receiver approaches are often used in situations where

sufficient stationary receiver coverage is not possible, such as large systems like the open ocean. In contrast, passive tracking enables much larger sample sizes both in terms of the number of animals (e.g., hundreds at a time), the duration for which each animal can be tracked (up to 10 years depending on the tag type), which in general makes it better-suited to informing fishery management than active tracking.

As noted above, one of the advantages to active tracking of individual animals is that more precise positions can sometimes be made than using stationary receivers that merely report the animal is within range of a receiver's omnidirectional hydrophone (in a dynamic range; see *Detection efficiency* below). In some instances, supplementing passive tracking with occasional, more precise position estimates by mobile tracking could provide useful information in a study relevant to fisheries management, such as confirming mortality events (i.e., whether a fish is still moving around). When the goal is to make precise position estimates for a tagged fish using a directional hydrophone, the relationship between signal strength and detection range (distance between transmitter and receiver) must first be established. Accuracies of up to 34 m have been reported when using 3–7 bearings to triangulate the position of an acoustic tag using a Vemco VR100 mobile receiver and a moored acoustic tag (Taylor and Litvak 2015), but to be accurate, this approach requires that the transmitter remains stationary during all detections that contribute to the position estimate (Schmutz and White 1990). Meckley et al. (2014) estimated that the precision of fish position estimates ranged from 50 to 180 m depending on distance between a directional hydrophone and tag when just direction and signal strength from a single point was used to estimate the location of a tagged fish with a Vemco VR100 receiver. Determining the bearing from receiver to transmitter can be time-limiting with coded acoustic transmitters that have relatively long intervals between transmissions (e.g., 1 min or longer). The direction, signal strength, and gain control can be used to position a boat over a non-moving tagged fish, yielding precisions of 10–30 m (Bassett and Montgomery 2011; Wall and Blanchfield 2012; Herrala et al. 2014). Perhaps the most precise positions with a mobile system can be obtained using hyperbolic positioning from time-difference-of-arrival on a single mobile receiver towed around a stationary tag (Nielsen et al. 2012). In addition, while

tracking animals by boat, a sonde can be lowered to varying depths in the vicinity of the animal to gain detailed insight into the animal's 'selection' of environmental properties (e.g., Cartamil and Lowe 2004). While following an animal closely and deploying sensors near its position provide precise data, it is also important to keep a sufficient distance from the animal to avoid disturbing natural behavior. Regardless of specific methods used or scale of inference, spatial precision and efficiency should be estimated in situ and estimates should be accompanied by measures of uncertainty (e.g., standard error, confidence interval). Quantifying spatial uncertainty in telemetry-derived locations remains a primary challenge and an area of important future development.

#### Passive receiver arrays

Telemetry receivers are imperfect sampling instruments that can be thought of in the traditional capture-mark-recapture framework that is often used in fisheries science, whereby the receivers are more analogous to continuously operating camera traps than to fishery survey gears normally used for mark-recapture studies with fishes. Fishery survey gears are inherently limited spatially and temporally compared to acoustic telemetry receivers—no fishery agency has the capacity to conduct fishery surveys in all areas of a water body and on every day of the year. In contrast, telemetry receivers can listen for tagged animals year-round in most aquatic habitats. To accomplish this effectively, consideration of how recapture effort (i.e., placement of acoustic receivers) is allocated across space and time is necessary, along with how well each receiver performs in terms of recapture (detection) efficiency (see *Detection efficiency* below). A well-designed telemetry receiver network may provide not only information about fish locations at the time of detection, but also allow inference of past locations or state of tagged fish (at temporal and spatial scales that are relevant to the questions of interest) between detections by interpolating animal movement paths or space use between detections (Heupel et al. 2006). The best allocation of receiver effort across space and time is one that helps to minimize the number of assumptions underlying conclusions drawn.

Heupel et al. (2006) recognized two common designs for arrays of stationary acoustic telemetry receivers. First, grids of receivers are commonly

deployed to examine space use and home range sizes of aquatic animals, and second, ‘gates’ (also sometimes called ‘lines’ or ‘curtains’) of receivers are useful for questions related to movements to and from areas of interest. A third (not mutually exclusive) strategy involves setting receivers in positions of interest (e.g., spawning areas) to examine connectivity between key locations, habitat types, or management zones. Positioning systems with overlapping receiver detection ranges can also offer insights into fish movements at finer spatial scales (e.g., Cooke et al. 2005b; Espinoza et al. 2011). Regardless of design, the key take-home message for researchers and managers is that the potential biases of a given receiver deployment design should be carefully considered when designing and interpreting telemetry studies. For example, having greater receiver coverage in one habitat than in another can bias sampling effort and study results, if not carefully considered. To this end, considering variability in detection efficiency and range is also important, especially for certain types of research questions (see *Detection efficiency* below). Radio telemetry arrays are similar in some ways to acoustic telemetry arrays when applied to studying bird movement (Taylor et al. 2017) but when studying fish movement (in freshwater), radio telemetry arrays are usually established as ‘gates’, with placement of receivers at key areas, or at regular intervals (e.g., along a river) in an area of interest. Because radio receiver stations have to be set up on shore, array configurations resembling grids are typically not possible. Because the large majority of fish telemetry studies now use acoustic telemetry, the rest of this section is written with acoustic telemetry in mind.

At present, the highest achievable spatial precision with acoustic telemetry (sub-meter accuracy) can be obtained using closely-spaced stationary receivers with overlapping detection ranges and a positioning algorithm that triangulates the position of the fish based on multiple receivers receiving the same tag transmission (O’Dor et al. 1998; Klimley et al. 2001; Niezgodna et al. 2002; Espinoza et al. 2011; McLean et al. 2014). Although methods for estimating spatial precision differ among manufacturers and equipment models (Ehrenberg and Steig 2002; Smith 2013), spatial precision can vary within the study area (e.g., due to receiver geometry, accuracy of receiver locations; Bergé et al. 2012; Meckley et al. 2014) and over time (e.g., due to variation in variables that influence

detection efficiency such as water temperature; Steel et al. 2014; Binder et al. 2016a, b). In situ testing can be incorporated to estimate spatial precision (1) at specific locations over the length of the study (e.g., using stationary test tags) and (2) throughout the study area at a specific time (e.g., using mobile test tags). In either case, precision can be estimated by summarizing the differences between “true” test tag locations and estimated test tag locations (derived from receiver detections). “True” test tag locations with sub-meter precision can be obtained by using a survey-grade GPS antenna placed directly over a test tag during such tests. For mobile tests, synchronization of telemetry receiver clocks to GPS clocks may also be needed to match each estimated tag location to the true tag location at that time. High-precision positional systems can offer impressive insights into fish ecology and behavior, but have been limited to relatively small areas (the largest ever such system based on the literature was  $\sim 30 \text{ km}^2$ ; Binder et al. 2016a, b).

Rather than using high-precision positional systems, most telemetry studies use coarser position estimates based on networks of acoustic receivers *without* overlapping detection radii, with the goal of capturing patterns of habitat use or broad-scale movements (i.e., tens to thousands of kilometers). Receivers are often arranged in lines to serve as gates to detect movement between discrete areas of interest (e.g., fishery management zones, marine protected areas). Such a setup, with a double-layered receiver line that indicates whether the line has actually been crossed (and in what direction), can be useful if fishery managers want to know with a high degree of certainty whether animals cross an important boundary (Hussey et al. 2017). Statistical approaches for estimating detection efficiency from receiver lines are well-developed (Skalski et al. 2002; Perry et al. 2012) and can enable unbiased estimation of movement and survival with minimal assumptions (Hayden et al. 2014, 2016). In both fine- and broad-scale spatial positioning systems, detection range is often variable spatially and temporally (Kessel et al. 2014; Hayden et al. 2016). Although estimates of detection range are often useful for designing telemetry receiver networks, detection range does not always need to be estimated or reported (e.g., for positional systems or when only efficiency is estimated with gates). However, when detection range is needed to determine if conclusions were supported by the data, it should be

reported for the full range of conditions present during the study.

Deploying acoustic receivers in grids can help better answer a greater variety of research questions than what is possible when receivers are arranged in lines. With grid arrays it is possible to estimate rates of movement between key areas of interest, which is typically also the main goal of having receivers set up in lines. Grid designs are powerful because they involve distributing receivers across the study area in an unbiased way, providing proportionally representative coverage of different areas. Such a system can reveal surprising movement patterns or important habitats or help to confirm prior expectations about an area *not* being important habitat, as opposed to only deploying receivers in areas where the researcher *a priori* expects tagged animals to go—an approach that is likely to yield biased answers to most research questions. In an important simulation study (with associated R scripts that can be adapted for different systems), Kraus et al. (2018) assessed the performance of grid arrays at describing fish movement tracks based on different numbers of receivers (different spacing between receivers) and different detection efficiencies and ranges for the receivers. Their study revealed that even with a widely spaced receiver grid (25 km spacing), reasonably representative tracks of animal movements across Lake Erie (North America) could be generated for wide-ranging animals moving across the whole system. This led to an acoustic receiver network in Lake Erie being reconfigured from receiver lines initially set up to assess movement between fishery management boundaries to a whole-lake receiver grid. Further work in that system using data from real fish movements will be useful for clarifying the costs and benefits of grids vs. lines as strategies for setting up an acoustic receiver network.

When working in large, interconnected ecosystems (i.e., large lakes or oceans), a major advantage of using acoustic telemetry is the ability to access large-scale tracking networks, which enable researchers to collaborate and share animal detections when they move between receiver arrays operated by different research teams. At the highest level of organization, the Ocean Tracking Network (OTN; [oceantrackingnetwork.org](http://oceantrackingnetwork.org)) is a global network that provides significant resources for data sharing, management, analysis, project planning, and acoustic receivers for animal tracking. Examples of more regional scale tracking networks,

many of which are partners of OTN, are the U.S. Animal Telemetry Network ([atn.ioos.us](http://atn.ioos.us)), the Great Lakes Acoustic Telemetry Observation System (GLATOS; [glatos.glos.us](http://glatos.glos.us); Krueger et al. 2018), the Integrated Marine Observation System (IMOS; [imos.org.au](http://imos.org.au)), and the Acoustic Tracking Array Platform (ATAP; [saiab.ac.za/atap.htm](http://saiab.ac.za/atap.htm)). Researchers participating in these networks must adhere to network-specific guidelines related to data sharing and project implementation to ensure secure and fair collaboration occurs. Importantly, these networks all use specific types of acoustic receivers and transmitters that enable cross-compatibility.

### Detection efficiency

For the transmission signal from a telemetry tag to be detected by a receiver, the signal must propagate through the water (and sometimes air) between the two devices. Various environmental conditions can disrupt effective transmission, most commonly physical obstructions such as benthic structures, as well as environmental noise commonly caused by wind, currents, aquatic organisms, or human activities (Gjelland and Hedger 2013; Kessel et al. 2014). Further, when multiple transmitters operating at the same frequency are within range of a receiver, signal collisions can occur (depends on coding scheme of the technology). For some telemetry systems, there is a period after a transmission is detected where reception is blocked out to increase the probability of effective reception of the original signal. Due to all of these variables, both detection range (i.e., the distance from the receiver that transmitters can be detected), and efficiency within that range can vary greatly across space and time (reviewed in Kessel et al. 2014). The result is a dynamic, three-dimensional ‘detection envelope’ that represents absolute receiver detection efficiency (*DE*). Typically, fixed or towed tag detection data show a high proportion of transmission detections near the receiver, which decreases with increasing distance between the tag and receiver (Kessel et al. 2014). However, patterns in detection efficiency within the detection range can be variable, likely due to spatial variations in localized obstructions and/or environmental noise. For example, Kessel et al. (2015) found that calm water and hard surfaces caused signal echos, interfering with transmissions in close proximity to receivers and impacting detection

efficiency. Similarly, Loher et al. (2017) also show varied patterns in detection efficiency with distance from receivers. While absolute  $DE$  is challenging to quantify, some relative measure of receiver performance is often essential to filter out the telemetry system performance and reveal true patterns in fish ecology. For example, failing to account for  $DE$  can lead to inaccurate estimates of survival rates, movement rates, site-fidelity, habitat use, and temporal patterns in space use (Payne et al. 2010; Kessel et al. 2014).

The importance of variations in  $DE$  and necessary approaches to quantifying it depend on study objectives. Melnychuk (2012) recognized four main types of  $DE$  related to study objectives, these are the probability of detecting: (1) individual tag transmissions ( $DE_{\text{single}}$ ); (2) tagged animals residing in a given area ( $DE_{\text{res}}$ ); (3) tagged animals moving past a specific location ( $DE_{\text{mig}}$ ); and (4) tagged animals being present during a mobile survey ( $DE_{\text{mobile}}$ ). Regardless of the study goal, assessments of receiver detection ranges (i.e., the proportion of known transmissions that were detected from transmitters set at a series of fixed distances from the receiver) should ideally be conducted at the start of a tracking study to inform passive array design or active tracking protocols. For example, when studies use receiver ‘gates’ (or ‘lines’ of receivers), knowledge of the detection range of each receiver can help to ensure overlap occurs between adjacent receivers, such that all (or most) animals are detected moving through the gate (Heupel et al. 2006; Welch et al. 2008). By positioning receivers along migratory routes, commonly as lines or single receivers at migratory pathway constrictions (choke points), migration and survival rates can be estimated between the lines or choke points (Heupel and Webber 2012; Perry et al. 2012). In these studies, assessing  $DE_{\text{mig}}$  is an essential component of data analysis (Melnychuk 2012), and can be estimated using the conditional nature of movement throughout the system (Skalski et al. 1998; Perry et al. 2012) or through detection range testing. Understanding how detection ranges are influenced by environmental conditions can also inform optimal receiver locations ensuring some minimum level of  $DE$  (Welch et al. 2012).

When study objectives relate to temporal dynamics of fish movement and space use, more extensive monitoring of  $DE$  is necessary. In passive arrays of receivers,  $DE_{\text{single}}$  can be quantified using reference

tags placed in strategic locations within the receiver array (e.g., Payne et al. 2010). Measures of receiver  $DE$  can be integrated directly into some statistical analyses (e.g., Winton et al. 2018). When longer term residency is of interest rather than individual detections (e.g. Lowe et al. 2009a),  $DE_{\text{res}}$  should to be assessed. If  $DE_{\text{res}}$  is low, the assumption that the animal is present could be inaccurate due to an increased probability the animal was elsewhere and returned but appeared to have been continuously in the study area based on intermittent detections in the area.  $DE_{\text{res}}$  can be assessed through systematically placing stationary tags at given locations or moving tags through the system. The greater the number of receivers, the higher  $DE_{\text{res}}$  will be, and well-designed receiver placements can result in nearly 100%  $DE_{\text{res}}$  for a given area (Heupel and Simpfendorfer 2002).  $DE_{\text{mobile}}$  should be assessed when mobile receivers are used to conduct surveys, either independently or in combination with a stationary receiver array, particularly when the studies aim to estimate the number of tags present in a defined area. In addition to variables that influence stationary receiver detection ranges, mobile receivers are influenced by boat speed and associated engine noise (assuming mobile surveys are carried out by boat; the typical method in most environments).

## Analysis

For any telemetry study, accounting for system performance, data processing and statistical analyses are necessary to translate detections/locations into a form that readily addresses a study’s specific research questions. The measurement of spatial precision and accuracy, sampling intervals, and types of analyses employed may strongly influence interpretations of tracking data. Further, relevant data may be derived from diverse sources with varied levels of spatial and temporal availability, accuracy, and precision. Establishing standardized protocols for data reporting, integration, and analysis ensures the highest level of data utility. This is particularly important as large datasets are amassing through integrated tracking networks, which enable exploration of broader scale research questions (Gazit et al. 2013). For example, Hoenner et al. (2018) outline a standardized approach to integrate animal detections, environmental data,



and tagged fish characteristics with a quality control protocol using data from the IMOS network, which interfaces with a set of analytical tools (Udyawer et al. 2018). The OTN and GLATOS networks also have similar standardized data management protocols and associated analytical tools (Binder et al. 2017). Regardless of whether a research project is integrated into a tracking network, the standardized data collection and management protocols developed and applied by these networks should be used as a reference, ensuring optimal data are generated for study objectives, and that the data can be potentially integrated into broader tracking data sets for potential future applications.

#### Data pre-processing

Accounting for data precision relative to spatial and temporal scales of movement is crucial in animal movement studies (Bradshaw et al. 2007; Schick et al. 2008); therefore data processing including data filtering (i.e., to reduce detection and spatial accuracy errors) and data interpolating (i.e., to reduce irregular sampling interval) is often required to obtain more accurate and interpretable telemetry data (Tremblay 2006; Bradshaw et al. 2007; Simpfendorfer et al. 2015). When transmissions are being sent out and recorded by a listening device, some level of transmission error will occur (Pincock 2012) leading to false-positive tag detections, or “ghosts in the data” in acoustic telemetry (Simpfendorfer et al. 2015). The potential for, and types of false detections depend on the type of technology used, and relevant literature and manufacturer recommendations should be considered when exploring the presence of false detections in a telemetry system. For example, with Vemco acoustic receivers, false detections occur when ambient noise or transmissions from multiple fish collide to produce either an unknown ID code (type A) or a known ID code of a tagged fish (type B) (Simpfendorfer et al. 2015). Type A codes are easy to distinguish in large databases, as the tag ID code is erroneous compared to the transmitters placed on the tagged fish. Type B codes are more difficult to identify and can be incorrectly included in the data used for analyses unless appropriate data filtering and/or analytical techniques are applied.

Well-established protocols provide means to filter erroneous tag detections from acoustic telemetry data

(Beeman and Perry 2012; Pincock 2012). Filtering protocols often focus on the realism of movement distances and speeds combined (e.g., Heupel et al. 2010). The frequency and timing of detections are often used as well, where multiple detections of an individual must occur within a given time window (Gutowsky et al. 2013; Lee et al. 2015). Pincock (2012) recommended that at least one short interval between detections (relative to tag transmission delay), and that more short than long intervals occur for the detections to be considered legitimate. With fine-scale positioning systems (e.g., Vemco Positioning System, Lotek MAP) each position has an associated value of positioning error. Smith (2013) describe a protocol for filtering out high-error positions. The level of error tolerated should depend on the spatial scale of interest; for example, Brownscombe et al. (2019) selected a level of error that ensured a high probability that fish positions would be assigned to the correct habitat type based on habitat patch size.

A major high-level goal of telemetry research is to understand the drivers of animal movement, including intrinsic (e.g., ontogeny, sex, physiological state) and extrinsic (e.g., light, temperature) factors (Nathan et al. 2008; Hussey et al. 2015). The mechanics underlying ecological phenomena are highly relevant to management decisions, especially when faced with uncertainty about the future state of an ecological system (Crossin et al. 2017). In order to elucidate the drivers of animal movement with telemetry, the derived animal movement data must often be combined with environmental sensor data from diverse sources, which may have been collected at different intervals, timescales or levels of precision. At this stage, careful consideration should be made of the appropriate data timescale required to address research questions, and whether the data fit, or can be aggregated or interpolated to this scale. In some cases, telemetry data are not well suited to answer certain research questions. A simple example of this is that broad scale telemetry (i.e., passive tracking with stationary omnidirectional hydrophones) is rarely applicable to fine-scale habitat use; fine-scale positioning systems are much better at addressing these questions.

The choice of sampling intervals is often defined by data (i.e., telemetry or environmental) availability rather than by biological or environmental processes (Johnson et al. 2017; Bastille-Rousseau et al. 2018;



Bruneel et al. 2018). Broad-scale telemetry records animal locations within the range of receivers, providing coarse-scale, discontinuous animal position records. If space use metrics such as utilization distributions or home range are of interest, broad-scale telemetry data must be converted to a suitable format for analysis using interpolation techniques such as correlated random walks (Johnson et al. 2008) or spatial weighted averaging approaches such as centers of activity (Simpfendorfer et al. 2002). These techniques require a number of important assumptions, can incur errors in location estimates, and may not be applicable to all types of telemetry data (Pace 2001; Hedger et al. 2008). Spatial interpolation is not always necessary; for example, network analysis is well-studied to address diverse study questions with broad-scale telemetry data (Cumming et al. 2010; Finn et al. 2014; Lédée et al. 2015).

In some cases, environmental sensors (e.g., weather stations) can have larger sampling intervals (e.g. every 10 min or every day) compared to that of the tracking system, which could be as low as 1 s (Tremblay 2006; Hussey et al. 2015; Bruneel et al. 2018). Therefore, tracking and environmental data are often reconciled before analysis; resulting in the reduction of animal movement resolution (Hebblewhite and Haydon 2010). However, certain analytical techniques (e.g., Gaussian random fields; Abrahamsen 1997) can handle this discrepancy statistically. Overall, finding the right balance between choosing an appropriate sampling interval, accessing/obtaining high resolution environmental data while minimising loss of animal movement information and study costs are important considerations when designing a telemetry study.

#### Accounting for system performance

A discussion of the various considerations and methods for measuring system performance is included above in *Detection efficiency*. Error estimates can be integrated into telemetry analysis in various ways, either through pre-processing the data to correct the position estimates prior to applying further statistical techniques (e.g., Payne et al. 2010) or by integrating estimates of error directly into models of fish movement (e.g., state-space modeling; Martins et al. 2013a).

#### Statistical analyses

Various types of data are generated by telemetry, from presence/absence at specific locations to individual continuous time-series locations, which vary in accuracy and sampling interval. Statistical analyses and/or modelling are necessary to translate telemetry data into a form that readily addresses a study's specific research questions. Given the diversity of research questions that can be addressed through telemetry a wide variety of statistical approaches can be used. Telemetry data, along with associated biological and/or environmental data and appropriate statistical approaches all have various assumptions and limitations that need careful consideration before use.

Telemetry data typically violate the assumption of independence; therefore, statistical approaches must have the ability to handle non-independent data (Cumming et al. 2010; Jacoby et al. 2012; Roberts et al. 2017). The lack of independence between successive observations in telemetry data or in the derived behavior or fates of tagged fish can give rise to pseudo-replication if treated as independent observations in analyses (Hurlbert 1984; Roberts et al. 2017). Failing to account for pseudo-replication can lead to incorrect conclusions in hypothesis testing frameworks as well as misinformed interpretations of the data. Multiple approaches exist for dealing with pseudo-replication. Including only a subset of location data in analyses is an option, but this is tantamount to throwing away collected data. Alternatively, many analyses (e.g., generalized linear or additive mixed effects models, Bayesian inferential approaches) can be performed where individuals are treated as fixed or random effects to account for observations being made on the same fish over time (Bolker et al. 2009; Zuur et al. 2009). Network analysis has randomisation tests, which must be performed prior to analysing data or included in theoretical concepts (such as network modelling, Exponential Random Graph Models and Multiple Regression Quadratic Assignment Procedures), to compensate for violation of the independence assumption (Cumming et al. 2010).

Telemetry data tend to be correlated in time and space (Boyce et al. 2010; Cagnacci et al. 2010; Frair et al. 2010; Roberts et al. 2017), including patterns that, if unaccounted for, can cause model assumptions to be violated (reviewed in Dormann et al. 2007). Temporal autocorrelation frequently occurs because

an animal's position or behaviour is often highly dependent on its previous one (Turchin 1998). Spatial autocorrelation, which stems from Tobler's First Law of Geography that "near things are more related than distant things" (Tobler 1970) may also be a statistical concern; for example, when analyzing habitat attributes at areas occupied by telemetered fish because habitat characteristics at nearby locations are likely similar. Multiple approaches can be used to assess (e.g., auto-correlation plots or variograms; see Zuur et al. 2010) and account for temporal and spatial autocorrelation in analyses, ranging from detrending observed data, including temporal or spatial information as explanatory covariates in fitted models, to using complex variance–covariance matrices for model error terms (Zuur et al. 2009, 2017). Modeling approaches such as state-space models and hierarchical spatio-temporal models with random fields allow for temporal or spatial autocorrelation to be accounted for directly (e.g., Carson and Mills Flemming 2014; Martins et al. 2014).

Critically appraising statistical approaches (e.g., via diagnostic plots) is crucial to check for violation of assumptions. Most statistical approaches (e.g., frequentist and Bayesian inference) require common assumptions about the response and predictor variables that need checking prior to analysis. The response variable will often dictate which type of analysis should be performed, (e.g., linear or generalised linear models; Zuur et al. 2010). For example, when looking at the influence of environmental variables on individual presence-absence within an acoustic array, the researcher may use a generalised linear mixed-effects model fitted with a binomial distribution assumed for the response variable, whereas when examining the environmental influences on the number of fish detections (count data), a Poisson distribution is commonly used. Over-dispersion can be an issue with count and proportion data, where observed variances are greater than that estimated by the statistical model, often causing parameter estimates to be biased (Zuur et al. 2010). Common sources of this issue in telemetry datasets are zero-inflation and outliers in the data (Brooks et al. 2017b; Harrison et al. 2018). Zero-inflation occurs when an excess of true "zero" observations in the data. This excess can be accounted for in some analyses with alternate link functions (e.g., negative binomial for count data, compound Dirichlet-multinomial for

proportion data), or by using a zero-inflated function or a hurdle model where zeros and non-zeros are fitted in two different stages (Brooks et al. 2017b). Outliers (i.e., relatively large or small values compared to other observations in dataset) may also be present in the response or predictors; in the latter case this problem can contribute to collinearity (Zuur et al. 2010). Collinearity occurs due to covariance amongst two or more predictors (e.g., rainfall and temperature), which may result in incorrect parameter estimates and interpretation of their significance or importance in many multivariate modelling approaches. Checking for collinearity between predictors is essential; this can be accomplished with pairwise scatterplots between predictors or variance inflation tests. Various selection techniques exist to identify which predictors to include in multivariate frequentist or Bayesian models; for example, via machine learning algorithms that are less sensitive to collinearity (Strobl et al. 2007).

Analyses of telemetry data often involve constructing models that are mathematical representations of hypotheses concerning the attribute being studied (e.g., movement, mortality). For example, models may be constructed explaining movement of telemetered fish in relation to their characteristics (e.g., age, sex) and/or environmental conditions (e.g., river discharge, temperature). Modelling approaches are constantly expanding as new techniques are developed and/or made accessible through user-contributed libraries (e.g., Comprehensive R Archive Network). As a result, researchers are increasingly using statistical modelling approaches. It is highly recommended to check model complexity and goodness-of-fit for validation (Bolker et al. 2009; Conn et al. 2018). Model complexity can affect the uncertainty of parameter estimates, so ideally, descriptions of analyses from a telemetry study will describe procedures used to avoid overfitting, such as conducting model selection using information criteria (Zuur, et al. 2009). When alternative models are fitted to telemetry data, information criteria (e.g., Akaike information criteria, Bayesian information criteria, Deviance information criteria) are common approaches used to identify the "best" model from a set of candidate models, while there are also statistical testing procedures (e.g., likelihood ratio tests, extra sum-of-square tests) available that can be used to test whether a model performs significantly better than another model for a

set of nested models (Burnham et al. 2011; Hooten et al. 2015).

Finally, multiple methods exist to check the model goodness-of-fit. With frequentist approaches (i.e., linear, additive and/or mixed-effect models), model goodness-of-fit can be tested using summary statistics such as a model's coefficient of determination ( $R^2$ , in linear models only), or simply plotting model residuals, or using cross-validation techniques (split collected data into training and testing data sets to determine how well a model constructed from a training set predicts observations from the testing set; Bolker et al. 2009; Zuur et al. 2009). Model checking in Bayesian analysis comes with its own analysis, from the use of simple Bayesian p-values (a more conservative approach), prior and/or posterior predictive checks, cross-validation techniques, or pivot discrepancies measures (see Conn et al. 2018 for review). Previous data or sub-setting of the data is required for the use of prior predictive checks, whereas, posterior predictive checks rely solely on properties of simulated and observed data (Conn et al. 2018).

## Interpretation

Diverse and complex considerations affect the interpretation of the validity and relevance of a given telemetry study, many of which are outlined above, including whether the appropriate tagging and tracking approaches were used and whether data were analyzed properly. Here we present some additional considerations for telemetry studies that should be addressed prior and during study implementation, as well as when interpreting a study's validity and management relevance.

What was the fate of tagged fish?

Inevitably, a portion of fish tagged for a telemetry study will experience natural or fishing mortality before batteries of implanted tags expire (e.g., Karam et al. 2008). Fish mortality has diverse potential causes, such as fisheries (Yuen et al. 1974), entrainment (Winter and Jansen 2006; Martins et al. 2013a), natural disasters (Waters et al. 2005; Young et al. 2010), extreme water temperature (Martins et al. 2012; Matich and Heithaus 2012), reproductive stress (Naughton et al. 2005; Mathes et al. 2010), or

predation (Raby et al. 2014; Thompson et al. 2015). Knowing if, how, and when fish die can be valuable information for data interpretation and to fishery managers (e.g., Bacheler et al. 2009; Friedl et al. 2013). For example, downstream entrainment of tagged fish at dams can provide population-level mortality estimates (Winter and Jansen 2006; Martins et al. 2013b). The predation of telemetry-tagged fish can be used to generate estimates of natural mortality that would be difficult to acquire (Hightower et al. 2001; Waters et al. 2005; Sammons and Glover 2013). Returned tags from a fishery provide researchers with data contributing to the calculation of fishing mortality, along with timing and location (Heupel and Simpfendorfer 2002; Bacheler et al. 2009; Friedl et al. 2013). When tags are recovered without the animal and not from fisheries, data interpreters must carefully consider potential causes of death or conclude the fate as “unknown” (Jepsen et al. 1998) because the cause could be death or tag expulsion. Tags have been found in the stomachs of birds, fish, and reptiles (Jepsen et al. 1998; Muhametsafina et al. 2014; Thompson et al. 2015). In cases where tags are found without a carcass, it may be possible to reasonably assume the cause of death based on the known predator guild. For example, cause of death of brown trout was inferred based on mammalian bite marks on a substantial proportion of stranded transmitters (Aarestrup et al. 2005). When tags cannot be recovered (e.g., in strong current or dangerous water, Martins et al. 2013b), the life history of the fish may provide some insight on fate (Gibson et al. 2015). For example, highly mobile species might be expected to move consistently in a certain season; thus, no movement over a relatively short period during that season may be suggestive that death has occurred. Several technologies exist that can pin-point the location of individual tags. These methods include manual tracking with radio antennae (e.g., on foot, land vehicle or plane) or with acoustic receivers to determine non-movement. Further, some radio tags can be equipped with sensors that increase the transmission rate when tags are motionless for a set period of time, effectively indicating that an animal has likely died (Sammons and Glover 2013; Bird et al. 2014). There are also acoustic tags available that have integrated pH sensors that detect predator stomach acids and alter signal characteristics to indicate predation (Halfyard et al. 2017).

When an animal is not recovered, determination of its fate can be challenging. For example, tagged animals frequently disappear from tracking systems, which could be due to animal mortality, emigration, or tag failure (Hays et al. 2007). However, in systems with sufficiently high receiver coverage, analytical techniques can be used to estimate annual fish survival and infer total mortality (Binder et al. 2016b; Hayden et al. 2018). Manual tracking may also be used to locate animals outside the study area or listening area of acoustic telemetry receivers, such is the case in the open oceans and connected river systems (Heupel and Simpfendorfer 2002; Aarestrup et al. 2005). Cessation of movement is often a sign of mortality in a tagged fish (Hightower et al. 2001; Waters et al. 2005; Karam et al. 2008; Sammons and Glover 2013), but fish may also expel transmitters (see **Tag retention and reporting** below), or fish may move very little for extended periods due to their behavioural tendencies, both of which can be addressed with certain analytical techniques that account for uncertainty (Stich et al. 2015; Bird et al. 2017). On the flip side, a moving tag does not necessarily indicate a tagged fish is alive. For example, a dead fish may drift down river in currents (Muhametsafina et al. 2014) or the tag, along with the fish, may be ingested by a mobile predator (Jepsen et al. 1998; Gibson et al. 2015; Thompson et al. 2015).

### Tag retention and reporting

With contemporary transmitters having longer lifespans than in the past, researchers are able to monitor the behavior and fate of individual fish for several years (Hussey et al. 2015). Telemetry research projects often vary in temporal scale according to research questions (e.g., post-release survival, habitat use, home-range analyses, predator–prey interactions, movement behaviour, personality) or the species (e.g., lifespan) being investigated. These variables dictate the tagging technique to be used. Researchers need to be confident that the chosen tag will be retained for an ecologically relevant time period suitable for answering study questions.

Interpretation of tag retention requires consideration of tagging method. With implanted tags, expulsion of the tag can occur either through the body wall, or trans-intestinally with exit through the anus, and can occur in days to months after being tagged (Jepsen et al. 2002; Lacroix et al. 2004; Cooke et al. 2011b;

Nowell et al. 2015). Sutures can also dissolve prior to incision healing leading to transmitter loss through the incision opening (Bunnell et al. 1998). Water temperature is a key variable associated with trans-intestinal tag expulsion or premature suture dissolution (Knights and Lasee 1996; Bunnell and Isely 1999). External tags are usually attached to the dorsal musculature, often being placed anterior to the dorsal fin (Thorstad et al. 2013; Jepsen et al. 2015). External transmitters are eventually shed by the tagged individuals, which affects studies of long duration and occurs earlier with large tag sizes (Haulsee et al. 2016). External tags can also become biofouled or abraded on bottom materials such as rocks which can further lead to tag loss (Bridger and Booth 2003; Jepsen et al. 2015). With intragastric insertion, transmitters are usually regurgitated eventually; retention is typically improved if tags are voluntarily consumed or if fish are not feeding (e.g., upstream migrating adult Pacific salmon).

Tag retention can be assessed by tagging individuals with more than one tag type and then monitoring which tags are reported from harvested or surveyed fishes (i.e., double-tagging studies). General approaches for estimating tag retention from double-tagging studies can be found in Kirkwood and Walker (1984), and Barrowman and Myers (1996). Because tag loss rates can vary by species and subtle differences in how tagging is conducted (Jepsen et al. 2002; Bridger and Booth 2003), simply assuming tag loss rates based on previously conducted studies should be used cautiously in data interpretations.

Telemetry studies are sometimes used as a basis for estimating harvest rates and/or mortality components of tagged individuals (Hilborn 1990; Pine et al. 2003). For studies of this nature, tagged fishes that are harvested must be ultimately reported back to study investigators. With intracoelomic implantation of transmitters, unintentional non-reporting may result from anglers simply not finding transmitters during the process of cleaning fish. To prevent unintentional non-reporting, external tags can be applied in addition to transmitters to help inform anglers of the presence of the internal tag. Intentional non-reporting can result from a variety of causes, including concern about the study's purpose and how it might affect future fishing opportunities, general apathy toward the study, or anglers' simply not willing to go to the effort to report the tag (Hoenig et al. 1998; Denson et al. 2002; Vandergoot et al. 2011). One way to encourage the

reporting of tagged individuals that are harvested is to offer rewards for recovery and reporting of transmitters. Intentional non-reporting of tags may also be discouraged by ensuring that the study is well advertised and that the purpose of the study is clearly articulated to stakeholder groups.

Reporting rates can be quantified in several ways. One of the most common approaches to quantifying reporting rates is to conduct a high reward tagging study, which involves releasing transmittered fish for which a high-enough reward is offered so as to “guarantee” high reporting rates if those fish are harvested (Pollock et al. 2001). The difference in return rates between high-reward and standard-reward individuals can then be used to estimate the reporting rates for standard-reward individuals (Pollock et al. 2001). The level of reward needed to elicit 100% reporting of harvested individuals is an important consideration for high-reward studies. In many tagging studies, \$100 has been used as a high-reward level (Denson et al. 2002; Taylor et al. 2006; Cadigan and Brattey 2006; Vandergoot et al. 2011). However, because of potential biases that may result if 100% reporting of high-reward tags is not achieved, it can be beneficial to conduct preliminary evaluations to determine the reward level necessary to elicit perfect reporting (Pollock et al. 2002). Other approaches for quantifying reporting rates include placing observers on fishing vessels or at cleaning stations who conduct independent checks for transmittered individuals and keep track of the fraction of total harvest examined or by planting tagged animals in the catch or creel of commercial or recreational fishers and monitoring how many planted tags are eventually reported (Pollock et al. 2002).

Did capture and tagging alter behaviour and survival?

The potential impacts of tagging on fish behavior, especially immediately after the tagging event, should be considered (Ross and McCormick 1981). For many studies, prior to analysis, fish movement data should be carefully evaluated and filtered to remove potential erroneous data that occurred within the first several days after a fish was released. Tagging effects can also be assessed by analyzing tracking data. For example, Moxham et al. (2019) examined post-release movement patterns of bonefish (*Albula* spp.) and inferred

that most of their animals were killed by predators due to tagging effects, resulting in predator tracking. An externally-placed transmitter or other external tag can also make tagged individuals more conspicuous to predators. In addition, acoustic transmissions could conceivably act as a “dinner bell” to predators (e.g., pinnipeds; Stansbury et al. 2015) able to detect high frequency acoustic wavelengths (Stansbury et al. 2015; Berejikian et al. 2016). However, no studies have documented this phenomenon in the wild. Whether transmissions would be frequent enough (typically every 1–5 min) for predators to locate tagged individuals in the wild is unknown.

Many of the challenges that fish face in the wild, such as predation, are not addressed by laboratory studies focused on assessing tagging effects. Thiem et al. (2011) found that only 7.7% of published fish telemetry studies addressed the potential effects of tagging procedures on behavior and survival, and only 11.3% of papers were able to refer previously published tagging effects assessments for their study species. Indeed, more research needs to be done on the effects of transmitters on fish (Jepsen et al. 2002; Bridger and Booth 2003), especially to support a telemetry studies designed to inform management actions. Negative tagging experiences (i.e., negative outcomes for fish) are rarely documented and reported, which complicates the knowledge of tag burden effects within the research community (Jepsen et al. 2002). Nevertheless, the fact that tagging effects studies are uncommon (Thiem et al. 2011) does not necessarily mean that a telemetry study’s findings are unreliable, especially considering the growing body of evidence about ‘best practices’ (Cooke et al. 2011a, b) that can be used to ensure fish welfare is maximized. However, there are inherent unknowns about tagging effects in many studies, especially those using novel species, tag types, and tag attachment styles.

Pre- and post-operative care of the fish tagged often have major effects on post-release behavior and survival. If a fish is in poor condition because of capture and handling, negative post-release outcomes become more likely. Given that fish tagging requires capture and handling, even in captivity, researchers should consider the vast literature related to commercial bycatch (reviewed in Davis 2010) and recreational catch-and-release fisheries (reviewed in Cooke and Suski 2005; Arlinghaus et al. 2007; Brownscombe et al. 2017). A variety of variables (e.g., gear set time,



hook type, net type, water temperature, fisher behaviour, depth of capture), can affect post-release mortality rates which can range from negligible (Beardsall et al. 2013) to over 90% (Bartholomew and Bohnsack 2005). Regardless of gear type used, all fish caught for tagging will experience some injury and stress. Any capture method that causes elevated levels of locomotor activity (e.g., struggling in a net, during handling, or while on rod and reel) will result in elevations in metabolic rate, depletion of tissue energy stores, shifts in acid–base balance, release of stress hormones, and buildup of metabolites (reviewed in Kieffer 2000; Barton 2002). These physiological alterations can be manifested as reflex impairments (Davis 2010) or behavioural alterations (reviewed in Wilson et al. 2015b). Negative effects of capture and handling even extend to some extent to a broad range of methods including dip-netting fish from a tank or captured them via electrofishing (Burns and Lantz 1978; Mesa and Schreck 1989). Although injuries can heal and physiological homeostasis can be restored, complete recovery may not be the case for all individuals. For example, disease may develop in some individuals as aquatic pathogens are opportunistic, taking advantage of even minor dermal injuries, especially when immune functions may be compromised due to stress (Miller et al. 2014).

Pre- and post-operative holding tanks should be matched to ambient water conditions with appropriate flow to maintain oxygen levels, temperature, pH, and salinity, while flushing out waste products. Although some have advocated holding fish in cooler than ambient temperatures or in hyperoxygenated waters, research suggests that physiological recovery is most rapid under ambient conditions (Suski et al. 2006; Shultz et al. 2011). For wild fish, confinement can be stressful (reviewed in Portz et al. 2006). In some cases, fish need to be held for a short period prior to release to ensure fish have minimal post-release behavioural impairment (e.g., Brownscombe et al. 2013), but longer holding periods can be detrimental. For example, holding adult migratory sockeye salmon (*Oncorhynchus nerka*) in an in-river net pen for 24 h led to near maximal levels of cortisol, and nearly all fish died within days of release whereas fish released immediately after tagging had comparatively low levels of mortality (Donaldson et al. 2011). In some cases, the method of release is also important. For example, devices that assist the fish to descend to certain water

depths and recover from barotrauma symptoms can improve survival (Fertter et al. 2015).

Were tagged fish representative of the study population?

Fish collection techniques are selective and thus potentially biased for individuals with certain life history, physical, behavioural, and physiological characteristics (Law 2007). As such, when evaluating studies, it is important to ask “who has been tagged”? The answer to this question is relevant to whether tagged animals are representative of the group of interest. Was bias for a certain sex, size, behavior, or personality of a fish introduced into the study? For example, were tagged animals the same size/age/growth rate, had typical representative behavioural syndromes, and showed the same behavioural repertoire as untagged conspecifics that were not captured and tagged? For managers, these questions could become large issues if information from tracking studies were being used to define stock assessment sampling strategies (Cooke et al. 2016a) or if using “Judas” fish to betray and locate conspecifics to eradicate (Lennox et al. 2017). A large body of research has developed in the context of selective fisheries and its role in fisheries-induced evolution (Heino and Godø 2002) and in the context of understanding sampling bias for stock assessment (Maunder et al. 2014).

Fish capture gear can be selective for a number of physical and biological characteristics. The most obvious form of selectivity is related to body size (which is often concomitant with age/ontogeny; see Rudstam et al. 1984; MacLennan 1992). Different sizes of fish may use space/habitats differently, often as a result of varying predation risk (Werner et al. 1983), nutritional requirements (Dahlgren and Eggleston 2000), or their interactions. Many gear types (e.g., nets) have inherent selectivity properties (e.g., net mesh size which dictates minimum fish size that can be captured). Given the manifold role of body size in biotic interactions (e.g., predator–prey and other forms of natural mortality; Gislason et al. 2010) and its relevance to population dynamics (Savage et al. 2004), tagging efforts that fail to represent the fish of interest could lead to incorrect conclusions about mortality, movement, or habitat use.



Other elements of capture selectivity relate to fish behaviour. For passive gears like long-lines or trap nets, highly mobile individuals are most likely to encounter gears (Uusi-Heikkilä et al. 2008; Diaz Pauli et al. 2015; Arlinghaus et al. 2016). For active gears such as trawling or trolling, capture may be more likely for individuals that are schooling with conspecifics. Even within a gear type, variable behaviour types may be caught. For example, with recreational fishing gear, different types of lures capture fish with different behavioural syndromes (Wilson et al. 2015a). With some gear types (especially passive gears that require fish to be hooked on bait or lure) components of the population may be simply “uncatchable”. Philipp et al. (2009) used a fishing catchability study to experimentally demonstrate that angling vulnerability is heritable (see Sutter et al. 2012). Bias can also occur if sex, maturation state, energetic state, or health state influences behaviour and catchability (Arreguín-Sánchez 1996).

Location and timing of fish collections are particularly important elements of study design that influence relevance to research objectives and management application. The objectives of a study (or any management application one tries to make with data) must be consistent with the spatio-temporal aspects of fish tagging. Tagging fish in specific geographic locations could potentially fail to assess the overall space use patterns of the broader population. Further, one could easily tag a non-random subset of the species such as more than one population with differing life histories (e.g., in impoundments you can have river residents and lake resident fish). Even the vertical distribution of fish can influence capture. Fishing with gear near the surface when fish are vertically distributed by body size or sex (e.g., Harrison et al. 2013), could lead to tagging a demographically biased part of the population.

Timing of fish collections can also influence the degree to which tagged fish were representative of the population of interest. For example, if collection efforts focused on the reproductive period, then tagged fish may include only individuals that are reproducing that year (e.g., excluding immature individuals or mature individuals on reproductive holiday). Moreover, sampling may be biased if tagging occurred on a single day or week rather than across the entire spawning season. For example, if migratory fish were tagged over a narrow period, the scope of inference

would not be the entire migration but fish from that migratory period and the environmental conditions that they faced. Research has shown that the physiology, behaviour, and fate of fish varies across migration periods (Cooke et al. 2006; Morais and Daverat 2016). These issues are most important at the analysis phase but can also be addressed a priori with appropriate experimental design or may become an inherent component of the objectives (e.g., comparing the fate of animals tagged at different times or in different locales).

### Translating telemetry to management

Telemetry research is often relevant to both fundamental ecological knowledge and applied environmental management (Crossin et al. 2017). To accomplish the latter, and underpinning all of considerations presented in this paper, early and sustained dialogue between managers and scientists can help to ensure that research design and findings correspond to management needs (Cvitanovic et al. 2015; Young et al. 2016b). Rather than researchers making decisions about trade-offs or which considerations to embrace or ignore, decisions might best be achieved collaboratively with managers, who are most often the end users of the information. This approach is better than simply “delivering” the science at the end with the assumption that it will be used by managers (Reed et al. 2014). With so many options available in types of technology and study designs in the field of telemetry, communication with managers may provide key guidance in selecting the appropriate approach. Further, if managers lack expertise in telemetry, additional reviews could be commissioned (after standard peer review associated with publishing) by experts that can assess the relevance and reliability of telemetry studies to a particular management context or decision.

Many other considerations exist for improving the mobilisation of telemetry knowledge into management practice. The first is the value of extending one’s social network to include people outside of one’s peer group. Existing research on knowledge transfer suggests that knowledge moves best through personal contacts and interpersonal relationships, so getting to know people beyond one’s organization or collegial network can have real benefits for putting knowledge

into practice (Gainforth et al. 2014). Growing one's network also provides opportunity to address misperceptions about telemetry research. Second, and related to time and patience, researchers should consider that managers are faced with multiple demands, tasks, and sources of knowledge. Managers and decision-makers are often constrained by stakeholder demands, lack of resources, legalities, administrative burden, changing priorities, and contradicting/conflicting information (Young et al. 2013; Nguyen et al. 2018). Framing research in a context that considers these multiple perspectives will help enhance its use. Third, researchers should be honest about the limitations of research tools and findings. Finding the best 'fit' between available knowledge and management needs means openly acknowledging where fit is imperfect or impossible. Transparency about these limitations is essential for building long-term trust among researchers and managers, as members of both groups can be confident that they are getting the whole story (Rice 2011). Lastly, researchers play an important role as gatekeepers of scientific knowledge more generally. Known and trusted researchers are often sought out by decision-makers and other stakeholders to give advice about a wide range of scientific findings, techniques, and arguments, including those outside the researcher's field of expertise. In these circumstances, researchers can adopt the role of the "honest broker" (Pielke 2007). Honest brokers help non-scientists to understand the full range of evidence and options available to them, without explicitly endorsing any one perspective, course of action, or policy option (Pielke 2007; Jasanoff 2008). Honest brokers serve the broad purpose of smoothing the path for the transfer of scientific knowledge into policy, practice, and decision-making (Turnhout et al. 2013; Fernández 2016). Engaging in these best practices can enhance the use and impact of particular types of knowledge, such as that derived from telemetry, with the potential to improve management and conservation.

## Summary

Above we outlined the key considerations for designing, implementing, and interpreting telemetry studies with a focus on acoustic and radio telemetry, as they are the most widespread approaches to evaluating fish movement, habitat use, behaviour and survival. It is

our hope that this review will serve as a useful reference for researchers seeking to conduct robust telemetry studies relevant to fish managers, and aid managers in interpreting the meaning and relevance of studies to their decision-making processes. Table 1 outlines these considerations as a checklist, which may be used as a quick reference for both researchers and managers. Failure to address a particular consideration (e.g., no tagging validation study conducted) does not invalidate the work but could reduce the confidence one has in its findings. Researchers should incorporate the technical components outlined here into their study to improve data reliability. However, no studies are perfect, especially with research on wild fish in the field. Technology is imperfect, and researchers often have to make trade-offs (e.g., tag size and its relevance to burden on fish vs longevity of tag, radio vs acoustic, fixed vs manual tracking, internal vs external tagging), all of which require considerable knowledge of technical aspects of study design and execution as well as the nuances of a given research question. Translating telemetry-derived knowledge into management relevant information requires consideration of management needs and decision-making processes, which is aided greatly by communication and collaboration between researchers and managers. With continued development and application of the telemetry practices outlined here, this research approach has great potential to generate impactful and disruptive knowledge on the natural environment relevant to fundamental ecology and applied conservation.

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## Compliance with ethical standards

**Conflict of interest** The authors declare no conflicts of interest.

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