Environmental factors influencing detection efficiency of an acoustic telemetry array and consequences for data interpretation

Michael Long[1,2*], Adrian Jordaan[2] and Theodore Castro-Santos[3]

Abstract

Background Acoustic telemetry is a commonly used technology to monitor animal occupancy and infer movement in aquatic environments. The information that acoustic telemetry provides is vital for spatial planning and management decisions concerning aquatic and coastal environments by characterizing behaviors and habitats such as spawning aggregations, migrations, corridors, and nurseries, among others. However, performance of acoustic telemetry equipment and resulting detection ranges and efficiencies can vary as a function of environmental conditions, leading to potentially biased interpretations of telemetry data. Here, we characterize variation in detection performance using an acoustic telemetry receiver array deployed in Wellfleet Harbor, Massachusetts, USA from 2015 to 2017. The array was designed to study benthic invertebrate movements and provided an in situ opportunity to identify factors driving variation in detection probability.

Results The near-shore location proximate to environmental monitoring allowed for a detailed examination of factors influencing detection efficiency in a range-testing experiment. Detection ranges varied from < 50 to 1,500 m and efficiencies varied from 0 to 100% within those detection ranges. Detection efficiency was affected by distance, wind speed and direction, wave height and direction, water temperature, water depth, and water quality.

Conclusions Performance of acoustic telemetry systems is strongly contingent on environmental conditions. Our study found that wind, waves, water temperature, water quality, and depth all affected performance to an extent that could seriously compromise a study if these effects were not taken into consideration. Other unmeasured factors may also be important, depending on the characteristics of each site. This information can help guide future telemetry study designs by helping researchers anticipate the density of receivers required to achieve study objectives. Researchers can further refine and document the reliability of their data by incorporating continuously deployed range-testing tags and prior knowledge on varying detection efficiency into movement and occupancy models.

Keywords Detection range, Detection probability, Range test, Passive monitoring, Spatial planning

*Correspondence:
Michael Long
mlong@cfrfoundation.org
[1] Commercial Fisheries Research Foundation, P.O. Box 278, Saunderstown, RI 02884, USA
[2] Department of Environmental Conservation, University of Massachusetts, 160 Holdsworth Way, Amherst, MA 01003, USA
[3] U.S. Geological Survey – Eastern Ecological Science Center, S.O. Conte Research Laboratory, One Migratory Way, Turners Falls, MA 01376, USA

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Background

Understanding animal habitat use and movements is necessary for a variety of applied uses, including spatial planning and other management decisions in aquatic and coastal environments. Information on movement and occupancy can be used to protect endangered and protected species, spawning aggregations, habitat corridors, nurseries, and important ecological areas [1–3]. Accurate and detailed information in these areas can assist management by helping to address conflicts between user groups and interested parties, and by promoting continued sustainability and productivity of natural resources [1–3].

Telemetry is used for a variety of purposes in aquatic and terrestrial environments, from understanding basic species movement ecology to addressing specific conservation needs, such as risk assessment and identifying causes and solutions for habitat fragmentation [4, 5]. Initially conceived in the 1950s, techniques have continued to improve over past decades with radio, satellite, acoustic, and GPS technologies [6]. Radio, satellite, and GPS telemetry methods all rely on transmission of radio signals to land- or space-based receivers. Radio transmissions are rapidly attenuated by water, making it challenging to employ in habitats greater than 6 meters (m) deep, and difficulties are even more problematic in saltwater environments [1]. However, acoustic signals can transmit well in these environments, making acoustic telemetry the preferred method in marine environments, as well as some freshwater systems.

Acoustic telemetry operates through uniquely coded transmitters (tags) that transmit ultrasonic pulses to allow identification of individuals [7, 8]. Tags transmit the coded pulses at fixed or random intervals and can remain active for several years depending on transmission rate, battery size, and power output. Receivers detect tag transmissions and store codes and detection times, along with other information specific to a given application such as tag depth, velocity, and temperature. Receivers are typically deployed at fixed locations to continuously monitor an area for extended periods of time. When receivers are fixed in place, they continuously collect data within a study area, providing a powerful framework for monitoring animal occupancy and movements [9, 10]. However, inference of occupancy or movement from the receiver data requires several assumptions about the probability of detections and the range over which the detections are being observed [11]. Typical telemetry analyses are based on the determination of presence and assumed absence of tagged animals at receivers due to the detections or lack of detections of transmission signals. If a tagged animal is detected on a receiver, it is assumed to be present within the area surrounding that receiver, and if an animal is not detected on a receiver, it is generally assumed to be absent [11–13], although some mark–recapture methods are able to account for missed detections [14]. This can lead to inaccurate interpretation of results, potentially leading to misinformed management decisions [11, 12].

Although each transmission has an associated probability of detection (i.e., detection efficiency operates at the level of a single transmission), most analyses treat the detection of individuals collectively, aggregating data over periods of time and so allowing for a higher cumulative probability of detection ([15, 16]. Although this issue has been recognized previously, and some of the associated risks have been described, the scope and scale of the problem of detection efficiency in acoustic telemetry remains poorly described, undermining reliability of existing data and its interpretation [11]. Throughout this paper we adopt the standard proposed by Kessel et al. [11], whereby efficiency is measured in units of proportion of transmissions that are successfully received and decoded, and rather than thinking of 'range' as a response variable we treat it as a covariate that affects detection efficiency.

Several physical processes reduce detection range and efficiency at a given distance, including wind, waves, rain, tide, depth, turbulence, dissolved gasses, thermoclines, etc. [7, 17, 18, 19]. Data and theory are limited, however, on the magnitude and relative importance of these effects, which vary widely among sites and applications; although performance appears to be robust in some pelagic situations, performance can be much more variable in near-shore and complex environments [11, 18, 20]. Here, we describe dramatic variability in detection performance of an acoustic telemetry system in a shallow, tidally influenced marine environment where tagged animals occur in close proximity to the bottom, and analyze the effects of a suite of environmental conditions on detection efficiency.

Methods

Data collection

From the spring of 2015 through fall of 2017, an array of 20 telemetry receivers (Vemco VR2W) was deployed in Wellfleet Harbor, Massachusetts, USA (Fig. 1). Wellfleet Harbor is a shallow sub-embayment off Cape Cod Bay with an intertidal range of up to 4 m. The bottom is almost entirely sand, mud, and shell, with minimal submerged vegetation and very few glacial erratic boulders scattered throughout. Receiver mounting hardware and design were replicated from the methods of Castro-Santos et al. [21]. Receivers were fixed to the bottom of 1.5 m PVC poles and buoyed at the water surface with two 20 cm floats at the top of the PVC pole, resulting in a
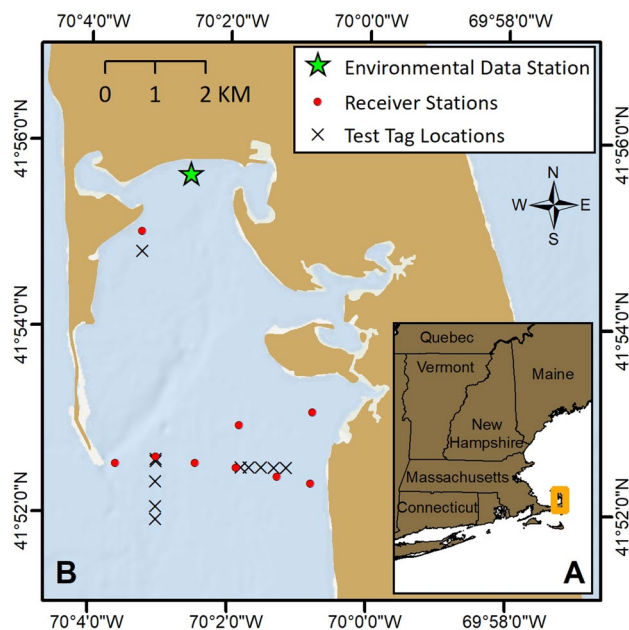
Fig. 1 Study area location on Cape Cod, Massachusetts, USA (A) and map of Wellfleet Harbor study area showing the 9 receiver stations, 11 test tag deployment locations, and the environmental water quality monitoring station used for this range test study (B)

receiver depth of approximately 1 m. This surface mounting was necessary because of the large intertidal range in

Wellfleet Harbor, and allowed for continuous coverage of the inundated portions of the harbor throughout the tidal cycle. The PVC float poles and receivers were anchored to 45 kg concrete anchors with sinking vertical lines that were 1.5 times as long as the high tide water depth at the location of each receiver station. This method allowed for some variability in position; at 10 m depth, the approximate maximum depth in the harbor, receiver location could deviate by a maximum radius of 11.2 m from the recorded central mooring location, or 2% of the a priori estimated detection range.

During the spring of 2015, preliminary mobile range testing on the full Wellfleet Harbor receiver array was conducted on multiple occasions by towing a test tag throughout the array at 1–2 m/s behind both a motorboat and kayak. The location of the towed tag was recorded with a handheld GPS (Garmin eTrex 10) on the same synchronized clock as the deployed receivers. Large gaps in detection history of the test tag were present when it was theoretically in range of a receiver, thus more in-depth detection range and efficiency testing was conducted during the spring and summer of 2016 using multiple fixed-location transmitters. Transmitters (Vemco V-13 high power tags, $n = 11$) were composed of 5 tags with precise fixed delay transmissions, and 6 non-precise fixed delay tags expected to drift in their transmission intervals by less than a second. Transmission intervals

Table 1 Range of test tag distances and observed environmental conditions during acoustic range test sessions in Wellfleet Harbor, and observed environmental conditions throughout the full year of 2016 within the harbor

Variable	Overall range test sessions 5/24/16–9/21/16				2016 (entire year)			
	Range	Mean	Median	Standard Deviation	Range	Mean	Median	Standard Deviation
Tag distance (meters)	50–1628	760	795	388	Not Applicable	Not Applicable	Not Applicable	Not Applicable
Transmission interval (seconds)	90–115	101	100	8	Not Applicable	Not Applicable	Not Applicable	Not Applicable
Wind speed (meters/second)	0.00–17.35	6.04	6.17	2.12	0–23.52	6.09	5.45	3.71
Wave height (meters)	0.08–0.83	0.38	0.36	0.10	0.04–3.60	0.53	0.39	0.43
Wind direction (°)	2–357	192	199	71	0–360	192	212	101
Dissolved oxygen (milligrams/liter)	5.61–10.36	7.21	7.12	0.72	0.84–13.31	8.07	8.08	1.87
Turbidity (nephelometric turbidity units)	0.01–45.24	5.55	2.39	7.04	0.00–125.87	7.64	2.68	12.36
Water temperature (°Celsius)	11.43–23.97	21.00	21.28	1.78	1.00–30.38	16.55	16.79	7.13
Receiver water depth (mean low water, meters)	0.62–11.29	3.21	3.23	1.39	Not Applicable	Not Applicable	Not Applicable	Not Applicable
Salinity (parts per thousand)	29.24–31.99	30.74	30.77	0.41	24.47–32.58	30.08	30.44	1.39
Wave direction (°)	0–359	211	216	86	0–359	208	239	125
Chlorophyll (micrograms/liter)	0.07–30.27	7.77	6.99	4.24	0.00–59.39	9.29	6.94	8.21

had staggered start times and ranged from 90 to 115 s, with extended intervals selected to accommodate a multiple second transmission duration and avoid collisions.

Tags were attached approximately 0.1 m above a fluke anchor on sinking vertical lines with a fastener system (Velcro), super glue adhesive (Pacer Technology Zap-A-Gap adhesive and Zap Kicker accelerator), and two zip ties. Tags were placed outside of channels to ensure a continuous, uninterrupted line-of-site between tags and receivers; all tags and receivers used in the analysis were fully submerged at all tide levels (Table 1). A small float was attached to the sinking vertical line just above the tag to prevent the tag from sitting in the bottom sediment. This method was chosen to closely replicate how tags were attached to benthic invertebrates [22, 23], and should also provide data representative of benthically oriented vertebrates. Transmitters were directed upward and not obstructed other than the two zip ties and overlapping beads of super glue.

Range test tags were deployed in two multiday sessions in the spring of 2016 (May 24–26, and June 17–24) and one single-day session in the fall of 2016 (September 21; Table 1). Five tags were deployed in each of the two main spring sessions, with only 1 tag deployed in the single-day fall session. Tags were deployed at various set distances away from a single reference receiver; however, the high density of receivers in the harbor allowed for tags to be detected on multiple other receivers within each test session. Where this occurred, distances from neighboring receivers were measured and data were included in analyses.

Environmental conditions were collected during the range test sessions through external data sources (Fig. 1). Water temperature, salinity, water depth (including variable tidal height), turbidity, chlorophyll, and dissolved oxygen data within Wellfleet Harbor were collected at 15 min intervals at a fixed station by the Barnstable County Cape Cod Cooperative Extension Water Quality Monitoring Program (www.capecodextension.org). Wind speed and direction data were collected at 5 min intervals at the Hatch Beach WeatherFlow DataScope station on the shore of Cape Cod Bay south of Wellfleet Harbor (41.817° N -70.003° W; www.weatherflow.com). Wave height and direction data were collected at 30-min intervals in Cape Cod Bay at a buoy station maintained by the United States Geological Survey (USGS) (Waverider 44090) within the National Oceanic and Atmospheric Administration (NOAA) National Data Buoy Center program (41.840° N 70.329° W; www.ndbc.noaa.gov).

Data analysis

Once all data had been collected, time sequences were created for all tags based on the date and time each tag was deployed and then retrieved in the field. The time sequences were setup as a series of ten non-overlapping transmission interval windows specific for the programming of each tag; for example, a tag with a transmission interval of 100 s would have its time sequence as a non-overlapping series of 1000 s windows from the time it was deployed until the time it was retrieved. The length of time for each window was always equal to ten expected transmission intervals, but varied based on the individual tag transmission interval. These ten transmission intervals will hereafter be referred to as efficiency windows, which served as the sampling unit for all analyses.

Efficiency window time sequences were established for each tag–receiver combination with at least one detection. This excluded combinations that never got any detections, which would have overly biased estimates of covariate effects. Detection efficiency was calculated by dividing the number of detected tag transmissions by 10 for each efficiency window. Environmental conditions were assigned to each efficiency window as the mean of all observed values within each efficiency window. Where efficiency windows spanned more than one recording interval for environmental data, the mean of the environmental data intervals was used to best approximate conditions that occurred during the efficiency window.

We tested a set of several hundred candidate logistic regression models using the environmental conditions and tag distance to receiver as predictors of detection efficiency. All feasible models were included as candidates, and only periods during which all environmental data were available were used to select the best models. Inclusion was determined based on interpretability of resulting candidate models, and included covariates with correlation coefficients < 0.60 [24]; where strong correlations occurred or were expected, interaction terms were included (see below). This approach balanced the risks associated with both data dredging [25] and confirmation bias [26]. To capture unmeasured effects associated with sessions and/or tags, we included test session or tag ID separately as factored predictors and random effects. Because tag and session were not independent, however, only one of these effects was included in any given model. Wind direction was included as a categorical variable discretized on the four cardinal directions, with south included as the reference in model intercepts. Because the harbor is protected by land from all directions but

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the south, wind direction was also separately tested as a binary predictor of south wind or non-south wind. All non-categorical predictor variables were standardized (z-scored to be compatible with the glmer function in the lme4 R package) [27].

Interactive predictor effects were also tested where appropriate. We tested interactions of wind speed with wind direction and wind speed with wave height because of the harbor's increased exposure to southern winds. Wind and wave direction alone were never tested as independent predictors because they hold no weight without a measure of wind speed or wave height. An interaction between water depth and wind speed was included in candidate models with expected impacts on detection efficiency being greater as water depth decreased and wind speed increased. Similar interactions were also included for water depth and wave height. Because of the intuitive correlation between wind speed and wave height, i.e., higher wind speed causing higher wave heights, those two independent predictors were not tested in the same model. However, the last interaction term we tested was between wind speed and wave height, thus incorporating wind gusts and potential effects of wind and waves travelling in either the same or opposite directions into candidate models.

Once a full set of candidate models was compiled, model fits were compared using Akaike information criterion (AIC) [25]. Only models with ΔAIC < 2 were considered in our interpretations as the most parsimonious models. The best model was then used to predict detection efficiency and range over the course of an entire year of study to assess temporal patterns in performance that could affect study outcomes.

Results

We logged 7,560 efficiency windows from which to parameterize and compare models. Environmental conditions varied widely over the period of testing, such that the range of most covariate values was greater than their mean value (Table 1).Covariates were largely independent (Additional file 1: Figure S1), except for turbidity and chlorophyll (Pearson's $r = 0.91$). All other potential combinations of environmental parameters were used in candidate models.

Two tags were undetected during the first test session. One, at 1,250 m distance from the nearest receiver was active and deployed properly throughout the session. The second, however, at 1,000 m, had become detached from its float and so was excluded from the efficiency analyses. All other tags were detected by at least one receiver during their deployments.

We did not observe any differences in performance between the fixed delay and the precise fixed delay tags

during our test sessions. The tag transmission intervals of both types of tags drifted within 1–2 s from their original specified transmission interval.

Detection efficiency and range

Raw data showed highly variable and dynamic detection ranges and efficiencies. The maximum distance between a tag and receiver which detected a transmission was 1,628 m; conversely, there were periods of time greater than 3.5 h during which tags as close as 100 m from a receiver were not detected.

There were 3 general patterns of the effect of tag distance on detection efficiency: periods when efficiency was generally high for all tag distances tested, periods when efficiency was generally low for all tag distances tested, and intermediate conditions with tags at short distances still producing high efficiency and tags at long distances producing low efficiency (Fig. 2).

Predictor variables

All tested environmental factors contributed to observed detection efficiency. Our AIC best fit model (inference model) included tag distance, wind speed, water depth, salinity, chlorophyll, dissolved oxygen, water temperature, and interactions of wind speed with wind direction (four direction categorical), wind speed with water depth, and wind speed with wave height. Tag distance, wind speed, wave height, chlorophyll, salinity, and dissolved oxygen all had negative effects on detection efficiency, while efficiency improved with water depth and temperature (Table 3; Fig. 3). Of these, the predictors that explained the most variance were tag distance, wind speed, and water depth (Tables 2 and 3, Fig. 3).

The magnitude of these effects is best described by the z-scored odds ratios (Table 3). These describe the multiplicative effect of the standard deviation of each covariate on detection probability (Tables 1 and 3). Thus a value near 1 indicates minimal effect, while values close to zero or much greater than 1 indicate strong effects. By way of example, distance had the strongest effect on efficiency, with a 1 standard deviation (SD) increase of 388 m reducing efficiency by a factor of 0.03, and conversely a reduction in distance of the same amount results in a 33-fold increase in detection efficiency.

The interaction terms for wind speed and wave height were important predictors in the inference model and most of the top models. Both wind speed and wave height had negative effects on detection efficiency, with wind speed having a stronger effect. The correlation with wave height likely affected the magnitude of the estimates: a negative effect for wave height as well as for northly wind speed suggests that the null condition (southerly wind direction) may be an underestimate, and

Fig. 2 Detection efficiency from a preliminary range test session showing the three main efficiency patterns (top) and the corresponding wind speeds during the session (bottom). The three main efficiency patterns are: high efficiency of all tag distances (2016-05-20), stratified efficiency observed with varying tag distance (2016-05-14), and low efficiency of all tag distances (2016-05-16)

Table 2 Top-ten models and corresponding model summaries for variable acoustic telemetry detection efficiency in Wellfleet Harbor, with the predictor variables present in each model marked by an x

Variable	Model rank									
	1	2	3	4	5	6	7	8	9	10
Tag distance	x	x	x	x	x	x	x	x	x	x
Wind speed	x	x	x	x	x	x	x	x	x	x
Water depth	x	x	x	x	x	x	x	x	x	x
Water temperature	x	x	x	x	x	x	x	x	x	x
Turbidity			x					x	x	x
Salinity	x		x		x		x		x	x
Chlorophyll	x	x		x	x	x	x			
Dissolved oxygen	x	x	x			x	x			x
Wind speed:wind direction	x	x	x	x	x			x	x	
Wind speed:water depth	x	x	x	x	x	x	x	x	x	x
Wind speed:wave height	x	x	x	x	x	x	x	x	x	x
Model Summaries										
K	13	12	13	11	12	9	10	11	12	10
AIC	16610	16613	16629	16643	16645	16647	16648	16661	16662	16664
Δ AIC	0	3.05	19.18	32.67	34.44	36.73	37.95	50.75	51.93	54.16
Weight	0.82	0.18	0	0	0	0	0	0	0	0
Cumulative weight	0.82	1	1	1	1	1	1	1	1	1
R^2	0.69	0.69	0.69	0.69	0.69	0.69	0.69	0.69	0.69	0.69

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Table 3 Model summary of AIC best fit model for variable acoustic telemetry detection efficiency in Wellfleet Harbor. Odds ratios are for z-scored continuous covariates (wind direction was categorical and untransformed)

Variable	Odds ratio (95% CI)	p
Intercept (south wind direction)	0.01 (0.01–0.02)	< 0.001
Tag distance	0.03 (0.03–0.04)	< 0.001
Wind speed	0.54 (0.51–0.56)	< 0.001
Water depth	2.33 (2.22–2.43)	< 0.001
Salinity	0.86 (0.82–0.90)	< 0.001
Chlorophyll	0.89 (0.85–0.92)	< 0.001
Dissolved oxygen	0.92 (0.88–0.96)	< 0.001
Water temperature	1.26 (1.16–1.36)	< 0.001
Wind speed:wind direction (East)	0.84 (0.74–0.95)	0.005
Wind speed:wind direction (North)	0.68 (0.62–0.74)	< 0.001
Wind speed:wind direction (West)	0.82 (0.74–0.92)	< 0.001
Wind speed:water depth	1.66 (1.59–1.74)	< 0.001
Wind speed:wave height	0.88 (0.86–0.91)	< 0.001

wave height effect might be overestimated. The results offer insights in how wind speed and wave height might be de-coupled (Table 3), but readers should bear the context in mind when interpreting them more broadly.

The strong effect of water depth was surprising due to the limited range of water depths that were tested, but this result demonstrates the extent to which shallow

depths can limit performance of acoustic telemetry. Even the change in depth from 1 to 10 m results in an increase in efficiency from nearly 0–100% when all other model parameters are held at their observed means and tag distance is held at 400 m (Fig. 3). The interaction term between wind speed and water depth was also important, with negligible effects of wind on detection efficiency under deep conditions, but a strong negative effect at shallow depths (Fig. 3).

Efficiency predictions for the full year of 2016 (Table 1, Fig. 4) illustrate the likely importance of the effects described here on ongoing studies in the area. Importantly, however, these predictions included covariate values well outside the range of what we tested, including temperatures ranging from 1–30 °C (Table 1, Fig. 4). Less severe extrapolation can also be seen in the 2016 model predictions for daily efficiency with other variables (Table 1), but water temperature has the largest impact because of the extreme efficiencies predicted for both high and low temperatures.

Discussion

For acoustic telemetry research in aquatic environments, proper interpretation of tag transmission detections is vital for determining tag presence and absence and inference of behaviors within the context of movement ecology and management decisions. Inference of presence or absence based on tag detections is commonly predicated
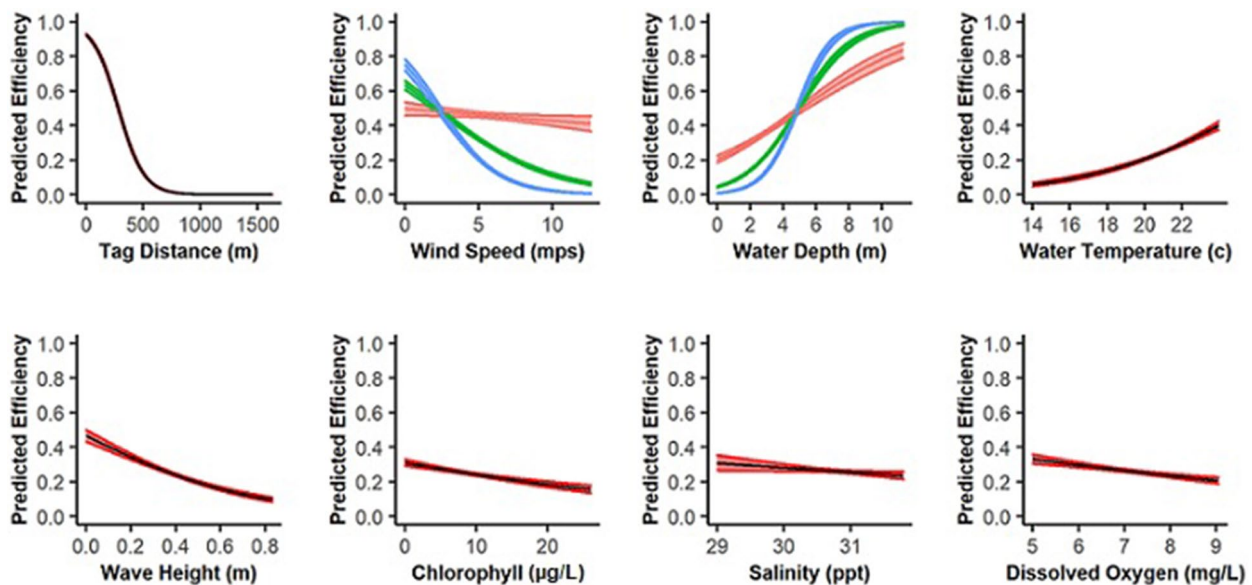

Fig. 3 Model prediction plots for each of the continuous predictor variables in our top performing inference model for variable acoustic telemetry detection efficiency in Wellfleet Harbor. All variables were fixed at their observed mean, with the exception of tag distance, which was fixed at 400 m for all but the tag distance plot. In addition, interactions of wind speed and water depth are illustrated with curves representing the mean value (green), the lower standard deviation (blue), and the upper standard deviation (red) for depth on the wind speed panel and for wind speed on the depth panel. X axis range is the observed range of data from the test sessions in this study
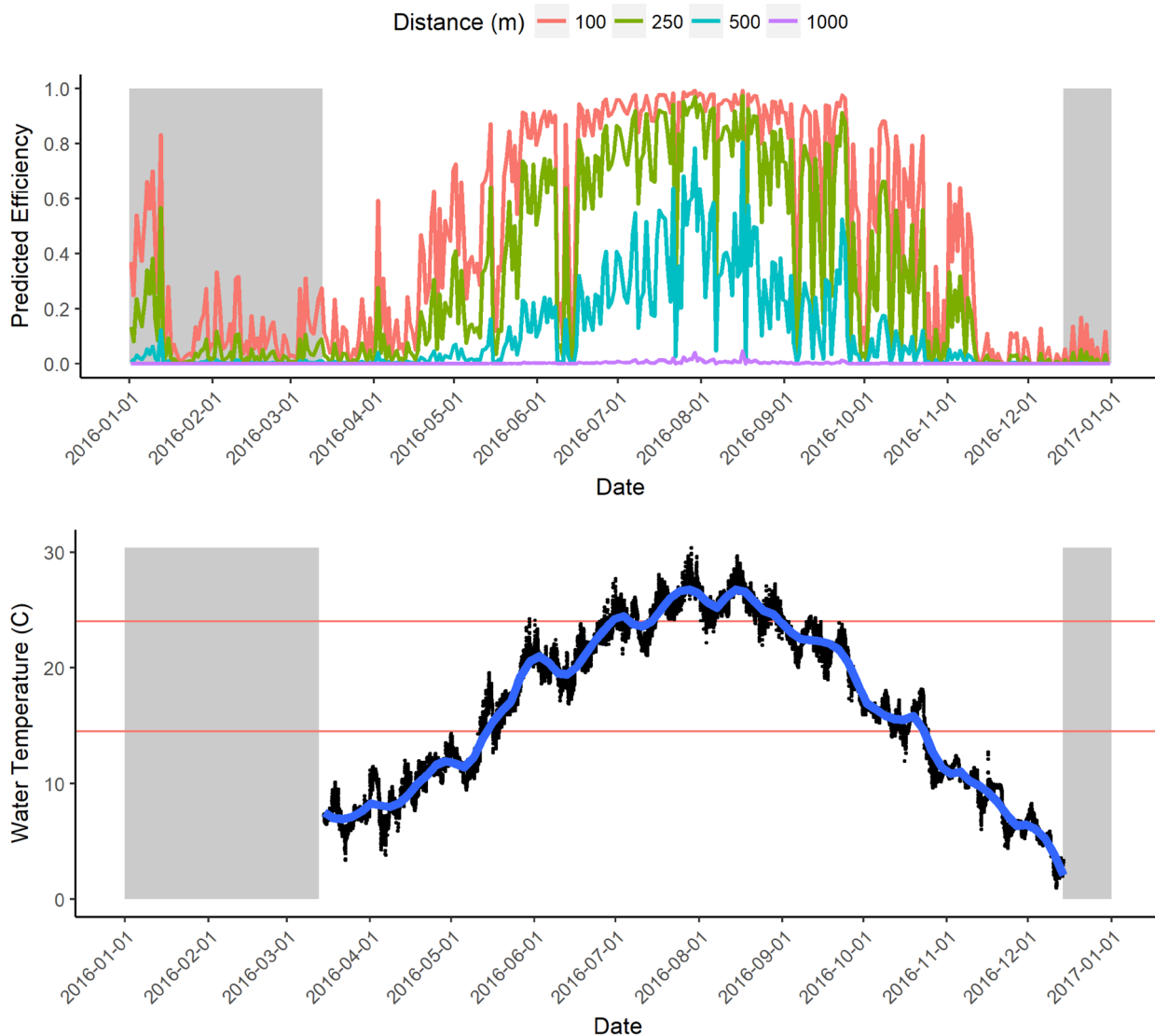
Fig. 4 2016 mean daily acoustic telemetry detection efficiency estimates (top) and observed water temperatures in the Wellfleet Harbor study site (bottom). Grey shaded areas represent time periods where water quality and water temperature data were not available. Red lines represent the range of water temperature observed in the range test sessions; dates with temperatures outside that range have model extrapolation. Other variables have similar extrapolation throughout 2016; however, water temperature provides the best visualization

on the assumption that detection ranges and efficiencies are consistent across time and space. Previous studies have identified environmental conditions that influence detection efficiency [7, 18] or accounted for it in modeling [20, 28]. Here we explicitly quantified the role and magnitude of a suite of environmental covariates, all of which had an influence on detection range and efficiency in a shallow-water, tidal marine environment with broad application to near-shore telemetry systems.

The environmental context of our study system is important; in tidal environments with large intertidal regions, channels, and sandbars, it is necessary to deploy receivers near the surface to maintain line-of-sight (or line-of-signal for telemetry equipment) surveillance of the study area, particularly for studying benthic-oriented species. This deployment allows continuous monitoring of submerged habitat, the geometry of which changes dramatically with the rise and fall of the tides [21, 29].

The sites selected for range testing in this study were not subject to the most extreme variation in bottom topography, being outside of the intertidal zone, and were selected for flat bathymetry with minimal structure to interfere with signal propagation. Nevertheless, the placement of receivers near the water surface likely

caused some reduction in overall detection range as they were more susceptible to wind and wave effects than might have occurred with bottom deployments and/or in more stable environments [7, 18, 30]. However, similar effects are possible regardless of receiver location, since benthic species can, and do, find positions in shadows within the benthic habitat or by burial [31]. In addition, as the depth shoals, effects from either surface or bottom fixed receivers are likely to converge as all the available water column is agitated. The ranges we observed here were much less than those found in studies performed in deep marine environments. Our models suggest that detection efficiencies < 50% at 100 m are likely to be common for much of the year. These results are similar to those described by Gjelland and Hedger [20], but contrast strongly with Huveneers et al. [18] who consistently detected > 50% of transmissions at ranges greater than 600 m.

Complex benthic habitats present greater potential for signal interference [19]. As a result, shallow complex systems have the highest probability of poor detection range, while deep continuous habitats have the highest detection ranges, regardless of the deployment location of receivers [18, 20]. Deployments similar to those described here are not uncommon for both fixed and mobile tracking [29], however, the results have broader relevance to deeper and bottom fixed receiver deployments as well. These examples, coupled with our data, emphasize the importance of local variability in transmission distances, and the importance of monitoring during studies [18].

With these deployment details in mind, it is striking that nearly all tested environmental parameters affected efficiency, with tag distance and wind speed having the strongest effects. The effect of distance, central to the concept of a range test, is the least surprising: acoustic signals are attenuated as a function of distance, owing to energy losses during transmission through the water as the signal expands into the environment [30]). This effect was entirely expected and its inclusion was required to characterize the remaining environmental factors that were of greater interest.

The second most important factor affecting detection efficiency was wind speed, which interacted with both wind direction and wave height. Importantly, wave height augmented the reduction in detection efficiency associated with wind speed. This effect is to be expected; wind generates noise as it passes over the water surface [7, 30, 32], and the depth that waves' orbitals penetrate is a function of wavelength [33]. Waves will interrupt the path of signals (particularly at distance), act to alter the orientation of the receiving hydrophone, and increase the mixing of air bubbles and water turbidity. As dissolved

gasses exceed saturation, they come out of solution creating micro-bubbles [34, 35]. The process of transitioning from dissolved to a gaseous state can itself produce noise, and once in the gaseous state bubbles are much more compressible than water and act to increase attenuation [7, 36, 37]. Thus, waves affect detection efficiency in several ways and should be an important environmental covariate to monitor, particularly in shallow-water environments. As waves enter shallower water the impact on the benthos increases, mobilizing sediment and stimulating algal growth, and thus increasing both turbidity and chlorophyll. In deep-water deployments, waves are unlikely to contribute to ambient noise unless they are actively breaking.

Several other factors (turbidity, chlorophyll, etc.) are unlikely to directly cause noise, although they may be correlated with noise-producing factors such as wind, biological activity, physical mixing, and scour. It is less clear how chlorophyll, suspended organic matter, and solids attenuated signals. It is likely that these suspended particles are themselves interfering with sound waves and contributing to attenuation of signals. Phytoplankton release gasses during photosynthesis and respiration, and thus contribute to the gaseous content of the water column.

There is a suite of other factors that can contribute to noise interference, but were not quantified, including boat motor noise, sonars, aquatic biotic activity, rainfall, etc. Some of these are transient events, and only by continuously monitoring the acoustic environment would it be possible to account for them [7, 17]. We are unaware of any studies that include continuous acoustic monitoring and its effects on detection range or efficiency, but such an addition would assist inferences regarding ecological patterns.

With a maximum of 69% explained variance in our inference model, there is still variability in observed detection efficiencies not captured by our predictor variables. Future studies may wish to expand the range of monitored environmental factors, both to address concerns of local conditions and to improve the generality of our results. Equipment performance also likely varied based on the physical condition of receivers and transmitters. Over time, receivers accumulate biological growth, biofouling, that influences the ability of receivers to detect tag transmissions [35, 38]. Similarly, tag attachment or insertion methods on study animals may lead to variability in tag performance [39], particularly for external tag attachments that may allow for biofouling [21].

Tag transmission collisions are a possible source for decreased detection efficiency values; however, any impact in this study likely only resulted a small effect. Although there was only a maximum of five range test

tags deployed in each session, there were other concurrent acoustic telemetry studies taking place in the area, including a horseshoe crab (*Limulus polyphemus*) study which had approximately 100 tagged crabs active within Wellfleet Harbor at the time of this study. However, these horseshoe crab tags were programmed with variable pulse intervals, meaning that although collisions may have contributed to reduced efficiency, these would have been rare events and not repeated within the intervals used here to calculate efficiency.

Inference implications and suggestions for future work

Methods are available to enhance the quality of acoustic telemetry data. Fixed receiver arrays require calibration and continuous monitoring with fixed transmitters to define the varying geographic limits of detection. Mobile tracking is even more susceptible to environmental effects, as environmental conditions change with each change in receiver position. Additionally, when receivers are towed, the turbulence of water moving around the receiver and hydrophone can cause additional effects, as can noise from engines, propeller cavitation, etc. Here again, known tag deployments in fixed locations can help quantify changes in detection range. Lastly, positioning studies requiring multiple detections of a single tag transmission can include detection variability in study design, helping to inform the number and placement of receivers to optimize coverage for intended testing [40–42]. These study types would all be impacted and biased if detection efficiency is non-constant among receivers, and recognizing the existence and causes of this bias can help inform various aspects of study design and interpretation [14, 43]. Monitoring and recording this interference and quantifying the effects on detection range and efficiency would be of great utility.

One technique that can help to offset the hazards of missed detections is to incorporate both detection efficiency and behavior into occupancy metrics [44]. The intervals between detections are distributed as a negative binomial, and when a tagged animal is within the detection zone these intervals can be used to provide an estimate of receiver efficiency. The distribution of intervals for animals in motion represent a mixture of at least two distributions, including the detection efficiency as well as movement in and out of the detection zone of the receiver array. Several objective methods are available for differentiating among these distributions [44–47]. An attractive feature of this approach is that it allows for an empirical estimate of bout frequency, and hence a threshold for delineating between occupancy events. This allows researchers to identify appropriate interval durations to delineate unique occupancy events, provided that the transmission interval is sufficiently smaller than this and the detection efficiency is sufficiently high, missed detections can be tolerated without substantial loss of information. Furthermore, this approach also allows for some variability in detection efficiency, and bias is minimized provided the above caveats are met. Regardless of the approach, it will be important for future studies to separate the detection probability as it related to environmental covariates and the movement ecology of the species of interest.

All of this highlights the fundamental constraints of telemetry studies in producing reliable results, given that decisions regarding transmission intervals, the inherent detection efficiencies and ranges, and rates of movement must all be considered to appropriately address the hypotheses being tested [48]. Slow-moving animals in systems with large detection ranges (e.g., crustaceans and gastropods) will be minimally affected by fluctuating ranges and efficiencies. Conversely, animals that move swiftly, are transient, occupy habitats with varying efficiencies and/or low ranges, as well as studies of fine-scale movements will require tags that transmit at a faster rate and a greater density of receivers. Thus, habitat preference studies of mobile species in heterogeneous environments with limited receiver coverage are likely to be most susceptible to biases imposed by environmental conditions.

This poses an intrinsic challenge for the technology tested here: the selected tag codeset, like many others in this frequency range, requires multiple seconds to deliver the complete code. When multiple tags are present, long and varying intervals between transmission are needed to reduce the risk of collision between transmissions. Alternative technologies do not have these same constraints [49–51], and technical solutions continue to be developed at a rapid pace. As new technologies emerge, it will be important to subject them to rigorous testing to understand reliability and to assist researchers to design studies that minimize bias.

In fine-scale studies examining residency within complex habitats [52] or fluctuating environmental conditions (Banks et al. [53]), a series of non-detected tag transmissions could bias results and miscalculate habitat preferences or other aspects of life history. For example, fish passage studies of migratory species often rely on brief occupancies of animals as they move up- and down-stream to access spawning areas, and a few missed transmissions on a receiver could result in miscalculated passage or movement rates [44, 48]. Triangulation studies would also be greatly impacted from poor detection efficiencies in their study areas, because each triangulated position requires detections on multiple receivers for each individual tag transmission [51].

The various factors affecting detection efficiency have implications for reliability of ecological data, including public safety. Series of receivers have been deployed along beaches of Australia, Cape Cod, and other locations as part of warning networks to inform lifeguards and the public when tagged sharks are likely to be in specific areas [54, 55]. Some of these beaches are popular for swimming and surfing during months when sharks are active, and specifically given that surfer activity is greatest when waves are large, the reduced efficiency of these receivers could contribute to reduced estimates of shark presences [56] and impart a bias to risk assessments. These challenges are not unique to shark detections, and any management decisions that are dependent on acoustic telemetry inference, including protection of spawning habitats, essential habitat determination and mitigation of human activities such as offshore wind energy development, will require a proper accounting of the detection probability change with environmental conditions. Communication of biases, uncertainty, and limitations are particularly challenging in the context of public engagement.

Improved knowledge of environmental conditions that impact detection efficiency in acoustic telemetry in future studies and analyses may allow better predictions of periods of time in which the likelihood of false absences of tagged animals are increased. Including temporal and spacial variability of detection range and detection probability in telemetry analyses could lead to substantially increased modeling power. This increased modeling power could lead to less biased study results and better-informed management decisions for aquatic species and areas.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s40317-023-00317-2.

> **Additional file 1: Figure S1.** Pearson correlation coefficient matrix for all predictor variables and observed detection efficiency throughout all test sessions.

Author contributions
ML was the primary contributor for all research field work, data analysis, and manuscript writing. AJ and TCS both served advisory roles on the study design, field deployment methods, data analysis, and writing review. All authors read and approved the final manuscript.

Availability of data and materials
Upon request, all data will be deposited in the USGS publicly accessible data repository.

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
Not applicable.

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