# A Systematic Review of Acoustic Telemetry as a Tool to Gain Insights Into Marine Turtle Ecology and Aid Their Conservation

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While widely applied in fisheries science, acoustic telemetry remains an underutilized method in the field of marine turtle biotelemetry. However, with the ability to provide fine-scale spatial data (tens to hundreds of meters, depending on array setup and receiver range) at a low cost, acoustic telemetry presents an important tool for obtaining key information on marine turtle ecology. We present a comprehensive and systematic review acknowledging how acoustic telemetry has been used to advance the field of marine turtle ecology and conservation. We identify the extent of current studies and discuss common and novel research approaches while addressing specific limitations of acoustic telemetry. Forty-eight studies were reviewed, representing six of the seven marine turtle species and all life stages, with most individuals identified as juveniles (45%) and hatchlings (36%). Most studies (83%) focused on the spatial distribution of marine turtles, including estimating home ranges, investigating drivers of habitat use, and identifying horizontal movement patterns and vertical space use. Additionally, acoustic telemetry has been used to study hatchling dispersal and marine turtle exposure and response to threats, as well as to monitor physiological parameters. We identified that acoustic telemetry directly or indirectly informs 60% of the top questions and research priorities related to marine turtles identified by experts in the field. With an increase in acoustic telemetry receiver networks and collaborations across taxa, the applicability of acoustic telemetry is growing, not only for marine turtles but for a wide array of marine species. Although there are limitations that need to be considered at a site/project-level, acoustic telemetry is an important, low-cost technology able to address key questions related to marine turtle ecology that can aid in their conservation, and therefore should be considered by researchers as they develop their projects.

Keywords: acoustic telemetry, spatial distribution, habitat use, sea turtle, tracking, biotelemetry, conservation

## INTRODUCTION

Marine turtles are charismatic species that have garnered support due to their listing on the International Union for Conservation of Nature Red List of Threatened Species (Campbell and Smith, 2006; IUCN, 2021). Recently, some populations have demonstrated stabilization and even growth, while others are still facing declines (Wallace et al., 2011; Mazaris et al., 2017;

Barrios-Garrido et al., 2020). To promote the recovery of declining populations as well as the continued success of growing populations, integrated conservation and management strategies that protect both individuals and key habitats are needed (IUCN/SSC Marine Turtle Specialist Group, 1995; National Marine Fisheries Service and U.S. Fish and Wildlife Service, 2008). In an effort to determine the strategies that will be most beneficial for aiding in this recovery, experts have identified key questions, research priorities, and knowledge gaps that need to be addressed. Priority topics range from demographics to nesting strategies to health parameters. Of particular importance is the topic of spatial distribution (Hamann et al., 2010; Hays et al., 2016; Wildermann et al., 2018). Indeed, understanding how individuals utilize space throughout time is imperative for identifying key areas to protect, as well as for assessing whether current and proposed protective measures are well placed to conserve species (Cooke, 2008; Gredzens et al., 2014; Lea et al., 2016; Santos et al., 2021).

Several research approaches have been used to study the spatial distribution and habitat use of marine turtles, such as mark-recapture studies (Blumenthal et al., 2009a; Llamas et al., 2017), visual transect surveys (Gorham et al., 2016), submersible camera recordings (Auster et al., 2020), drone surveys (Sykora-Bodie et al., 2017), stable isotope analyses (Bean and Logan, 2019; Pearson et al., 2019), epibiont identification (Silver-Gorges et al., 2021), biotelemetry studies (Berube et al., 2012; Santos et al., 2021), and a combination of the aforementioned techniques (Scales et al., 2011; Haywood et al., 2020; Siegwalt et al., 2020). Biotelemetry in particular, or the tracking of individuals, has emerged as a common method for obtaining habitat use information of species (Cooke et al., 2004; Hussey et al., 2015; Hays and Hawkes, 2018). Most marine turtle tracking studies have utilized satellite telemetry, with hundreds of studies tracking thousands of individuals (Hussey et al., 2015; Hays and Hawkes, 2018). Less common and perhaps underutilized in marine turtle biotelemetry is acoustic telemetry (Hussey et al., 2015). This method is widely used in fisheries and has the ability to provide fine-scale spatial information on a scale of tens to hundreds of meters at a lower cost than other biotelemetry technologies, depending on receiver set up and detection ranges (Heupel et al., 2006; Hussey et al., 2015; Zeh et al., 2015; Matley et al., 2021b).

Acoustic transmitters are attached to or implanted within an individual and emit coded ultrasonic signals which are logged by receivers. Individuals can be actively followed and tracked with a single receiver or tracked passively via an array of receivers moored throughout the study site. Because individuals must pass within the detection range of a receiver to be detected, acoustic telemetry provides presence-only data and studies are spatially constrained by the receiver array, limiting their applicability for highly migratory species. Passive array designs as well as study site characteristics will dictate what questions can be answered and how the data is analyzed and interpreted (Heupel et al., 2006; Heupel and Webber, 2012; Whoriskey and Hindell, 2016). However, since signals transverse through water easily, acoustic telemetry allows for near-continuous monitoring of marine turtles, who spend 91–97% of their time submerged

(Renaud et al., 1995; Schmid et al., 2002), As a result, acoustic telemetry provides higher numbers of detections, improved resolution, and lower positional errors than other tracking techniques, such as satellite telemetry, which only transmits location data when turtles surface (Hazel, 2009; McClellan and Read, 2009; Hart et al., 2012; Whoriskey and Hindell, 2016). Therefore, when within the range of receivers, acoustic telemetry presents an opportunity for effectively collecting spatial information for marine turtles (Matley et al., 2021a; Pillans et al., 2021).

While acoustic transmitters themselves are low-cost compared to other biotelemetry devices, installing and maintaining an array of receivers and facilitating data retrieval can be quite costly (Whoriskey, 2015; Zeh et al., 2015). However, acoustic receivers are not species specific (Lea et al., 2016; Matley et al., 2019), which allows multiple taxa to be tracked simultaneously within the same receiver array, enabling cost-sharing among projects to reduce the financial burden to any one study (Selby et al., 2019; Bangley et al., 2020; Reubens et al., 2021). Tens of thousands of passive receivers exist throughout the world and as more are deployed, opportunities for collaborations and data sharing emerge (Hussey et al., 2015; Whoriskey, 2015; Whoriskey and Hindell, 2016). Organizations such as the Ocean Tracking Network (OTN) and FACT Network create regional and global networks that facilitate data sharing among members and encourage standardized data collection and analysis protocols. While challenges still exist in creating compatibility between transmitters and receivers of different manufacturers, these networks are working toward increasing the spatial scale of studies as well as the overall capacity of acoustic telemetry to address questions related to the ecology of marine species, such as marine turtles (Whoriskey, 2015; Bangley et al., 2020; Young et al., 2020; Matley et al., 2021b; Reubens et al., 2021).

To provide marine turtle researchers and managers with a comprehensive understanding of how acoustic telemetry can contribute to marine turtle conservation, we conducted a systematic literature review to investigate how acoustic telemetry has been used to study the ecology of marine turtles. We document the extent of marine turtle acoustic telemetry studies, identifying the regions, species, life stages, and approaches that have received the most attention. We detail the contribution of acoustic telemetry studies to the knowledge of marine turtle ecology and its application toward understanding complex concepts important to aiding their conservation, while also highlighting challenges and identifying knowledge gaps associated with acoustic telemetry. The approaches and limitations discussed here are applicable to many marine taxa and present a broad overview of the relevancy of acoustic telemetry to marine conservation.

## MATERIALS AND METHODS

A systematic literature search was conducted on the 28th of January 2021 following the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) standard (Moher et al., 2009) to identify studies that have utilized acoustic

telemetry to obtain information on marine turtles. The search was performed within EBSCO Host and Google Scholar using the below search string:

("chelonia mydas" OR "caretta caretta" OR "eretmochelys imbricata" OR "lepidochelys kempii" OR "lepidochelys olivacea" OR "natator depress*" OR "dermochelys coriacea") AND ("acoustic telemetry" OR "acoustic transmitter*" OR "sonic telemetry" OR "sonic transmitter*").

The above string was also searched in Web of Science ("All Databases"), prefaced with "TS = " per the database's search requirements. An additional, broader search was conducted in Web of Science using the search string:

TS = [("marine turtle*" OR "sea turtle*") AND ("acoustic telemetry" OR "acoustic transmitter*" OR "sonic telemetry" OR "sonic transmitter*")].

For inclusion, papers must have been published in peer-reviewed academic journals and have utilized acoustic telemetry (also referred to as sonic/ultrasonic telemetry) to gain insight and knowledge on marine turtles during any life stage. Studies in laboratory settings and/or those focused solely on the efficacy of acoustic tag use were excluded, as well as reviews. The original search strings returned 316 unique results. After applying the selection criteria, 39 published journal articles fell within the scope of our review (**Supplementary Figure 1**). Backward and forward searches were conducted to identify additional papers for inclusion, which required scanning the reference sections of all 39 original papers, as well as scanning the titles of all articles that cited the selected papers. The same selection criteria were applied when determining whether additional articles should be added. In total, 48 studies were selected for inclusion in this review.

To understand the spatial, temporal, and demographic trends of existing marine turtle acoustic telemetry studies, we extracted the following information from each article: date of study and publication, study location, type of tracking method used, number of individuals successfully tracked, species, life stage, sex, duration of tracking, transmission interval, and transmitter attachment method, fate, and retention. It was also noted whether studies conducted range tests to estimate the detection probabilities of the receivers used in the study. Occasionally, the same tracking data was used in multiple published studies for different analyses. Individual turtle parameters that were the same between studies were omitted from our analysis, such as species, sex, life stage, and transmitter details. We used the life stage specified by the study; if the authors did not identify the life stage, individuals were classified as "unknown" due to varying growth rates and age at sexual maturity across species and populations (Avens and Snover, 2013). The study period was defined as the overall time between the first and last tracking events included in a study's analysis. For active telemetry studies, tracking duration was considered to be the cumulative time an individual was actively followed, while for passive studies it was defined as the time between which the individual was released or the study began and when the study ended or the transmitter was evidenced as being dislodged. Some studies limited their analyses to a specific period of time (e.g., a period when all passive receivers were operable). For these studies, we included only the tracking duration used in analyses. Transmitter retention was only determined for those known to be lost.

Additionally, the research question(s), study goal(s), and major findings of all 48 studies were reviewed and grouped to identify the overarching broad research topics that acoustic telemetry studies have addressed, as well as to explore common and novel approaches utilized. Findings were synthesized to illustrate what information acoustic telemetry has provided for marine turtle ecology thus far. To assess the applicability of acoustic telemetry in eliciting high-priority information on marine turtle ecology and conservation, we reviewed three publications that employed expert opinions to identify top research priorities and key questions: Hamann et al. (2010), Hays et al. (2016), and Wildermann et al. (2018). These studies focused on marine turtles on a global scale, marine megafauna movement ecology, and immature marine turtles, respectively. After removing similarities, we critically reviewed the questions presented in these publications to assess whether acoustic telemetry could address key topics of importance for further marine turtle research.

## RESULTS

The 48 studies that met our criteria for inclusion in this review (**Supplementary Table 1**) were published between January 1983 and January 2021. The number of studies published per year has increased, with an evident shift from active to passive tracking methods (**Figure 1**). While 63% of the studies utilized active tracking methods, these studies generally had smaller sample sizes (avg: 16 individuals; range: 2–94) than passive studies (avg: 28; range: 3–89). Therefore, of 870 individuals tracked with acoustic telemetry, 66% were tracked passively. Studies were found to be globally distributed with most (46%) conducted in the Caribbean and Gulf of Mexico, followed by 31% in the Pacific, 13% in the Indian Ocean, and 10% in the North Atlantic (**Figure 2**).

All marine turtle species except the olive ridley (*Lepidochelys olivacea*) have been tracked acoustically, with most studies focusing on green (*Chelonia mydas*) turtles (**Figure 3**). Green and hawksbill turtles (*Eretmochelys imbricata*) are the only species that have been tracked with both active and passive telemetry (**Figure 4A**). Individuals from all life stages have been tracked, although the vast majority have been juveniles (45%) and hatchlings (36%; **Figure 4B**). Transmitters were most often (78%) applied to the dorsal posterior marginal scutes (3% to the ventral posterior marginal scutes) of juvenile and adult individuals. Attachment methods included wiring or bolting the transmitter through the marginal scutes (34%), using an epoxy, putty, or glue to affix the transmitter (25%), or a combination of both methods (36%). For hatchlings, acoustic transmitters were attached to the plastron with adhesive (71%) or attached via a tether (29%).

Overall study periods ranged from 4 days to 8 years, with longer studies typically tagging new individuals throughout the study or replacing individuals' transmitters periodically to increase tracking time. On average, individual tracking durations
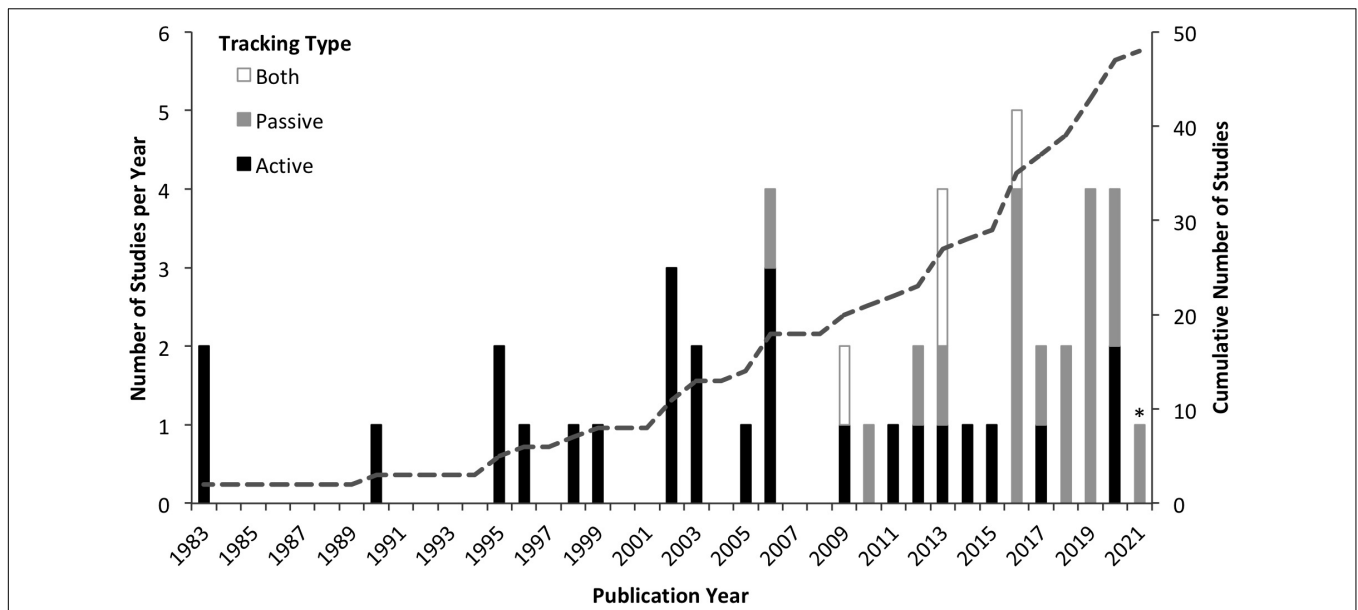
**FIGURE 1 |** Number of acoustic telemetry studies published per year utilizing active tracking (black), passive tracking (gray), or both types of tracking (white). Cumulative number of studies shown by dotted line. *Data from 2021 only includes studies published prior to January 28th and therefore is not comparable to other years.
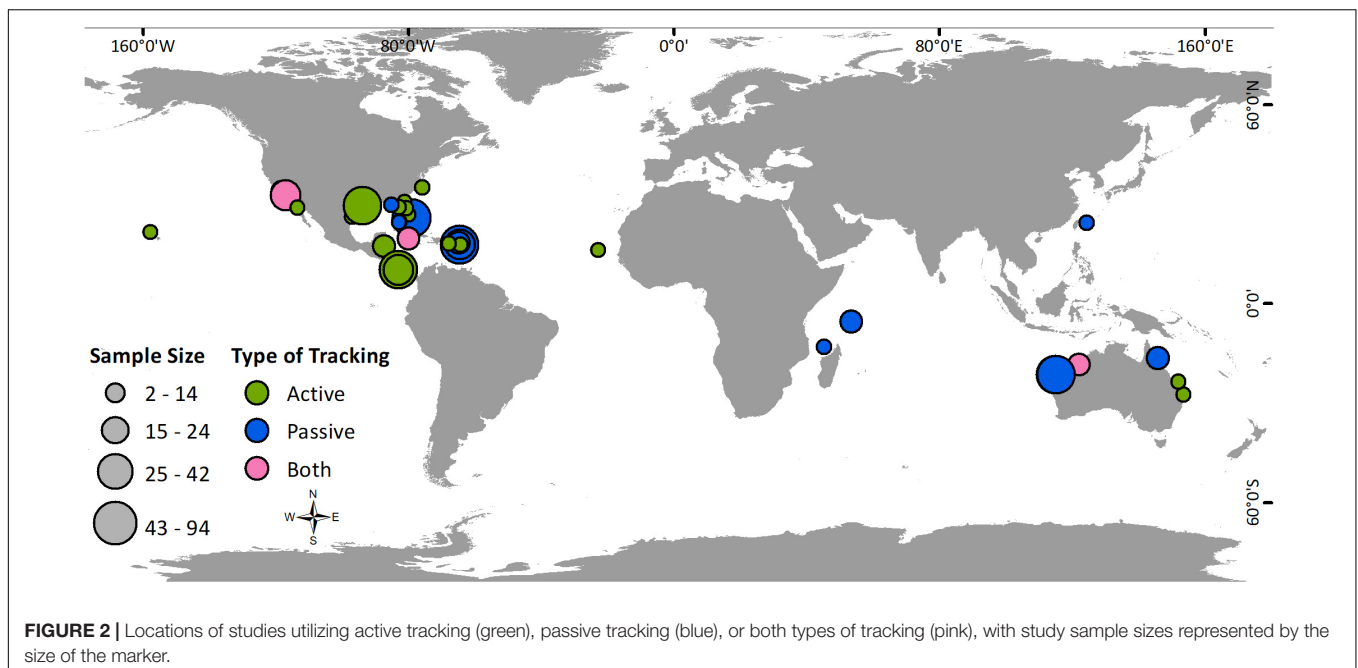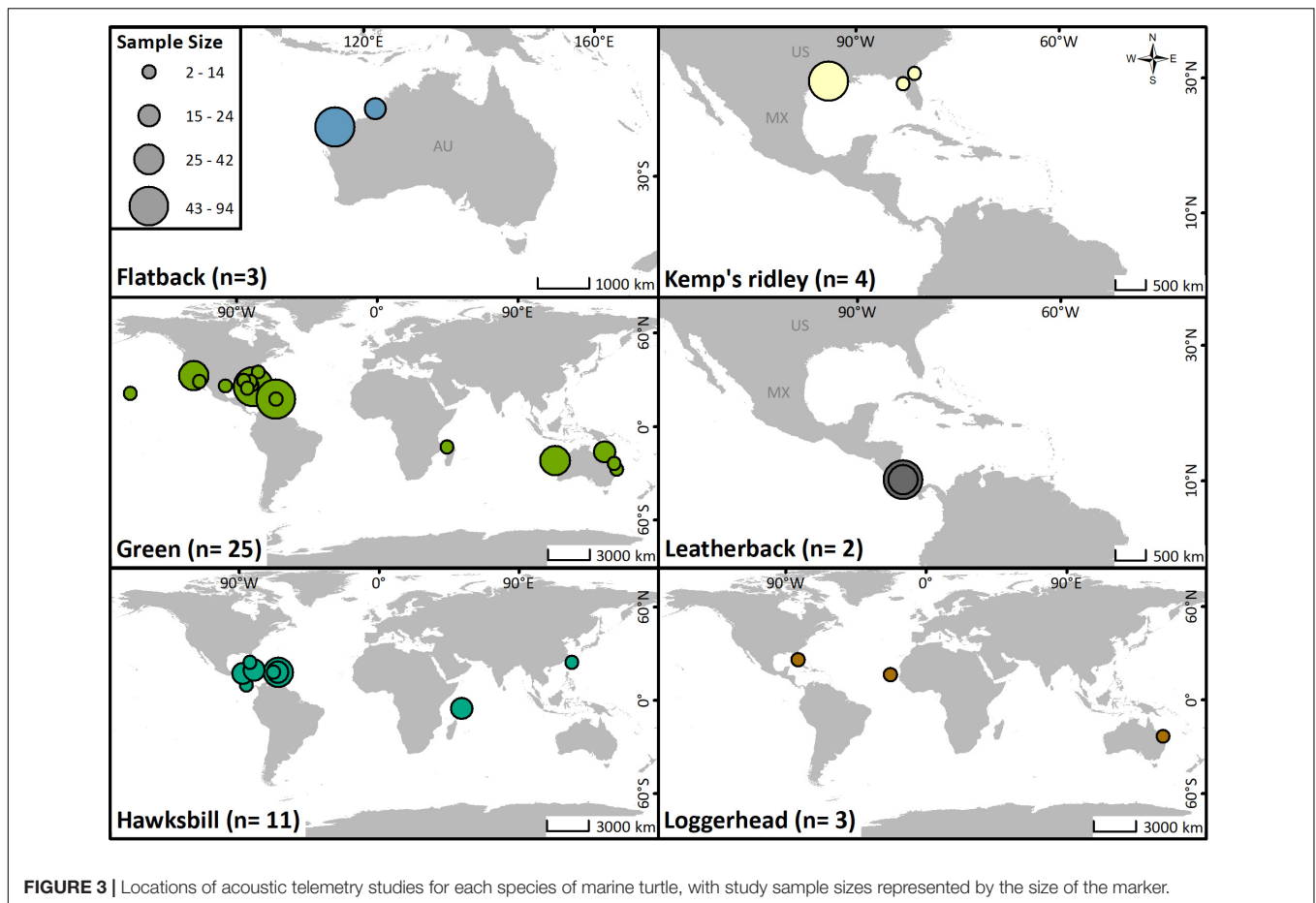


**FIGURE 2 |** Locations of studies utilizing active tracking (green), passive tracking (blue), or both types of tracking (pink), with study sample sizes represented by the size of the marker.

were less than 1 day (range: 5 min to 3.5 days) for active studies and 186 days (range: 7 min to 1,414 days) for passive studies. Short tracking durations were mostly those of hatchlings that traversed the study site quickly during their dispersal. Transmitter retention was largely unknown since in many cases (72%) it could not be discerned whether the transmitter was lost, the turtle never returned to the study area, or tracking ceased due to the end of the study. There were 55 known instances of tags becoming dislodged or lost from an individual,

of which the average tag retention was approximately 255 days (range: 1–1,414 days).

Acoustic telemetry has been used to obtain information on a variety of topics related to marine turtle ecology and conservation. Most studies (83%) to date have focused on the spatial distribution of juvenile, sub-adult, and adult marine turtles and have addressed questions related to their home range and site fidelity, movement, vertical space use, and the drivers that influence these (**Figure 5**). Additionally, acoustic telemetry

**FIGURE 3 |** Locations of acoustic telemetry studies for each species of marine turtle, with study sample sizes represented by the size of the marker.

has been used to explore hatchling dispersal, assess spatial proximity and response to threats, and monitor turtle health and physiological parameters (**Figure 5**). Several of these topics fall within the research priorities identified by experts in the field, with acoustic telemetry directly or indirectly addressing 60% of key questions identified by Hamann et al. (2010), Hays et al. (2016), and Wildermann et al. (2018) (**Supplementary Table 2**).
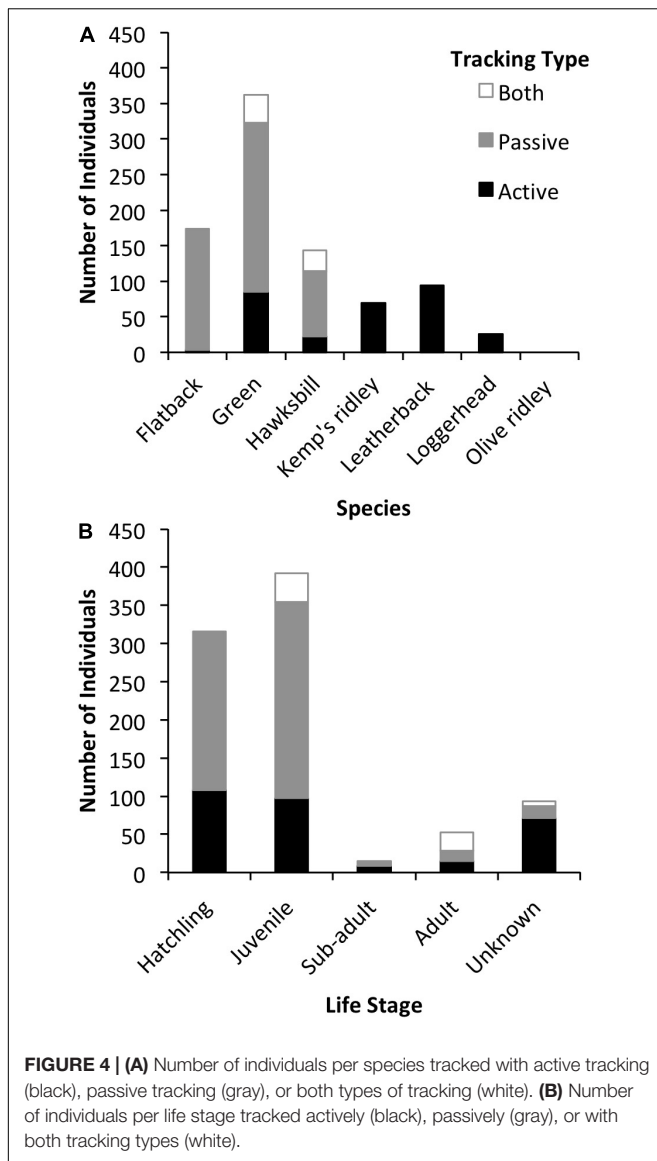
## DISCUSSION

While acoustic telemetry has been utilized by a relatively small number of marine turtle studies, the technology has provided a wealth of information regarding marine turtle ecology, particularly regarding spatial distribution and movement within study sites. Here, we detail the contribution of acoustic telemetry to our knowledge of marine turtle ecology and explore both commonly used approaches as well as those less routinely used. We discuss the application of acoustic telemetry toward marine turtle conservation, while also acknowledging its limitations.

## Spatial Distribution
### Home Range and Site Fidelity
Acoustic telemetry was utilized by over a third of studies to estimate the space use of individual marine turtles, including

minimum complex polygons, home ranges, and core use areas (**Supplementary Table 3**). In addition to identifying and quantifying these areas of regular use (**Supplementary Table 1**), studies also investigated the overlap among individuals, providing insight into simultaneous habitat use among marine turtles (Mendonca, 1983; Ogden et al., 1983; Schmid et al., 2003; Makowski et al., 2006; Scales et al., 2011; MacDonald et al., 2012; Hazel et al., 2013; Lamont et al., 2015; Fujisaki et al., 2016; Crear et al., 2017). Nearly half of all studies used acoustic telemetry to explore site fidelity (**Supplementary Table 3**), which, when combined with information on home ranges and overlap between individuals, can distinguish areas of high importance for marine turtles (Renaud et al., 1995; Blumenthal et al., 2009b; Hazel et al., 2013; Selby et al., 2019). Space use data from acoustic telemetry studies should be interpreted with care since detections are only possible when an individual is within the range of a receiver (Heupel et al., 2006; Whoriskey and Hindell, 2016). In our review, passively tracked marine turtles were detected on an average of 85% (n = 152) of the days they were tracked, indicating that individuals may utilize areas beyond the bounds of passive receiver arrays (Blumenthal et al., 2009b; Hart et al., 2012). Consideration of the spatial extent and design of arrays is necessary to avoid misinterpretation of results and underestimations of home ranges and fidelity indices (Heupel et al., 2006; McClellan and Read, 2009; Hart et al., 2012;

FIGURE 4 | (A) Number of individuals per species tracked with active tracking (black), passive tracking (gray), or both types of tracking (white). (B) Number of individuals per life stage tracked actively (black), passively (gray), or with both tracking types (white).



FIGURE 5 | Broad topics investigated by marine turtle acoustic telemetry studies with the number of studies ($n$ = 48) that explored or discussed each topic indicated.

Kessel et al., 2014; Whoriskey and Hindell, 2016). For home range analyses, receiver arrays should ideally be designed with overlapping detection ranges to avoid gaps in coverage, but costs of additional receivers and site characteristics prevent this in some cases (Heupel et al., 2006; Hazel et al., 2013; Chevis et al., 2017). Multiple factors (e.g., bathymetry, habitat type and rugosity, background noise) affect the detection probabilities of receivers and tests should be conducted to ensure that coverage is even across the study site to reduce spatial bias (Heupel et al., 2006; Kessel et al., 2014; Selby et al., 2016; Swadling et al., 2020). Of the passive studies included in this review, 73% conducted receiver range tests or modeled detection probability based on study site characteristics. With a well designed and tested array, or with the incorporation of analytical methods to account for inconsistencies in receiver detection ranges, acoustic telemetry is extremely useful in providing fine-scale spatial information to estimate home ranges (Heupel et al., 2006; Kessel et al., 2014).
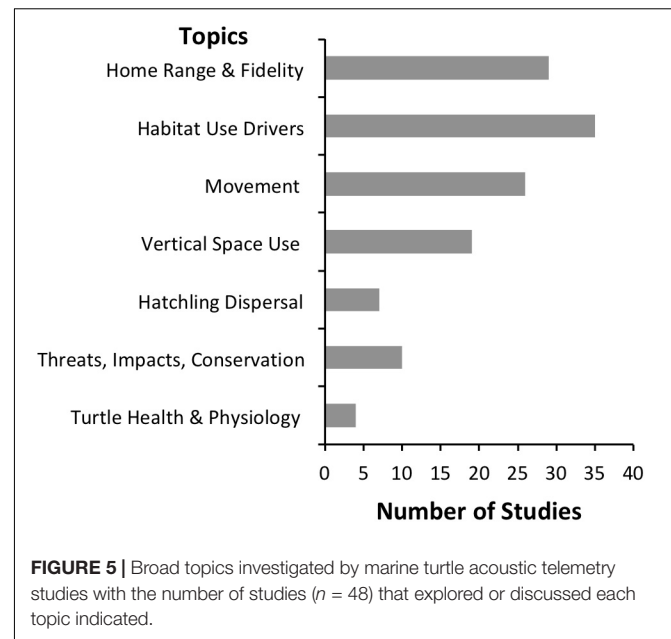
For marine turtles, it is best utilized in areas where turtles are known to aggregate and where arrays can be designed to cover the entire study area, such as juvenile and adult foraging areas where fidelity is high either within or across years.

## Habitat Use Drivers

Identifying the factors that drive home range size and selection can assist managers in predicting current and future habitat use, which can guide management decisions (Hazen et al., 2013; Schofield et al., 2013). Seventy-three percent of acoustic studies coupled space use data with additional data sets (e.g., habitat type, water temperature, diel patterns) to investigate the factors that drive marine turtle habitat use (**Supplementary Table 3**). For example, several studies examined habitat type associations (**Supplementary Table 3**) and found benthic substrate to be a main predictor of marine turtle spatial distribution (Renaud et al., 1995; Seminoff et al., 2002; Schmid et al., 2003; McClellan and Read, 2009; Lea et al., 2016; Griffin et al., 2019, 2020; Selby et al., 2019). Acoustic telemetry was used to further investigate patterns of habitat type use throughout the day to understand the influence of diel patterns and behavior on space use (**Supplementary Table 3**). Acoustic telemetry has also been used to analyze the influence of food availability and selection on marine turtle habitat use by pairing spatial data with esophageal lavages (Mendonca, 1983; Brand-Gardner et al., 1999; Makowski et al., 2006; Carrión-Cortez et al., 2013).

However, care should be taken when interpreting habitat type usage results derived from acoustic telemetry, as studies typically used broad habitat classifications and considered the habitat type to be homogenous within the entire detection zone of a receiver (Hart et al., 2012; Selby et al., 2019). Since detection ranges potentially reach distances > 500 m, this may not always be true or representative of the habitat type the individual was using at the time of the detection

(Heupel et al., 2006; McClellan and Read, 2009; Crear et al., 2016; Selby et al., 2019). If fine-scale information on habitat type associations is desired, geographic coordinates of an individual's location can be derived if it is simultaneously detected by three receivers (Wilson et al., 2019). While passive receiver arrays must be designed in a tight grid to enable this, specific habitat types at the individual's coordinates can be confirmed (Hart et al., 2012). Some habitat types, such as reefs and rocky structures, can also block acoustic signals leading to lower detections that underrepresent actual use of that habitat (Okuyama et al., 2010; Selby et al., 2016; Chevis et al., 2017). Regardless of these limitations, acoustic telemetry is commonly regarded as an appropriate tool for identifying general habitat type associations (Donaldson et al., 2014; Selby et al., 2019).

Other environmental habitat use drivers that have been investigated are season (Mendonca, 1983; Renaud and Williams, 2005; McClellan and Read, 2009; MacDonald et al., 2012, 2013; Carrión-Cortez et al., 2013; Crear et al., 2016), water temperature (Mendonca, 1983; Lamont et al., 2015; Madrak et al., 2016; Matley et al., 2020), moon index (Taquet et al., 2006), and air pressure (Matley et al., 2020). Individual metrics have also been studied, with a third of studies analyzing the relationship of turtle size and habitat use (**Supplementary Table 3**). Fujisaki et al. (2016) investigated how sex mediates space use among marine turtles which provided insight into attraction and territoriality between individuals (Fujisaki et al., 2016). Since sex can only be determined in the field for mature individuals by the presence of a large tail in males or the absence of such in females, this application is limited to specific populations of sexually mature individuals (Wibbels, 2003). However, this topic should be explored further as it has important implications for mate encounter frequency and levels of multiple paternity and their effects on populations (Uller and Olsson, 2008; Hays and Hawkes, 2018).

## Movement Patterns
Over half (54%) of marine turtle acoustic studies identified movement patterns, including displacement, rate of movement (**Supplementary Table 1**), movements between habitats, and the drivers that influence those movements (**Supplementary Table 3**). Additionally, Addison et al. (2002) utilized active tracking to explore the movement patterns of post-nesting females up to 12 km offshore. An advantage of active telemetry is that location points can be taken as often as desired as an individual is followed, allowing researchers to discern even small variations in movement paths (MacDonald et al., 2013; Crear et al., 2017). With passive telemetry, movement patterns within a study site are inferred as an individual is detected on various receivers along its path through an array (Heupel et al., 2006; Whoriskey, 2015). Some studies have also placed receivers in a linear fashion to monitor upstream and downstream movements of marine turtles in rivers (Crear et al., 2016). Movement between locations and the strength of those connections has been explored through network analyses, which have found that even when links to other suitable habitats exist, turtles rarely travel between sites (Lea et al., 2016; Griffin et al., 2019). Within sites, movements are predominately driven by behavior, diel patterns, and environmental factors, such as temperature and

tide (Mendonca, 1983; Renaud et al., 1995; van Dam and Diez, 1998; Schmid et al., 2002; Renaud and Williams, 2005; Seminoff and Jones, 2006; McClellan and Read, 2009; MacDonald et al., 2013; Crear et al., 2016, 2017; Griffin et al., 2019; Matley et al., 2020). Studying movement with acoustic telemetry is limited by short temporal durations of active tracking and the unknown path and direction of an individual between detections during passive tracking, both of which can affect displacement and rate of movement measurements (Heupel et al., 2006; Chevis et al., 2017). The interval at which transmitters send signals should be taken into consideration, as this will affect the timestep of location points used for movement analysis. Short intervals will increase the likelihood of signal collisions and autocorrelation of the data, but longer intervals decrease the temporal resolution of the data (Heupel et al., 2006). For the studies in this review, transmission intervals ranged from 1 s to 3 min. Compared to other technologies such as satellite telemetry, acoustic telemetry provides a higher number of detections for marine species and therefore may present a more representative picture of movement patterns within the extent of the receiver array (Hart et al., 2012; Dwyer et al., 2015). If very detailed movement patterns, displacement measurements, or rates of movement are of interest, active telemetry should be considered (Seminoff and Jones, 2006; Lamont et al., 2015; Crear et al., 2017).

## Vertical Space Use
With information of passive receiver depths or with depth measurements taken during active tracking, acoustic telemetry has been used to infer vertical space use of marine turtles. With the incorporation of depth sensors or radio telemetry devices, further insights into submergence and surfacing patterns, dive patterns, and depth usage can be explored. Indeed, 40% of studies have investigated vertical space use in coastal habitats (**Supplementary Table 3**). This topic is important to understanding exposure to certain threats, such as boating and fishing, as well as energetics associated with diving and depth usage (Southwood et al., 2003, 2006; Blumenthal et al., 2009b; McClellan and Read, 2009). Since radio signals do not transmit well through water, the addition of radio transmitters to the acoustic transmitter can provide information of how often a turtle surfaces, and for how long (Addison et al., 2002; Schmid et al., 2002). Depth sensors can also be easily incorporated into the acoustic transmitter to provide timed depth information (Gitschlag, 1996; Blumenthal et al., 2009b). Exploring depth usage is vital to understanding habitat use in the three-dimensional space that turtles occupy. It has been suggested that vertical habitat partitioning may occur, which has implications for individuals' access to food and shelter (Makowski et al., 2006; Blumenthal et al., 2009b; Hart et al., 2012; Carrión-Cortez et al., 2013). Further exploration of how depth mediates space use is necessary, but the cost of additional sensors may be a limitation to incorporating this data into acoustic telemetry studies (Matley et al., 2021a).

## Beyond Spatial Distribution
Information obtained by acoustic telemetry can help answer more complex questions beyond spatial distribution of marine turtles, such as whether certain behaviors are learned or innate

and the role of marine turtles within the ecosystem (Hays et al., 2016). Habitat use and movement patterns between groups of individuals can be easily compared with acoustic telemetry, an approach used by Okuyama et al. (2010) to gain insight into marine turtle behavior. By comparing acoustic telemetry data of wild-caught and head-started turtles, the study provided evidence that turtles may exhibit learned behaviors, such as the ability to navigate to previous locations and utilize rocky ledges for assisted resting (Okuyama et al., 2010). The role of marine turtles within the ecosystem also remains an understudied area and is a complex combination of habitat use, movement, foraging ecology, and predation (Hamann et al., 2010; Heithaus, 2013; Rees et al., 2016). Marine turtles affect seagrass growth and coral reef ecology through foraging and are responsible for small scale transportation of nutrients throughout their environment (Hill, 1998; Moran and Bjorndal, 2007; Schmitz et al., 2010; Heithaus, 2013; Rodriguez, 2018). Acoustic telemetry has been essential in identifying the extent of movement between foraging and resting sites, and provides insight into turtles' role in nutrient cycling (Taquet et al., 2006; Schmitz et al., 2010; Heithaus, 2013; MacDonald et al., 2013). Additionally, mapping the spatial overlap of turtles and their predators can inform trophic ecology and community dynamics (Heithaus et al., 2008; Hammerschlag et al., 2015). While studies on ecosystem role remain limited (Rees et al., 2016), acoustic telemetry may present an effective tool to gain the spatial information needed for future research in this area.

## Hatchling Dispersal

With the smallest transmitters weighing just under 0.4 g (Thums et al., 2013; Whoriskey and Hindell, 2016), acoustic telemetry offers a novel approach to gain *in situ* insights into the factors affecting nearshore marine turtle hatchling dispersal. It has been used to monitor movements of hatchlings to study the influence of oceanic conditions (Scott et al., 2014; Thums et al., 2016; Wilson et al., 2018; Barbour et al., 2020; Hoover et al., 2020), artificial light (Thums et al., 2013, 2016; Wilson et al., 2018, 2019), swimming speed and fitness (Scott et al., 2014; Barbour et al., 2020), and predation (Wilson et al., 2019) on dispersal patterns. These studies have found that while hatchlings exhibit active, directed swimming, oceanic conditions and anthropogenic factors (e.g., artificial lights, increased predation due to jetties) greatly affect their trajectories (Thums et al., 2013, 2016; Scott et al., 2014; Wilson et al., 2018; Barbour et al., 2020; Hoover et al., 2020), which has important implications for dispersal patterns, especially when considering the short- and long-term variability of oceanic conditions (Scott et al., 2014; Barbour et al., 2020). Data from acoustic studies can contribute to more accurate models and simulations of hatchling dispersal to better predict how changes in global climate, ocean currents, and coastal development will affect the survival and oceanic distributions of marine turtles (Scott et al., 2014; Thums et al., 2016; Wildermann et al., 2017; Putman et al., 2019).

Tracking hatchlings with acoustic telemetry comes with limitations. Passive studies are short in duration and distance, as hatchlings quickly transverse the receiver array (range: 5–35 min) and leave the nearshore area (Thums et al., 2013, 2016). Active

telemetry allows for longer tracking durations (range: 20 min to 8 h) over greater distances (12 km), but is labor intensive and can be affected by weather conditions (Heupel et al., 2006; Scott et al., 2014). While acoustic telemetry can only track hatchlings in the nearshore environment and does not allow tracking over the entirety of their dispersal pathway, tracking hatchlings is a unique benefit of acoustic telemetry. Other tracking approaches, such as satellite telemetry, currently do not have tags small enough to accommodate hatchlings (Mansfield et al., 2017).

## Threats, Impacts, and Conservation

Marine turtle spatial data can be coupled with information on threats, such as boating and fisheries, to identify and map areas of high exposure (Hart et al., 2018; Fuentes et al., 2020). However, only 10% of acoustic studies have taken advantage of this approach, possibly due to increased probability of loss or damage to receivers and decreased detection probability in areas of high vessel traffic (Clements et al., 2005; Heupel et al., 2006). Regardless, McClellan and Read (2009) used acoustic telemetry to analyze the overlap of small-scale fisheries operations with green turtle habitat, while four other studies assessed the presence of turtles within boating channels (Brill et al., 1995; Renaud et al., 1995; MacDonald et al., 2012, 2013). Findings from these studies can inform management strategy decisions, such as implementation of "go-slow" zones or marine protected areas (MPAs) (Schofield et al., 2013; Shimada et al., 2017; Fuentes et al., 2020). These strategies require planning and evaluation to ensure they are reaching their intended goals (Day, 2008). The effectiveness of MPAs at protecting marine turtle habitat has been evaluated with acoustic telemetry by assessing the percentage of habitat use that occurs within current or proposed MPA boundaries (Blumenthal et al., 2009b; Carrión-Cortez et al., 2013; Lea et al., 2016; Fuentes et al., 2018; Griffin et al., 2020). Acoustic telemetry has also facilitated a multispecies approach to MPA evaluation by tracking multiple species simultaneously (Lea et al., 2016). Effective evaluation of MPA success requires that passive receiver arrays overlap completely with the extent of the MPA.

Acoustic telemetry data can also help assess and predict the response of marine turtles to climate change (Madrak et al., 2016; Matley et al., 2020). Data from acoustic studies has shown that marine turtles make fine-scale changes in habitat use, movement patterns, and speed in response to changes in water temperature (McClellan and Read, 2009; Lamont et al., 2015; Madrak et al., 2016; Matley et al., 2020). As climate change progresses, distributions may shift as turtles adjust their habitat use to fit their thermal range and foraging preferences (Patel et al., 2021; Patrício et al., 2021). In addition, acoustic telemetry has shown that some juvenile marine turtles actively select for manmade structures over natural habitats, which could prompt small-scale shifts in habitat use as the number of jetties and other shoreline stabilization structures increase with rising sea levels (Renaud et al., 1995; MacDonald et al., 2013; Crear et al., 2017; Matley et al., 2019; Oppenheimer et al., 2019). As storm frequency and intensity increase, knowledge of marine turtles' response and survivability to storms is important (Fuentes and Abbs, 2010; Fuentes et al., 2019; Crowe et al.,

2020). Matley et al. (2020) and Lamont et al. (2021) assessed this response when separate Category 5 hurricanes moved over their passive array study sites. While turtles showed short-term changes in habitat use, all turtles survived and no long-term changes were observed (Matley et al., 2019; Lamont et al., 2021). An important caveat in analyzing data collected during storms is that wave action likely caused significant background noise and drastically reduced the detection probability of receivers (Heupel et al., 2006; Kessel et al., 2014; Matley et al., 2019; Lamont et al., 2021). Swells associated with extreme weather can also displace passive receivers, affecting spatial data collection. Indeed, Matley et al. (2019) noted the permanent loss of three receivers during the storm event.

## Health and Physiological Parameters

While less commonly utilized, acoustic telemetry has also been used to provide insights to turtle health and physiological parameters, with 8% of studies tackling this topic. Brill et al. (1995) compared the spatial distribution, movement, and depth use of turtles with fibropapillomas (FP) tumors and those without, noting no differences between the two groups. Additionally, three acoustic telemetry studies took advantage of active tracking to recapture individuals for subsequent physiological sampling. Wibbels et al. (1990) relocated and collected blood samples from adult female loggerhead turtles up to 9 times each over 4 months to assess reproductive hormone production. Southwood et al. (2006) used acoustic telemetry to recapture individuals injected with doubly labeled water to measure water flux and field metabolic rates. The same team also relocated and resampled turtles to determine differences in body and water temperatures across seasons (Southwood et al., 2003). While this approach is limited to areas where turtles can be reliably recaptured (e.g., foraging grounds where turtles display high site fidelity), these studies illustrate how acoustic telemetry can provide information beyond spatial distribution.

## FUTURE DIRECTIONS

Future marine turtle acoustic telemetry studies can build upon the approaches already established to develop novel ways to answer outstanding research questions. For example, further use of active tracking to recapture individuals can increase studies on physiological parameters over time (Wibbels et al., 1990; Southwood et al., 2003, 2006). Subsequent sampling of individuals can also inform epibiont colonization rates (Silver-Gorges et al., 2021), as well as provide additional data for growth rate curves (Patrício et al., 2014). Further, active tracking can be used to retrieve additional bio-logging equipment and sensors from individuals, allowing incorporation of *in situ* environmental data or video footage into studies (Harcourt et al., 2019; Jeantet et al., 2020; Smulders et al., 2021). Improved demographic information, including survivorship and timing of ontogenetic habitat use shifts, could be achieved with increases in acoustic studies investigating long-term home ranges and site fidelity (Hamann et al., 2010; Wildermann et al., 2018). Additionally, further studies analyzing predation and storm response could

inform survivorship rates. Acoustic arrays placed offshore of known nesting beaches could provide insight into the movement patterns of internesting females (Addison et al., 2002). While only 10% of current acoustic telemetry studies analyzed the spatial overlap of marine turtles with threats, this approach can be expanded upon to further conduct threat assessments of chemical spills, pollution (e.g., plastic, light, noise) and a variety of human activities (e.g., boating, snorkeling, fishing) (Hamann et al., 2010; Sequeira et al., 2019).

As the field of acoustic telemetry grows, it will be important to look to other taxa to learn new approaches. For example, fisheries and elasmobranch studies have utilized tightly gridded arrays to triangulate locations of individuals for more fine-scale location data and have analyzed social interactions among individuals (Armansin et al., 2016; Binder et al., 2018; Becker et al., 2020). While differences in life histories, morphology, and behavior may deem some approaches inapplicable to marine turtles, there is much to gain from reviewing studies from fields where acoustic telemetry has been more widely utilized, such as fisheries (see reviews: Heupel and Webber, 2012; Donaldson et al., 2014; Hussey et al., 2015; Matley et al., 2021b). Currently, one of the main limitations to marine turtle acoustic studies is that transmitters are applied externally, which reduces the retention time compared to transmitters surgically implanted in fish and shark species (Smith et al., 2019; Smukall et al., 2019; Kennedy et al., 2020). Although marine turtle transmitter retention varies by species, the longest recorded duration (hawksbill) was just under 4 years (Chevis et al., 2017; Smith et al., 2019). Further research is needed to identify the effect of transmitter application techniques on tag retention rates. Meanwhile, active telemetry can be used to recapture individuals and proactively replace transmitters that are loose or near the end of their battery life in order to increase tracking durations (Selby et al., 2019).

Despite its limitations, acoustic telemetry's capacity for answering important research questions is growing due to its advantages in providing spatial information on hard-to-monitor species and with the proliferation of acoustic tracking networks (Bangley et al., 2020; Matley et al., 2021b). With data-sharing within networks, acoustic studies can potentially span coastal regions and even ocean basins and inform migration paths and long-distance movements of marine species (Guttridge et al., 2017; Young et al., 2020). Networks, such as the OTN, are dedicating resources toward establishing standardization of metadata and analysis protocols and are working with manufacturers to resolve differences between transmitter models and encourage open decoding protocols (Whoriskey, 2015; Bangley et al., 2020; Reubens et al., 2021). New technologies are being developed to aid in data retrieval, such as autonomous underwater vehicles (AUVs) that can retrieve data from receivers, as well as systems that can transmit detection data to the surface with a modem and hydrophone. Advancements are also being made in utilizing marine organisms and AUVs as roving receiver platforms to increase detection probabilities (Whoriskey, 2015; Davis et al., 2018; Bangley et al., 2020; Ennasr et al., 2020). A proposed framework for standardization of data across all biotelemetry technologies will increase compatibility of data and

improve biotelemetry's ability to inform spatial distribution of marine species (Sequeira et al., 2021).

The combination of these advances provides opportunities for the exploration of a wider scope of topics related to marine species ecology and conservation. Data sharing can lead to studies that track multiple species to identify global hotspots for biodiversity and examine both intra- and interspecies interactions to understand social behavior among individuals, as well as predator-prey relationships. The advancement of multispecies studies can lead to ecological rather than species-level approaches to conservation and management (Lea et al., 2016; Brodie et al., 2018; Bangley et al., 2020).

## DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author/s.

## AUTHOR CONTRIBUTIONS

MF developed the initial concept for this review and provided critical edits to the final manuscript. EH designed and conducted the systematic search, extracted and analyzed the data, and wrote the original manuscript. Both authors contributed to the article and approved the submitted version.

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