Autonomous acoustic telemetry monitoring systems have been deployed in aquatic ecosystems around the globe – from under ice sheets in the Arctic to coral reefs in Australia – to track animals. With tens of thousands of tagged aquatic animals from a range of taxa, vast amounts of data have been generated. As data accumulate, it is useful to reflect on how this information has advanced our understanding of aquatic animals and improved management and conservation. Here we identify knowledge gaps and discuss opportunities to advance aquatic animal science and management using acoustic telemetry monitoring. Current technological and analytical shortfalls still need to be addressed to fully realize the potential of acoustic monitoring. Future interdisciplinary research that relies on transmitter-borne sensors and emphasizes hypothesis testing will amplify the benefits of this technology.

In a nutshell:

• Acoustic telemetry monitoring is widely used in freshwater and marine ecosystems and has provided invaluable information on aquatic animals from various taxa and life stages
• Most acoustic telemetry monitoring studies focus strictly on animal movement, but this technology provides opportunities to take more integrative and comparative approaches to ask “big questions” in aquatic ecology
• Future telemetry-based studies should emphasize hypothesis testing and investigate more complex research questions to better understand how aquatic animals interact with their environment
• To maximize the information gained from acoustic telemetry monitoring, scientists must address existing technological, analytical, and data management needs

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Figures for multidisciplinary studies are emerging, and researchers are currently on the verge of important new findings in the study of aquatic animals using acoustic monitoring.

**Individual-level responses**

**Behavior and survival**

The most common application of acoustic monitoring has been to study aquatic animal behavior and survival (e.g., Blumenthal et al. 2009; Jorgensen et al. 2010; Figure 1). Studies have helped to reveal seasonal and developmental changes in organism behavior (Andrews et al. 2010), and specially designed transmitter-receiver tags coupled with a receiver array have enabled explorations of group behavior and social interactions (Guttridge et al. 2010). A variety of migration behaviors have been examined, from juvenile salmon (Oncorhynchus nerka; Figure 3) behavior and survival as they transition from freshwater rearing habitats to coastal Pacific Ocean waters (Welch et al. 2009), to movement behaviors of gray seals (Halichoerus grypus; Figure 4) in the northwestern Atlantic Ocean (Lidgard et al. 2012). Although much knowledge has already been gained, field-based acoustic monitoring applications have the potential to address emerging questions regarding animal behavior. For example, investigating behavioral anomalies, such as the presence of individuals outside their typical ranges, can provide information on migration behaviors and home ranges. Such findings may be particularly valuable in a climate-change context, given that the ranges of some species are expected to shift (Hampe and Petit 2005). Even a relatively small dataset can provide important insights, for example, into potential rarely observed offshore foraging behaviors of northern elephant seals ([Mirounga angustirostris]; Hayes et al. 2013), particularly when investigated with novel modeling techniques.
Although various electronic tagging technologies exist (e.g., radio, satellite, archival), acoustic telemetry is designed specifically for use in aquatic ecosystems, including both marine and freshwater habitats (Figure 2). Acoustic receivers contain an integrated hydrophone that is submerged to detect transmissions via fixed position receivers for passive monitoring or by mobile receivers for active tracking.

**Acoustic transmitters**

Over several decades of refinement, acoustic transmitters have benefited from increased battery life and increasingly smaller transmitter sizes. Juvenile Salmon Acoustic Telemetry System (or JSAT) transmitters, for instance, measure only 12 mm × 5 mm × 4 mm and weigh ~0.4 g in air (McMichael et al. 2010). Transmitters can be implanted internally (Figure 3a) or may be attached externally (Figure 3b), have uniquely coded identification numbers, and can be equipped with sensors to store or transmit information about the animal’s internal and external environment. Novel technologies and sensors have been incorporated into transmitter design (e.g., combined acoustic transmitter/GPS; Lidgard et al. 2012; Figure 4). New tracking approaches include Business Card Tags (Holland et al. 2009) that function as an animal-borne transmitter and receiver unit, which detects free-swimming individuals outside the confines of moored receivers but can also be incorporated into existing networks to expand detection coverage (Hayes et al. 2013).

**Acoustic receivers**

Acoustic receivers are submerged in aquatic systems (Figure 5). A range of configurations can be used, including arrays of receivers organized in a grid formation (e.g., often used in systems such as lakes or bays) or lines of receivers deployed as a curtain (e.g., typically used along continental shelves, within riverine systems, or along key migration routes). Nodes can be small and geographically isolated or connected to much larger international networks such as the Ocean Tracking Network (OTN; Cooke et al. 2011). Depending on the system being used, some acoustic receivers may be wired (i.e., cables attached to computers, such as Vemco [Halifax, Canada] Radio-linked Acoustic Positioning [VRAP] or Lotek Wireless Inc [Newmarket, Canada] MAP systems), others may be wireless but retrieved to download, while others still enable remote downloading to mobile computers through wireless technologies such as modems and Bluetooth®.

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**Panel 1. Acoustic telemetry monitoring**

**Context**

**Figure 2.** (a) A blacktip shark (Carcharhinus limbatus) and (b) a silvertip shark (Carcharhinus albimarginatus) being released following acoustic tagging.

**Figure 3.** (a) An acoustic transmitter being surgically implanted into a juvenile sockeye salmon (Oncorhynchus nerka); (b) an acoustic transmitter externally attached to a Mary River turtle (Elusor macrurus).

**Figure 4.** A gray seal (Halichoerus grypus) tagged with an acoustic transceiver used to detect other nearby tagged animals and a satellite transmitter used to track movements of the seal itself.

**Figure 5.** (a) An acoustic receiver being programmed prior to deployment in a coastal habitat in Canada; (b) an acoustic receiver attached to a mooring prior to deployment in a shallow tropical habitat in The Bahamas; (c) an acoustic receiver moored in a marine habitat in Australia.
(WebPanel 2). Investigations into anomalous behaviors should be coupled with data on broader-scale, population-level patterns to avoid potentially misleading interpretations. Taking integrative approaches to animal behavior studies by combining multiple endpoints such as morphology, performance, and physiology (WebTable 1) will help provide context for movement data.

**Morphology**

Various measures of individual morphology and size are commonly included as covariates or factors in statistical analyses in acoustic monitoring research. Most studies collect only one measure of length and/or mass, but there are opportunities to take more detailed morphological measurements. Tagging typically requires animals to be restrained and handled during the tagging procedure, enabling researchers to make observations on the animals’ physical condition (eg previous injuries or abnormalities) and to record more detailed body dimensions using digital photography and imaging software (eg Hanson et al. 2007). Morphology can also be used to test hypotheses relating to fitness (eg Moland Olsen and Moland 2011; see “Life history” section below). Integrating morphology and allometry (the relationship of body size to shape) variables into acoustic monitoring studies could strengthen hypotheses related to predator–prey relationships (eg prey-size selection), habitat use (eg foraging site selection and competition), and morphology-based social hierarchies, as well as animal performance.

**Performance**

A range of remote-sensing options are now available to study animal movements in the field (Ropert-Coudert and Wilson 2005; Goldbogen et al. 2013). Acoustic monitoring allows for the near-continuous tracking of aquatic animal performance. For instance, acoustic tags equipped with sensors (eg pressure, acceleration, tailbeat frequency) have provided information on diving performance (eg the freshwater Arafura filesnake [Acrochordus arafurae]; Pratt et al. 2010), swimming speeds (eg Atlantic cod [Gadus morhua L]; Fernö et al. 2011), and tailbeat frequency (eg juvenile scalloped hammerhead sharks [Sphyma lewini]; Lowe et al. 1998). Where researchers were previously required to conduct time-intensive and difficult manual tracking (Carey and Scharold 1990), large-scale telemetry nodes and networks now enable sophisticated and automated passive monitoring over larger spatial scales, using receiver curtains and high-resolution tracking, including three-dimensional telemetry arrays. Hanson et al. (2010) used a three-dimensional, whole-lake acoustic telemetry array with sub-meter accuracy to assess the swimming performance (ie daily distance traveled and mean daily swimming speed) of largemouth bass (Micropterus salmoides)
over multiple seasons. Results obtained from acoustic accelerometer tags and flow-through respirometry (technique for estimating metabolic rate) in laboratory studies can be used to calibrate acceleration sensor tags to make correlations between acceleration and oxygen consumption and swimming performance (Wilson et al. 2013), which can then be applied to acoustic monitoring data from free-swimming individuals in field settings. Tags with depth sensors can facilitate examination of diving performance and foraging attempts in mammals (Lydersen 1991) and other species (eg snakes; Pratt et al. 2010).

**Physiology and energetics**

Acoustic monitoring provides a platform for taking the laboratory into the field in order to understand how animal physiology and energetics relate to behavior, ecology, and fitness in situ. The two most common methods of measuring physiological and energetic variables are through transmitter or animal-borne sensors or loggers, or by collecting biological samples (eg biopsies) at the time of transmitter attachment and relating that data to subsequent activity determined with telemetry. Sensors can measure activity or acceleration in near real-time and can be used to infer metabolic rate and energy expenditure (eg Lowe et al. 1998). Combining acoustic telemetry and physiological loggers will help in linking behavior with physiological parameters, such as heart rate (Block 2005). Biopsy approaches typically include the collection of blood or other tissue samples at the time of capture and transmitter attachment. Although the additional handling may further stress the target organism, biopsy methods are designed to be as rapid and non-invasive as possible to minimize these effects (Panel 2). Biopsy could enable integration of gene expression, biochemical processes, nutrition, stable isotopes, cellular responses, cardiovascular data, and toxicology data into acoustic monitoring studies, yet many of these research avenues have so far remained unexplored.

- **Population-level responses**

**Population dynamics**

Given the characteristically small sample sizes in telemetry studies, it can be challenging to extrapolate results from individuals to populations for variables such as demography, recruitment, and productivity. However, statistical modeling approaches are continually improving inferences from telemetry studies at the population level. For example, Payne et al. (2011) used acoustic monitoring for a giant Australian cuttlefish (*Sepia apama*) with a highly male-biased sex ratio to quantify adult sex ratio (ASR) at the population level; these authors found that the ratio of breeding durations was equal to the operational sex ratio, suggesting a balanced ASR. The concept of using individual telemetry data to make population-level inferences has received recent attention in the literature (Panel 2; Perry et al. 2010).

**Fitness and evolutionary biology**

Fitness correlates, such as measurements of behavior and reproductive output (eg spawning aggregation behaviors of common snook [*Centropomus undecimalis*]; Lowerre-Barbieri et al. 2003) provided valuable, albeit indirect, insight into evolutionary outcomes when combined with acoustic monitoring. Acoustic monitoring is often used to assess survival, and an animal’s fate can be used to elucidate fitness outcomes. By using acoustic telemetry to test hypotheses related to evolutionary biology, Moland Olsen and Moland (2011) identified a trade-off between body size and fisheries-harvest-induced selection in G morhua; the authors found that while natural selection favored large fish, commercial harvesters selectively removed them. Fishing mortality was considerably higher than natural mortality, providing evidence of how different mechanisms of selection can alter the fitness landscape.

**Life history**

Life-history traits, such as age of maturity, number and size of offspring, and growth and development rates, can be studied either directly or indirectly through acoustic monitoring. These topics typically require monitoring over longer durations, but are becoming more tractable with improvements in technology, specifically the miniaturization and improved longevity of acoustic tags. Understanding the early life history of aquatic animals is important for estimating survival, yet until recently there have been relatively few studies that focus on juvenile life stages relative to adults for most taxa (but see Heupel and Simpfendorfer 2002). The miniaturization of acoustic tags has provided information on the early life history of aquatic animals, including the timing of juvenile development and key events in their life history. For instance, McMichael et al. (2010) highlighted miniaturized acoustic tags, called the Juvenile Salmon Acoustic Telemetry system, which enable tagging of individuals ~95 mm to study this early life stage.

- **Ecosystem-level responses**

**Habitat associations**

The advent of satellite telemetry has been important for understanding how individuals interact with their habitats, but spatial and temporal imprecision have made it hard to study fine-scale movements relating to trophic ecology, habitat utilization, and interactions with conspecifics (Lidgard et al. 2012). Acoustic monitoring is immensely powerful for understanding ecosystem-level
research questions because it can provide near-continuous monitoring of individuals at a fine scale (Espinoza et al. 2011). However, collecting quality data is dependent on strategic positioning of receivers and/or integration with technologies such as those associated with the global positioning system (GPS). Integration of such approaches is fundamental to asking complex research questions regarding aquatic habitat associations. For example, Furey et al. (2013) incorporated habitat variables, physicochemical conditions, and bathymetry (measurement of depth in a watery body) with acoustic monitoring to quantify estuarine habitat use by juvenile southern flounder (Paralichthys lethostigma). Acoustic monitoring has also been used to successfully identify home ranges and habitat use by ocean whitefish (Caulolatilus princeps; Bellquist et al. 2008), and to understand how habitats influence activity and behavior of reef sharks (eg Papastamatiou et al. 2009). Acoustic monitoring revealed the home range of juvenile hawksbill turtles (Eretmochelys imbricata) to be much larger than previously thought for developmental habitat at an atoll in Belize (Scales et al. 2011). Similar studies on sharks have provided information on site fidelity to specific habitats (Jorgensen et al. 2010).

**Inter-individual and multi-taxon interactions**

Innovative technologies such as Business Card Tags (BCTs) provide information on inter-individual and multi-taxon interactions, and help to address questions relating to trophic and other multi-species interactions. BCTs are animal-borne acoustic tags that also detect other acoustic-tagged animals (Hayes et al. 2013), provide information on interactions among tagged conspecifics (Holland et al. 2009), and could be applied to assess multi-taxon interactions. For example, Lidgard et al. (2012) equipped gray seals with BCTs and archival (ie logging) GPS telemetry units and were able to track spatially and temporally referenced associations between individuals and foraging habitats. Exploring hypotheses related to social interactions, social networks, and fine-scale animal behavior (ie personality; Krause et al. 2010) in the wild is an interesting area of research, and while acoustic monitoring has already provided information on such topics (eg Guttridge et al. 2010), BCTs could open up new avenues of research. Tagging individuals from different taxa with BCTs provides opportunities to investigate basic ecological relationships such as predator–prey associations, resource competition, and native–invasive species interactions. One could, for instance, tag individuals from a prey population with standard positional transmitters and tag individuals in a predator population with specially designed BCTs to track predation attempts. Fixed receiver nodes in key foraging areas would provide temporal and spatial information on predator–prey interactions.

- **Integrating environmental data**

By using positional telemetry in combination with environmental, oceanographic, or meteorological datasets, researchers can investigate how abiotic conditions influence animal behavior, activity, and habitat associations. Acoustic monitoring studies have focused on responses of aquatic animals to changes in environmental conditions such as salinity and temperature (Ubeda et al. 2009), as well as ocean currents and wind (McMichael et al. 2013). Parameters related to weather events have also been investigated (eg Udyawer et al. 2013). Acoustic monitoring revealed that an extreme cold snap in the Everglades resulted in a high proportion of tagged juvenile bull sharks (Carcharhinus leucas) either permanently leaving their estuarine habitat or dying, leading to long-term demographic changes in the population (Matich and Heithaus 2012). Payne et al. (2013) used acoustic monitoring to show that, while the yellow-fin bream (Acanthopagrus australis) was most active during the day, rainfall coupled with changes in conductivity and turbidity resulted in a reversal of diel activity patterns. Childs et al. (2008) used acoustic monitoring to reveal that the abundance of spotted grunter (Pomadasys commersonnii) in a South African estuary was correlated with barometric pressure, wind direction, and sea temperature. With improved monitoring of environmental data as well as data-sharing capabilities between research groups, such information is becoming increasingly accessible, which should facilitate future integrative research. Incorporation of environmental data may also be fundamental to predicting and understanding how climate change influences individual–ecosystem interactions.

- **Aquatic organisms as indicator species**

Aquatic vertebrates are often described as being indicator or sentinel species for ecosystem and human health (Bosart 2006). Tracking animals has great potential to directly monitor sentinel species (Block 2005). With the help of acoustic monitoring, they could potentially be used as environmental indicators for habitat quality or loss, degradation, or connectivity (eg Pecl et al. 2006), as well as for studying anthropogenic impacts, including boat traffic, chemical spills, or fisheries activities, on behavior and survival (Donaldson et al. 2012). For instance, it was found that juvenile hawksbill turtles were more abundant in a protected area habitat relative to unprotected habitat, likely due to superior quality habitat and/or protection from capture as bycatch in gill net fisheries (Scales et al. 2011). Acoustic-tagged sentinels could also act as indicators for environmental change, helping to document responses to climate regime shifts, extreme weather events, or ocean acidification, while temperature sensor tags or loggers could measure shifting micro-scale climatic changes and habitat associations over time. Aquatic organisms could
potentially also be used as socioeconomic indicators for ecosystem services, monitoring of invasive species, fisheries catch monitoring, and ecotourism costs and benefits. Acoustic monitoring is increasingly being used in freshwater ecosystems, including the Laurentian Great Lakes (reviewed in Cooke et al. 2013a), enabling researchers to ask questions related to the valuable recreational and commercial fisheries that occur there.

### Conservation science

An understanding of the general ecology of imperiled species – such as identifying breeding habitats (Paragamian et al. 2002) and quantifying survival during challenging life-history stages such as migration (Welch et al. 2009) – can be obtained through acoustic telemetry. Tracking the prey of imperiled species could also be important for understanding their behavior and habitat associations (eg to understand the foraging ecology of narwhal [Monodon monoceros], one could use acoustic monitoring to track Arctic cod [Arctogadus glacialis] and Greenland halibut [Reinhardtius hippoglossoides]). Simpfendorfer et al. (2010) relied on a series of telemetry techniques to track critically endangered juvenile small-tooth sawfish (Pristis pectinata) in southwest Florida to identify key habitats on which to focus conservation efforts, including shallow mud and sand banks and mangrove shorelines. The identification of discrete population structures using this technology could have important implications for vulnerable species or populations. For example, Jorgensen et al. (2010) combined satellite and acoustic tagging data with genetic analyses to show that eastern Pacific white sharks (Carcharodon carcharias) follow a persistent migration pattern consistent with genetically distinct populations. Acoustic monitoring can help to prioritize habitats to receive conservation efforts; this approach has recently garnered much attention with respect to establishing and monitoring Marine Protected Areas (Chapman et al. 2005). The same techniques can be integrated into new directions in conservation science, such as conservation physiology, an emerging conservation subdiscipline rooted in comparative physiology research (Metcalfe et al. 2012).

### Management

Acoustic monitoring studies can inform management either directly (eg providing survival estimates related to fisheries bycatch; Donaldson et al. 2012) or indirectly (eg establishing baseline survival rates and population monitoring; Welch et al. 2009). Other management issues that could benefit from this approach include biological invasions (reviewed in Cooke 2008), fisheries operations (eg catch-and-release fisheries; Donaldson et al. 2008), and habitat management, particularly in a climate-change context. Acoustic tracking data can also be applied to the management of fish stocks, quotas, and management regions. As an example, an acoustic telemetry study on Greenland halibut (R. hippoglossoides) provided evidence that individuals caught in the winter months by Inuit fisheries in Canada’s Arctic were from the same population as those harvested to the south in the summer months, suggesting that the fisheries boundary should be adjusted; this result was expedited by acoustic monitoring as compared with traditional mark–recapture studies (Cooke et al. 2011). The management of highly migratory species and species with extensive transboundary ranges can also be enhanced, with potential relevance for ocean governance (VanderZwaag et al. 2013).

### Conclusions

Although most acoustic monitoring studies to date have focused exclusively on animal movement, several fundamental research questions remain unanswered. We have highlighted basic and applied research topics, provided key examples, and suggested subjects that warrant further inquiry. Numerous technological and data needs remain unfulfilled, but important innovations – for instance in data management and analysis – are opening new areas for research. Future investigations that integrate different tools and specialties, rely on transmitter-borne sensors, and emphasize hypothesis testing and experimentation will not only enhance acoustic monitoring applications but also help to address the unresolved questions identified in this paper.

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