Does transmitter placement or species affect detection efficiency of tagged animals in biotelemetry research?

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ABSTRACT

Acoustic telemetry has quickly become a powerful tool for ecological research in aquatic systems, yet our knowledge of in situ transmitter performance remains limited. Here, we used an experimental approach to test the influence of three biotic factors on the detection range of acoustic transmitters: (1) internal versus external placement of the transmitter on a model finfish species, red drum (*Sciaenops ocellatus*); (2) attachment of a transmitter on an animal host (red drum) versus a fixed object; and (3) species comparison between internally tagged red drum and southern flounder (*Paralichthys lethostigma*). Significant differences in detection probability were observed between internally and externally placed transmitters as well as between transmitters attached to an animal host (red drum) and those attached to a fixed line, while no effect was observed between the two species tested. External transmitters were detected significantly more than corresponding internal transmitters in red drum, and outperformed internal transmitters by 2–7 fold at distances >100m. Similarly, detection probability declined more quickly as a function of distance for transmitters attached to red drum relative to transmitters attached to a fixed line, with greater differences observed at distances >300m. Findings from this study challenge commonly held assumptions in acoustic telemetry research and suggest that traditional range testing methods are likely to considerably overestimate detection range of tagged animals in situ. Accounting for the influence of transmitter placement will enhance study design in acoustic telemetry research and ultimately improve detection efficiency and data interpretation in animal movement studies.

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1. Introduction

The study of animal movement is rapidly increasing amid growing efforts to assess the effects of habitat loss/fragmentation and climate change on animal distributions (Nathan et al., 2008; Schick et al., 2008). Animal movement patterns can provide researchers with a better understanding of how animals interact with their environment across a range of spatial and temporal scales (Morales and Ellner, 2002; Patterson et al., 2008; Morales et al., 2010). In recent years, technological advances in biotelemetry and geographic information systems have greatly improved our ability to track animals and relate patterns of movement to their environment (Cooke et al., 2004; Cagnacci et al., 2010; Hussey et al., 2015). Although the study of animal movement has progressed rapidly in a relatively short period of time, studies identifying potential uncertainty and limitations associated with animal tracking technologies are lacking and are needed to improve interpretations of movement data (Frair et al., 2010; Fieberg et al., 2010).

The ability of researchers to characterize animal movements is considerably impaired in aquatic systems, and acoustic telemetry has quickly become a powerful tool to examine movement patterns of marine and freshwater taxa (i.e. fishes, crustaceans, cephalopods, mammals) (Donaldson et al., 2014; Hussey et al., 2015). Acoustic receivers can be deployed in a variety of configurations to address different research questions and range in size from small arrays to examine site fidelity to a particular habitat, to mesoscale gridded arrays for estimating home range and activity spaces across larger water bodies (i.e. bays, lakes), to widely dispersed receiver lines (i.e. curtains or gates) deployed at intervals along a coast or river to monitor fish passage associated with broad movements or migrations (see Heupel et al., 2006). In addition, recent advancements have given researchers the ability to deploy high-density arrays of receivers with overlapping listening areas (acoustic positioning systems) to triangulate animal positions and
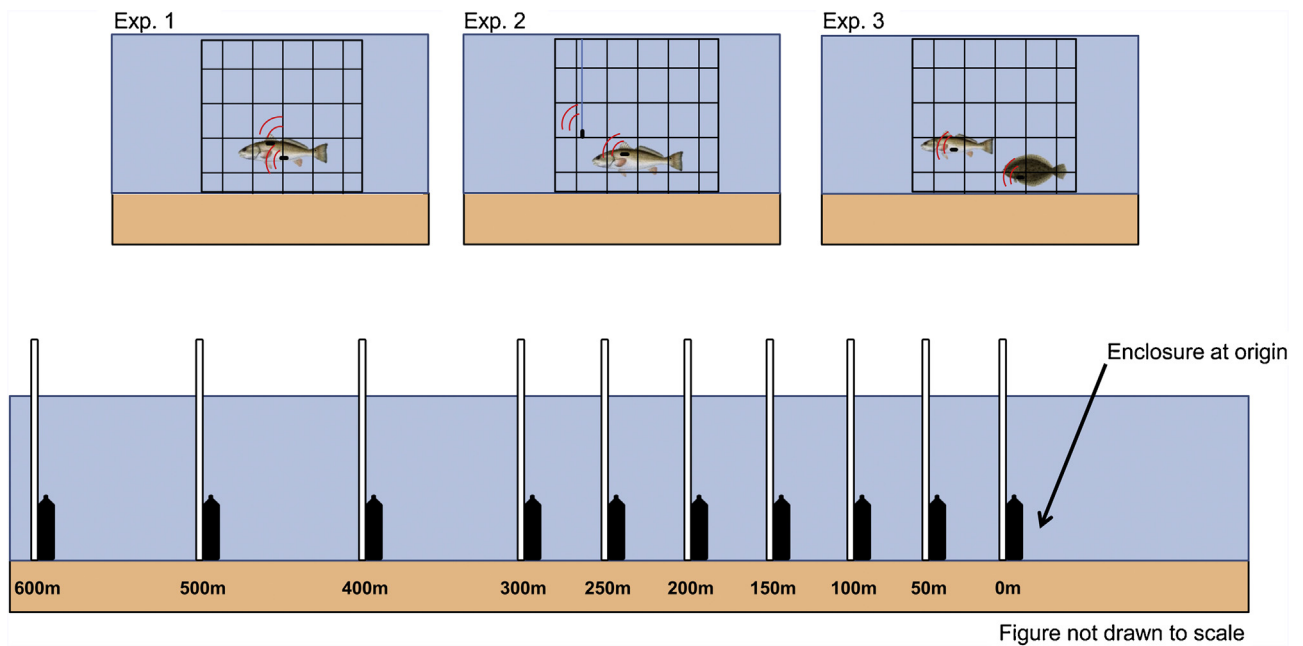
Fig. 1. Schematic of experimental design, which consisted of a 1-m^3 enclosure and a line of acoustic receivers secured to polyvinyl chloride (PVC) moorings at set distances from the enclosure (0, 50, 100, 150, 200, 250, 300, 400, 500, 600 m). In the first experiment (Exp. 1) red drum were simultaneously fitted with an internal and external transmitter. In the second experiment (Exp. 2), red drum were fitted with an external transmitter and a second transmitter was attached to a fixed monofilament line. In the third experiment (Exp. 3) both a red drum and southern flounder were fitted with an internal transmitter. Distances and sizes are not drawn to scale.

provide fine-scale animal tracks (Espinoza et al., 2011; Grothues et al., 2012; Capello et al., 2013; Furey et al., 2013). Despite the sharp increase in acoustic telemetry studies over the last decade (Kessel et al., 2014), our understanding of the range at which receivers can detect transmitters is still surprisingly limited. This discrepancy between application and understanding can lead to poorly designed receiver configurations and ultimately misinterpretation of acoustic telemetry data (Payne et al., 2010; Gjelland and Hedger, 2013).

A variety of factors can affect the ability of acoustic receivers to detect transmitters including environmental and meteorological conditions (Gjelland and Hedger, 2013), ambient noise (Welsh et al., 2012), biofouling (Heupel et al., 2008), transmitter type/power (How and de Lestang, 2012; Cagua et al., 2013), depth (Gjelland and Hedger, 2013), and diel (Payne et al., 2010) or tidal (Mathies et al., 2014) cycles. The influence of many of these factors varies across systems, and thus it is generally recommended that researchers conduct range tests within a study site prior to and/or during a study to estimate the distance from a receiver that a tag can be reliably detected within an array (Heupel et al., 2006; Payne et al., 2010). The majority of range tests are aimed at determining the impact of environmental variables, and therefore detection range is typically estimated from fixed transmitters in water despite the fact that the most common method of attachment for fish is to surgically implant the transmitter into the coelomic cavity rather than attaching it externally (Cooke et al., 2011; Johnson et al., 2015). Thus, range tests are largely conducted under the assumption that transmitter performance in water will not differ from transmitter performance when internally implanted within or externally attached to the host animal (Kessel et al., 2014). Moreover, if the body wall of the tagged animal does indeed affect transmission, it might then be further expected that these effects would be dependent upon body morphology. Nevertheless, the effect the tagged organism (or tagging method) has on detection range of acoustic transmitters is poorly understood.

Here we utilize an experimental approach to test the effects of three biotic factors affecting acoustic telemetry studies. We first examined the effect of transmitter placement (internal vs. external) on detection range of a common estuarine finfish, red drum (*Sciaenops ocellatus*). Next, we assessed the impact of the host animal (red drum) on detection range by comparing detection range of a transmitter fixed to a line to that of a transmitter attached to an animal. Lastly, we compared detection range of internal transmitters in red drum to another common estuarine fish that differs in body type, southern flounder (*Paralichthys lethostigma*), which has a laterally compressed body ("flatfish").

2. Materials and methods

Experiments were conducted between February and December 2013 in Galveston Bay, a large estuary in the northern Gulf of Mexico. Benthic structure of the study site was homogenous, and characterized by bare sand substrate and relatively uniform depth [1.02 ± 0.03 m (mean ± SE)]. Tagged fish and transmitters used in experiments were placed inside a 1-m^3 enclosure comprised of a polyvinyl chloride (PVC) frame and plastic mesh that was secured to a PVC pole at the origin of a line of receivers (Vemco VR2W, n = 10) attached to fixed (PVC) moorings located 0, 50, 100, 150, 200, 250, 300, 400, 500, and 600 m from the enclosure (Fig. 1). This structure allowed for movement of tagged individuals within a restricted area to account for some natural variability in detection probability due to fish movement and orientation, while also controlling for transmitter location and preventing predation. The order of receivers was randomized for each replicate trial to reduce the effects of individual receiver performance on detection range (Heupel et al., 2008).

Red drum was chosen as a model fish species and was used in all three experiments, while southern flounder was used as a contrasting species in the third experiment. Both species have been previously used in telemetry studies (Furey et al., 2013; Fodrie et al., 2015; Dance and Rooker, 2015) and co-occur over much of their range. Individuals were captured via hook and line and held in 1.7 m^3 tanks at the Texas A&M University Sea Life Center. Fish were anaesthetized with clove oil prior to tagging and fitted with Vemco

Table 1

Mean difference (±SE) in detection probability as a function of distance between paired samples for three experiments testing biotic factors influencing detection efficiency of acoustic transmitters: (1) Ext-Int (difference between paired external and internal transmitters on red drum), (2) Fix-RD (difference between transmitter attached to a fixed line and transmitter externally attached to a red drum), (3) SF-RD (difference between transmitters internally implanted in southern flounder and red drum). Asterisks represent significant differences at $\alpha = 0.05$ (paired t-test; P < 0.05), while q-values represent p-values adjusted to control the false discovery rate (also set at 0.05). Effect size is given as Cohen's d (d), where the corresponding effect size magnitudes using the thresholds defined in Cohen (1992) are: negligible (|d| < 0.2), small (0.2 < |d| < 0.5), medium (0.5 < |d| < 0.8), large (|d| > 0.8). Large effect sizes are indicated with bold font. Experiment 3 was only conducted between 0 and 400 m.

Distancece	Experiment 1			Experiment 2			Experiment 3		
	Ext-Int	q	d	Fix-RD	q	d	SF-RD	q	d
50 m	0.06 (0.03)	0.11	**1.33**	0.00 (0.02)	0.81	−0.35	0.01 (0.01)	0.56	0.52
100 m	0.35 (0.13)	0.07	**1.68**	0.01 (0.04)	0.81	0.29	0.11 (0.06)	0.56	0.79
150 m	0.48 (0.13)*	0.03	**2.64**	0.04 (0.06)	0.32	**1.55**	0.13 (0.13)	0.71	0.49
200 m	0.57 (0.09)*	0.02	**3.14**	0.14 (0.09)	0.32	**1.74**	0.06 (0.14)	0.98	0.16
250 m	0.60 (0.14)*	0.03	**2.34**	0.17 (0.1)	0.34	**1.64**	0.00 (0.11)	0.98	0.01
300 m	0.64 (0.11)*	0.02	**3.19**	0.23 (0.08)*	0.20	**3.10**	−0.01 (0.09)	0.98	−0.03
400 m	0.51 (0.12)*	0.03	**1.99**	0.26 (0.15)	0.28	**1.99**	−0.04 (0.04)	0.71	−0.46
500 m	0.50 (0.14)*	0.03	**1.87**	0.24 (0.12)*	0.20	**1.62**			
600 m	0.31 (0.09)*	0.03	**1.66**	0.22 (0.11)	0.20	**1.19**			

V9-1H coded transmitters (69 kHz, 9 mm diameter × 24 mm length, 151 dB) with a nominal delay of 15 s (range 10–20 s). V9 transmitters are commonly used to study movement patterns of fishes and invertebrates in a range of systems (e.g. Welch et al., 2011; Bloor et al., 2013; McMahan et al., 2013). External tagging followed a protocol modified from Furey et al. (2013) in which each transmitter was fixed to a vinyl Peterson disc tag (FloyTag Inc) with heat shrink wrap and mounted to the dorsal musculature of the fish. Two sterilized nickel pins held in place by another vinyl Peterson disc tag were passed through the dorsal musculature and secured to the vinyl disc tag holding the transmitter with rubber earring backings and a metal crimping sleeve. Internal transmitters were surgically implanted into the coelomic cavity via a small ventral incision and closed with one or two interrupted sutures (4-0 Ethicon vicryl). Overall, six V9-1H transmitters were used in the study and transmitter pairings for each trial were rotated to minimize the effect of any individual transmitter on detection range.

To test the effect of internal versus external placement on transmitter performance, we conducted replicate trials on five consecutive days with similar environmental conditions. Prior to each trial, a single red drum (55.9 ± 1.5 cm; mean ± SE) was fitted with both an internal and external V9-1H transmitter and placed in the field enclosure after a recovery period (minimum 1 h). Receivers (random order) were then deployed at the fixed moorings located at set distances from the enclosure (see Fig. 1). Data were recorded for approximately three hours, after which the fish and receivers were recovered and data were uploaded. Five V9-1H transmitters were used for this experiment and the pairing of transmitters used in each trial was unique. No transmitter was used more than twice as either an internal or external transmitter.

The second experiment tested for differences in detection range between transmitters on an animal host (red drum) and attached to a fixed line. This experiment followed a similar procedure to the first, with the exception that red drum (TL: 55.0 ± 3.0 cm) were fitted with only an external transmitter and placed in the enclosure with a fixed transmitter that was suspended from the top of the enclosure via monofilament line 0.5 m above the substrate (Fig. 1). A unique red drum was used for each of the three replicate trials, with receiver order and transmitters again randomized for each trial. Because we were unable to conduct this experiment on consecutive days, each trial lasted 24 h to account for variability in weather conditions and daily cycles (tide, day/night) among replicates (n = 3).

The third experiment tested for differences in detection range between red drum and southern flounder, two species that differ in body morphology. Prior to each trial, a red drum (39.8 ± 4.5 cm; total length ± SE) and southern flounder (39.8 ± 2.9 cm) of simi-

lar size were fitted with internal transmitters and placed in the enclosure (Fig. 1). The rest of the trial followed a similar procedure described previously for the other two experiments, with the exception that detection range was tested to 400 m (set distances of: 0, 50, 100, 150, 200, 250, 300, 400 m) rather than 600 m. Different red drum and southern flounder were used for each of five replicate trials, with receiver order and transmitters randomized before each trial. Similar to the second experiment, we were unable to conduct the experiment on consecutive days, and therefore, we used 24-h time periods to account for variability in weather conditions and daily cycles among days.

Transmitter detections recorded per receiver during each trial were converted to a detection probability by dividing the number of detections at a given receiver by the number of detections recorded by the receiver at the origin (0 m). This methodology was used rather than dividing by the theoretical number of transmissions to eliminate transmissions not detected by receivers due to acoustic collisions (Heupel et al., 2006). Mean collision rate across all experiments (46.3 ± 0. 7%; mean ± SE) was nearly identical to the predicted collision rate (for two transmitters with a 15 s nominal delay) of 46.5%, and no significant differences in collision rate were observed between treatments in experimental trials (paired t-test, P > 0.05). Analysis of covariance (ANCOVA) was used to test the variation in the relationship between detection probability and distance among treatment groups for each of the three experiments. Detection probability was the dependent variable for each ANCOVA model with transmitter treatment as the independent variable and distance from transmitter as the covariate. In each case, preliminary models were run first (slopes test, interaction regression) to determine if slopes of the regression lines differed between treatments. The main effects test of the ANCOVA (y-intercept) was only performed for experiments in which the assumption of parallel slopes was met. Mean differences in detection probability between paired samples in each experiment were assessed with paired t-tests to determine the magnitude and specific distances at which differences occurred in each experiment. Adjusted p-values (q-value) were used to control the false discovery rate (FDR) at $\alpha = 0.05$ (Benjamini and Hochberg, 1995), which is the preferred adjustment to correct for multiple comparisons in ecological studies (Nakagawa, 2004; Pike, 2011). Although it is generally acceptable to use the uncorrected p-value in this case, given that each comparison tested a different distance-specific null hypothesis (Cabin and Mitchell, 2000), we present both corrected and uncorrected values. We then calculated effect size for each paired comparison using Cohen's d (Cohen, 1992) to examine the magnitude of the treatments tested, where effect size magnitudes are: negligible (d < 0.2), small (d = 0.2–0.5), medium (d = 0.5–0.8), and large (d > 0.8).
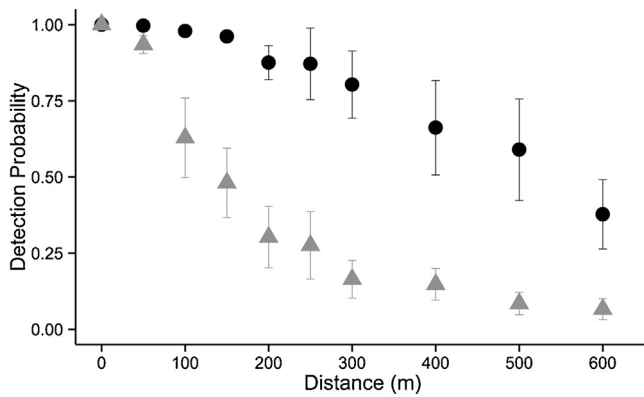
Fig. 2. Mean detection probability as a function of distance for external (●) and internal (▲) transmitters simultaneously attached to red drum. Error bars are ± 1 SE of the mean from five replicate trials.

Fig. 4. Mean detection probability as a function of distance for transmitters internally implanted in southern flounder (●) and red drum (▲). Error bars are ± 1 SE of the mean from five replicate trials.

3. Results

Detection probability declined with increasing distance from transmitter for all experiments. Mean detection probability was significantly greater for external transmitters than internal transmitters (ANCOVA y-intercept; P < 0.001), and ranged from 1.00 (50 m) to 0.38 (600 m) for external transmitters compared to 0.93 (50 m) to 0.07 (600 m) for internal transmitters. External transmitters outperformed internal transmitters in paired comparisons at all distances in every trial (see Table 1, Fig. 2), and mean differences in detection probability between paired external/internal transmitters at each distance ranged from a minimum of 0.06 at 50 m to a maximum of 0.64 at 300 m. Differences in detection probability were significant between treatment pairs at all distances greater than 100 m (paired t-tests; P < 0.05), with external transmitters detected 2–7 times more frequently at these distances (Fig. 2). While large effect sizes were observed for all comparisons (Cohen's d > 1.3), smaller but consistent differences in detection probability between internal/external pairs at 50 m (mean difference = 0.06) and 100 m (0.35) were not significant (paired t-tests; P > 0.05).

The rate of decline in detection probability as a function of distance differed between transmitters attached to an animal host (red drum) and those attached to fixed line (ANCOVA slopes test; P < 0.01), with transmitters on red drum detected less frequently as distance increased. Mean detection probability ranged from 1.00 (50 m) to 0.47 (600 m) for transmitters attached to the line, and from 1.00 (50 m) to 0.25 (600 m) for transmitters externally attached to red drum. While transmitters performed
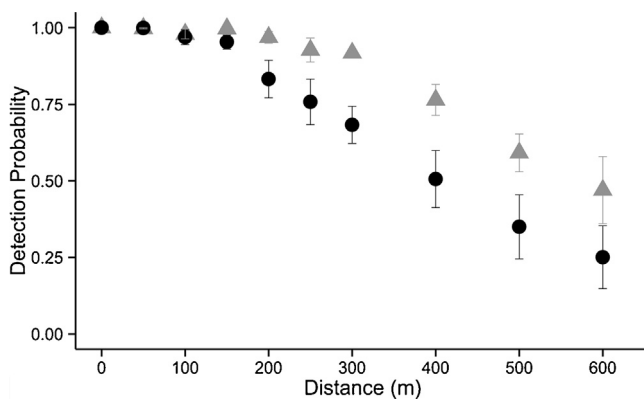
similarly between treatments from 50–150 m (mean paired difference < 0.05 m), transmitters attached to the line were consistently detected more frequently than transmitters on red drum at distances greater than 150 m (range: 0.14–0.26, Table 1, Fig. 3). We also observed very large effect sizes at most distances (d > 1.5), yet despite the magnitude of these differences, paired comparisons at each distance indicated that transmitter treatments were significantly different at only two distances: 300 m and 500 m (paired t-tests; P < 0.05), and no differences were detected at any distance after controlling for FDR (q > 0.05) (Table 1).

Red drum and southern flounder were used as model species to test for species-specific differences in detection range. Detection probability for transmitters internally placed in red drum and southern flounder did not differ statistically (ANCOVA y-intercept test; P > 0.05). Mean detection probability ranged from 0.99 (50 m) to 0.08 (400 m) for red drum and from 0.99 (50 m) to 0.05 (400 m) for southern flounder. Examination of differences in paired treatments indicated that transmitters placed in southern flounder were often detected more frequently at closer receivers (<150 m) than transmitters placed in red drum (Table 1, Fig. 4). However, differences in detection probability between the two species were variable across the 5 trials, and no significant differences in detection probability were found at any distance (paired t-tests; P > 0.05).

4. Discussion

Here we demonstrate that the placement of acoustic transmitters affects their performance, with detection probabilities of external transmitters on red drum being 2–7 fold higher than internal transmitters at receiver distances >100m. This finding suggests that intracoelomic implantation of acoustic transmitters in fish may reduce the detection range of transmitters. Our results are in accord with previous studies that reported reductions in detection efficiency and/or signal strength associated with internal transmitters in both radio-telemetered finfish (Cooke and Bunt, 2001) and acoustically-tagged cuttlefish (Jackson et al., 2005). In fact, cuttlefish simultaneously tagged with internal and external transmitters were detected four times more efficiently with the external transmitter (Jackson et al., 2005), which is similar to our findings and suggests that signal attenuation likely occurs at a higher rate for acoustic transmitters placed inside the body cavity of the host species.

While the exact mechanism of signal attenuation is unknown, submerged aquatic vegetation, biofouling, mineralized hard parts, and several different biological tissues have all been shown to reduce the detectability of acoustic transmissions (Jackson et al., 2005; Heupel et al., 2008; Wilson et al., 2013). Still, any reduction

Fig. 3. Mean detection probability as a function of distance for transmitters attached to a fixed line (▲) and externally to red drum (●). Error bars are ± 1 SE of the mean from three replicate trials.
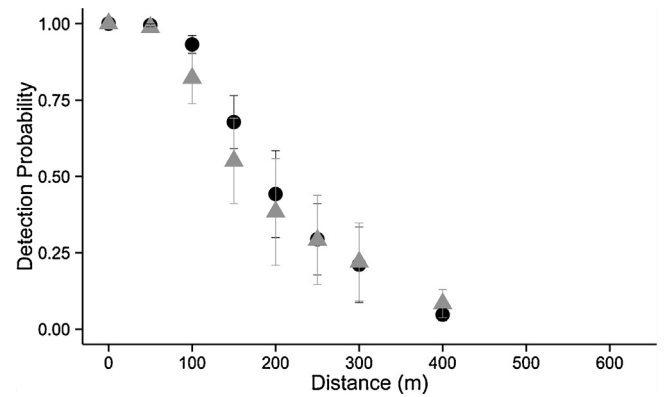
in detection range caused by intracoelomic implantation of acoustic transmitters is widely assumed to be negligible because the density and sound properties of animal tissues are thought to be similar to that of water (Kessel et al., 2014). This may be true for tissues with high water content, as acoustic attenuation is negatively correlated to tissue water content and those tissues with high water content are more likely to have similar sound properties to water (Olerud et al., 1990). However, attenuation is positively correlated with collagen concentration in tissue (O'Brien, 1977; Olerud et al., 1990; Mast, 2000), and therefore we might expect tissues with higher collagen content such as bones, tendons, and fish scales to have higher acoustic impedance (Pohlhammer and O'Brien, 1980), potentially increasing signal attenuation from transmitters placed in the body cavity of the host animal. While we cannot unequivocally determine the direct cause of the observed reduced detection range for internal transmitters in this study, the consistent and substantial difference in detection probability between internal and external transmitters across a range of distances suggests that traditional range tests of transmitters, which are often performed by attaching the transmitter to a fixed structure, will overestimate the detection range of surgically implanted transmitters.

The detectability of acoustic transmitters can also be influenced by the behavior of the study animal (Heupel et al., 2006; Grothues et al., 2012), and therefore the movement or orientation of a tagged animal may likewise impact detection range. Our second experiment showed that detection probability declined more rapidly for transmitters attached to an animal host relative to transmitters attached to a fixed line. This finding suggests that attaching transmitters to fixed or stationary objects during range tests may not accurately represent the detection range of externally tagged animals in situ. Coupling this result with findings from our first experiment showing reduced performance for internally placed transmitters, it is likely that conventional range testing (i.e., transmitter attached to a nonliving object) considerably overestimates the detection range achieved for internally tagged fish or other animal hosts. In the current study, tagged red drum were free to move within a limited area inside the experimental enclosure, and observed differences in detection probability between transmitters attached to red drum and the fixed line were likely reflective of red drum movement or orientation within the enclosure. Similarly, other studies have shown that animal orientation or transmitter movement can negatively affect the accuracy of acoustic telemetry systems (Espinoza et al., 2011; Grothues et al., 2012).

Given the observed reduction in detection range for internal acoustic transmitters in the first experiment, it might be expected that variation in body type between red drum and southern flounder would lead to differences in transmitter performance. Multi-species acoustic telemetry studies are increasingly utilized to examine species interactions (Speed et al., 2011; McMahan et al., 2013; Dance and Rooker, 2015; Hussey et al., 2015), and the ability to make comparisons between or among species is dependent on the assumption that internal transmitters perform similarly among species. In the current study, we observed that detection range was statistically similar between these two species even though their body types differ markedly, suggesting that species-specific differences in detection range may be minimal. This was surprising given that the body wall of a red drum is significantly thicker than that of a southern flounder (Dance, 2016), and makes it seem unlikely that the thickness of the body wall is the sole mechanism reducing detection range of internal transmitters relative to externally attached transmitters. Although we did not detect differences between red drum and southern flounder, it is possible that we were unable to detect differences that may actually occur in situ due to behavioral differences. The enclosure likely precluded fish from natural behaviors (i.e. active swimming, burying, association with submerged aquatic vegetation, etc.) that could affect transmitter performance (see Grothues et al., 2012), reducing our ability to detect behavior related differences. Future studies that examine the influence of swimming speed, position in the water column, or habitat preference on detection range would be beneficial to our understanding of the impacts of species-specific behavior on transmitter performance.

A variety of factors can affect the detection range of acoustic transmitters (Kessel et al., 2014), and it is possible that relationships described here could vary across different transmitter types or ecosystems. Previous studies have shown that transmitter type and power output impacts detection range (How and de Lestang, 2012), and thus it is possible that transmitters with a higher or lower power output than those used in this study may not respond in the same manner. Nonetheless, the conspicuous difference in detection range for internal and external transmitters presented here suggest a similar effect is likely for other transmitter types (i.e. power outputs), although further testing would be needed to determine the magnitude of this effect. Detection range for our transmitters attached to a fixed line (>50% detection probability at 500 m) was comparable to or exceeded reported detection ranges (150–500 m) for fixed transmitters of similar power output in previous estuarine or coastal studies (Chittenden et al., 2008; Sulak et al., 2009; Francis, 2013) and far exceeded that of transmitters in reef systems (50–150 m) (How and de Lestang, 2012; Welsh et al., 2012). Because detection range can vary across systems of varying complexity and depth (i.e. reefs, coastal, riverine, offshore), there may be variability in the magnitude of the effects of the host animal on detection range. However, comparisons to previous studies also suggest that our system may represent a favorable acoustic environment and the reduction in detection range associated with transmitter placement shown here could be conservative relative to systems with greater influence from environmental factors that attenuate acoustic signals (e.g. noise, wind/sea surface variability, depth).

Our results highlight the value of in situ range testing using animal hosts and suggest that the use of external transmitters may be beneficial, depending on the research aims of the study, as it will likely improve detection range. Still, the use of internal transmitters is often advantageous to other research goals (i.e. increased study duration) and intracoelomic implantation remains the most common attachment method in fish. Therefore, in such instances, researchers should consider range testing with an internally tagged animal to provide the most realistic estimates of detection range for transmitters in situ. Because it is not always feasible to use animals during range testing, caution should be used when interpreting traditional range tests, particularly during the planning phase of studies that deploy arrays such as curtains, gates, and acoustic positioning systems that rely on receiver spacing to effectively cover an area of interest (see Heupel et al., 2006; Espinoza et al., 2011). Overestimating detection range can lead to inadequate receiver spacing and reduced detection efficiency, ultimately impairing the ability of researchers to detect movement patterns, fish passage, and fish-habitat relationships. As a result, there is increased potential for animals to be present but not detected within acoustic arrays, which can lead to spurious conclusions such as reduced home range or residency estimates, underestimation of connectivity among locales, and/or overestimation of mortality in migration studies (if detection efficiency is not estimated from the study animals directly; i.e. Welch et al., 2011 and Clark et al., 2016). Given the increasing use of acoustic telemetry as a tool to monitor animal movements in aquatic environments, there is a need to improve range testing procedures to more accurately predict in situ transmitter performance and minimize methodological errors.

Acknowledgements

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