CSIRO PUBLISHING

SHORT COMMUNICATION
https://doi.org/10.1071/MF21042

MARINE & FRESHWATER RESEARCH

Habitat-specific performance of high-frequency acoustic telemetry tags in a tropical marine environment

J. K. Matley[A,E,*], L. Vargas-Araya[B,C], A. T. Fisk[A] and M. Espinoza[B,D]

For full list of author affiliations and declarations see end of paper

*Correspondence to:
J. K. Matley
Department of Aquatic Resources,
St Francis Xavier University,
Antigonish, NS, B2G 2W5, Canada
Email: jordanmatley@gmail.com

Handling Editor:
Daniel Deng

Received: 4 February 2021
Accepted: 25 January 2022
Published: 2 March 2022

Cite this:
Matley JK *et al.* (2022)
Marine and Freshwater Research
doi:10.1071/MF21042

ABSTRACT

High-frequency (>175 kHz) acoustic telemetry transmitters are increasingly being used to track the movements of small fishes and other aquatic organisms. These transmitters, which are often smaller than conventional types, have primarily been used in freshwater, yet limited information is available on their efficacy in estuarine or marine environments. This study quantified detection ranges (DR) of 180-kHz tags and potential environmental factors influencing detection probability in three different habitats within a large embayment in Costa Rica. Mangrove (DR at 50% detection efficiency; DR_{50} = 121.0 m ± 8.1 s.e.) and transitional estuarine (DR_{50} = 145.6 m ± 12.2) habitats had relatively high detection ranges, albeit smaller than similar studies in freshwater, highlighting the effectiveness of using this frequency in tropical marine environments. By contrast, performance within rocky reef habitat was poor (DR_{50} consistently <0 m), which may have been caused by the heterogeneous bottom structure or close proximity detection interference (CPDI) due to ambient noise. This study provides novel information on the performance of high-frequency acoustic tags in a tropical marine environment serving as an important case study as investigations of the spatial ecology of small fishes in both marine and freshwater become more common.

Keywords: acoustic tracking, biotelemetry, CPDI, detection efficiency, fish movements, high-frequency acoustic tags, range test, spatial ecology, Vemco.

Introduction

Conducting preliminary investigations on the efficacy of acoustic telemetry systems is a key aspect of aquatic animal tracking research (Kessel *et al.* 2014). These studies provide knowledge of how far transmissions reliably travel between acoustic transmitters and receivers – both fundamental components of acoustic telemetry (Matley *et al.* 2022). When conducted for an extensive period, they can also inform how environmental or other relevant factors influence a receiver's ability to detect a transmitter (Gjelland and Hedger 2013). The list of environmental parameters that influence detections is vast (see Kessel *et al.* 2014) including ambient noise, water temperature, thermocline, wave action, biofouling, and transmitter type, among many others. Understanding the dynamic nature of the aquatic environment and its role in detectability can have a significant effect on interpreting the behaviour and space-use patterns of aquatic animals using acoustic telemetry. For example, without insight on temporal drivers that affect detectability of tagged animals (i.e. implanted with a transmitter), erroneous conclusions about presence within the study area can be made (Payne *et al.* 2010). Similarly, quantifying the use of specific areas (e.g. spawning sites, protected areas, focal habitat) (Simpfendorfer *et al.* 2008; Melnychuk 2012) or even distinguishing detections from deceased or living individuals (Klinard and Matley 2020) is further complicated if the distance that a tagged animal is detected by a receiver is not known.

Acoustic telemetry systems utilise the transmission of coded signals from a transmitter to a receiver, typically at a specific frequency between 63 and 417 kHz. Lower frequency transmissions are composed of longer wavelengths than higher frequencies, often resulting in waves travelling further due to less energy loss into the surrounding medium.

Although smaller transmitters suffer from reduced battery life, greater sound attenuation and are limited to higher frequencies compared to larger transmitters (Sherman and Butler 2007; Rechisky *et al.* 2020), the trade-off is that smaller animals are suitable for tagging. The development of transmitters that enable tracking of juvenile or small fishes (or other organisms), has broadened the potential application and effect of acoustic telemetry in both marine and freshwater environments. To date, the majority of research using high-frequency transmitters, defined here as >175 kHz, including investigations of detectability, has been conducted in freshwater (e.g. Larocque *et al.* 2020; Leander *et al.* 2020; Weinz *et al.* 2021). Considering the vast potential to track small animals in the marine environment, there is very limited information regarding common questions researchers may have; for example, how far is a signal expected to be reliably detected?

In this study, we conducted detection range testing of high-frequency (180 kHz) transmitters in three different habitats within an embayment in the tropical eastern Pacific Ocean. Specifically, we (1) quantified effective distances that transmitters could be detected by receivers in each habitat, and (2) investigated potential spatio-temporal factors that influence detectability throughout the deployment period. This study provided baseline detection information to help inform researchers for an under-utilised technology in the marine environment – but one that will likely grow as smaller animals continue to be targeted in acoustic telemetry research.

Materials and methods

Study area

This study was conducted in Santa Elena Bay (10°56′35″N, 85°48′16″W), a ~728-ha semi-enclosed bay, located along the eastern Pacific Ocean in the north-western region of Costa Rica (Fig. 1). The bay was declared a Marine Management Area in 2018 (Sistema Nacional de Áreas de Conservación 2017) and is subject to strong seasonal upwelling between December and April resulting from the intensification of the trade winds during the dry season (Amador *et al.* 2006). This study was conducted in shallow (<15 m) coastal areas within the bay (Fig. 1). Around the mouth of

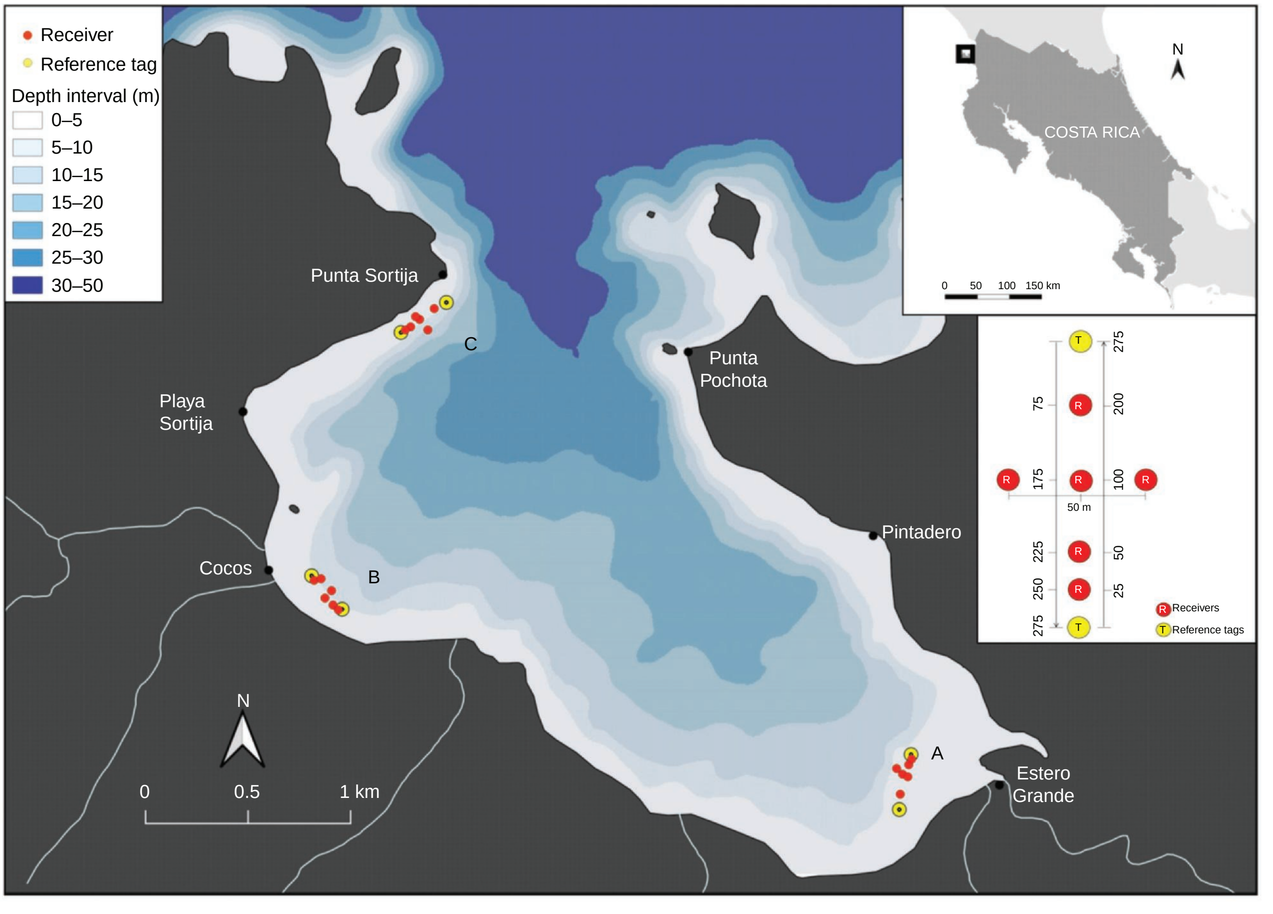

Fig. 1. Range test array positioning (receivers and reference tags) at different habitats (A: mangrove, B: transitional estuary, C: rocky reef) in Santa Elena Bay, north Pacific, Costa Rica (see upper right panel). The lower right panel is an example schematic of receiver and reference tag configuration at each location (spacing varied across locations).

the bay, the bottom composition is composed of sand with isolated rock formations (i.e. rocky reef). In the middle section of the bay, a transition environment is found with some rocky bottoms and mangrove patches (i.e. transitional estuary). The inner region of the bay contains dense mangrove cover (i.e. mangrove), where the bottom is composed by a mix of silt, sand and some submerged rocks. The bay is considered an estuary due to multiple small rivers and creeks discharge into the inner and middle regions of the bay during the wet season (May–November).

Range test

Detection range testing took place in the three areas of Santa Elena Bay described above (i.e. rocky reef, transitional estuary, mangrove). An acoustic telemetry array, consisting of six acoustic telemetry receivers (180-kHz VR2W; Vemco Ltd, Innovasea, Bedford, NS, Canada) and two transmitters (also known as a reference tag; Vemco V9-2H 180-kHz, 143 dB, nominal delay: 600 s, coding system: pulse position modulation, PPM), was deployed at each area between 26 September and 21 October 2020. Receivers were moored off the bottom with stainless steel rods or rope attached to concrete anchors and a subsurface float (hydrophones facing up; Supplementary Fig. S1). See Huveneers *et al.* (2016) for example of similar mooring arrangement. Transmitters were similarly deployed on separate lines at different distances from receivers (Fig. 1). The configuration of the array was designed to incorporate a distance range between high detectability (i.e. low distance) and poor detectability (i.e. high distance) while also maximising the number of transmitter–receiver combinations (i.e. 12 in each area). Receivers and transmitters were deployed at depths between 2.1 and 12.2 m (Table 1). Environmental variables, including wind speed, wind direction, and rain accumulation were collected from a nearby oceanographic mooring (Instituto Meteorológico Nacional 2020) and bottom water temperature was recorded on-site in each area (Table 1; HOBO water temperature Pro v2 logger, Onset Computer Co., Cape Cod, MA, USA) programmed to record temperature every 5 min.

Data analysis

Data management and analysis were conducted using the R programming language (ver. 3.61, R Foundation for Statistical Computing, Vienna, Austria, see https://www.r-project.org/). Detection range (DR), a measure that indicates the distance between a transmitter and receiver at which a specified proportion of detections (known as detection efficiency; DE) are estimated to occur (Melnychuk 2012), was estimated in each area of the bay throughout the study period. This was done by calculating the proportion of recorded detections every 6 h relative to the expected amount based on transmitter specifications at each transmitter and receiver combination (defined here as detection probability, DP – as opposed to detection efficiency, which is estimated from detection probability across a range of distances). The duration of these intervals was selected to optimise the total number of detections each sampling period while enabling diel categories to be incorporated into investigations of environmental effects (see section below). The relationship between measured detection probability values and their associated receiver–transmitter distance (i.e. $DR_{\%\ DE}$) was determined for each habitat using a generalised linear mixed model (GLMM) with a binomial distribution (*MASS* R package, ver. 7.3-51.4, see https://CRAN.R-project.org/package=MASS; Venables and Ripley 2002). Receiver–transmitter ID was incorporated as a random effect, as well as an autocorrelation structure following Klinard *et al.* (2019). Detection range at 25% (DR_{25}), 50% (DR_{50}), 75% (DR_{75}), and 95% (DR_{95}) detection efficiencies were then estimated from the fitted models of each habitat.

Changes in detection patterns over time were explored by testing the relationship between detection probability in each area of the bay with local environmental conditions using generalised additive mixed models (GAMM, *mgcv* R package, ver. 1.8-31, see https://cran.r-project.org/web/packages/mgcv/; Wood 2011). Environmental variables included water temperature (specific to each area), wind speed, wind direction, and rain accumulation. Measurements were grouped and averaged (except sum was used for rain) every 6 h to coincide with detection probability, which was also calculated at 6-h intervals. Additional variables included the receiver–transmitter distance, diel category (0000–0600, 0600–1200, 1200–1800, 1800–2400 hours), receiver depth, and a category representing whether receiver depth was higher or lower than transmitter depth. Collinearity among covariates was tested using the variance inflation factors (VIF, <3 representing no collinearity; *car* R package, ver. 3.0-5, see https://CRAN.R-project.org/package=car;

Table 1. Summary of receiver and transmitter deployment among the three different habitats in Santa Elena Bay, Costa Rica between 26 September and 21 October 2020.

Habitat	Number of receivers	Receiver depth (m)		Number of transmitters	Transmitter depth (m)		Temperature logger depth (m)
		Mean ± s.e.	Range		Mean ± s.e.	Range	
Estuary	6	3.4 ± 0.2	2.1–4.6	2	4.1 ± 0.8	3.3–4.8	3.8
Mangrove	6	6.5 ± 0.7	3.8–11	2	5.3 ± 0.3	5.0–5.6	2.1
Rocky Reef	6	6.3 ± 0.9	2.5–12.2	2	7.4 ± 2.2	5.2–9.5	12.2

Fox and Weisberg 2011). Similar to Klinard *et al.* (2019), interaction terms were included between each variable and receiver–transmitter distance to examine any effects of distance on other variables. Random effects and autocorrelation structures were the same as described above. A pool of candidate models was explored for each habitat using the *MuMln* R package (ver. 1.43.17, see https://CRAN.R-project.org/package=MuMIn; Burnham and Anderson 2002), and the optimal model was selected based on the lowest ΔAIC. Adjusted R^2 values were used to assess model fit of the optimal model for each habitat and statistical significance was set at $\alpha = 0.05$.

This study was conducted under the permit R-ACG-PI-031–2020 and ADENDUM R-SINAC-ACG-PI-033–2020.

Results and discussion

Detection profiles between 26 September and 21 October differed among areas with the transitional estuary ($DR_{25} = 181.3$ m ± 15.8 s.e., $DR_{50} = 145.6$ m ± 12.2, $DR_{75} = 109.9$ m ± 11.1, $DR_{95} = 49.8$ m ± 15.9) and mangrove ($DR_{25} = 141.3$ m ± 8.2 s.e., $DR_{50} = 121.0$ m ± 8.1, $DR_{75} = 100.7$ m ± 8.8, $DR_{95} = 66.5$ m ± 11.3) areas of the bay exhibiting the highest detection ranges (Fig. 2). Compared to similar transmitters deployed in freshwater, detection ranges in this study are smaller, but that is expected given the different absorption properties between marine and freshwater (Ainslie and McColm 1998). For example, using the same transmitters as this study, Weinz *et al.* (2021) calculated a maximum daily DR_{50} of ~206 m in a flat, soft-sediment, shallow (<2 m) freshwater channel in the Great Lakes, although notably, when present, vegetation greatly reduced this detection range. Despite detection ranges being smaller than in freshwater, these results are positive (e.g. coral reefs or rocky environments often have low detection ranges with lower frequency transmitters) and demonstrate the effectiveness of this frequency to track small animals in marine habitats.

Reporting of detection ranges derived from high-frequency transmitters in the marine environment is limited. A literature search for tropical studies provided only a few articles that directly investigated detection patterns. For example, Kessel *et al.* (2016) calculated DR_{60} estimates between 130 m (open-water) and 198 m (ice-covered) in a shallow, low-ambient noise, Arctic marine environment (Vemco V6-4 × 180-kHz). Additionally, a DR between 80 and 100 m was estimated in a flat and soft bottom, marine harbour in the Strait of Georgia, Canada along a depth gradient between 0 and 55 m using 180 kHz (Vemco V6-4x, 140 dB) transmitters (Rechisky *et al.* 2020). An even greater reduction in detection range (<50 m) was found using higher frequency tags (Lotek JSATS system: 416.7 kHz) in a high-resolution positioning experiment in the Mediterranean Sea (Aspillaga *et al.* 2021). Detection performance in the tropical transitional estuary and mangrove habitats fit within detection range estimates of the studies using the same frequency, supplementing the sparse resources available to inform study design of acoustic telemetry research in the marine environment.

The rocky reef area, which is characterised by sand and isolated rock formations had considerably lower detection ranges (some with negative estimates) with high variation: $DR_{25} = 22.4$ m ± 47.3 s.e., $DR_{50} = -11.7$ m ± 59.6, $DR_{75} = -45.8$ m ± 72.5, $DR_{95} = -103.0$ m ± 94.8 (Fig. 2). Differences in detection range between the rocky reef and the transitional and mangrove areas were likely driven by differences in the benthic structural composition. The mangrove and transitional habitats are characterised for having a dense mangrove cover and relatively homogenous sandy bottom respectively, whereas the rocky reef within the outer bay is structurally more complex. Despite the rocky reef being low-profile compared to other reef systems where structures physically block acoustic transmissions

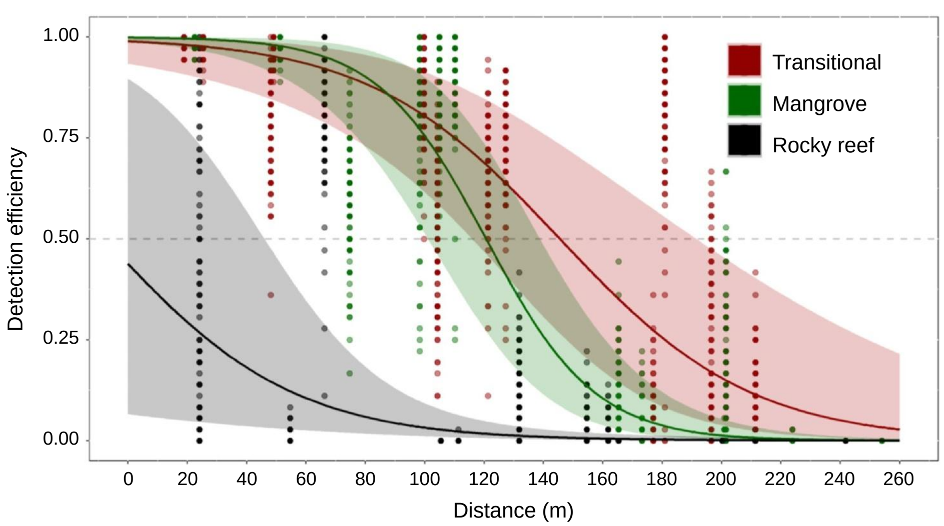

Fig. 2. Predicted detection curve fitted from generalised linear mixed models (GLMM) for each habitat between 26 September and 21 October 2020. The solid line represents the predicted detection efficiency (DE) and the grey shaded area represents the 95% confidence intervals. Points represent 6-h detection probabilities (DP), and the grey dashed line denotes 0.50 DE (DR_{50} estuary: ~145.6 m, DR_{50} mangrove: ~121.0 m, DR_{50} rocky reef: ~−11.7 m.

(e.g. Simpfendorfer *et al.* 2002), the habitat complexity still created greater surface area for acoustic signals to bounce or scatter likely resulting in reduced successful transmissions (Cagua *et al.* 2013). Also, reefs are often loud environments due to the abundance of animal life (Heupel *et al.* 2006), which could have resulted in transmitter signals being distorted before reaching the receiver. Similarly, a higher ambient noise level at the rocky reef compared to the mangrove and estuary, may have contributed to decreased range due to close proximity detection interference (CPDI; Kessel *et al.* 2015), indicating that less powerful transmitters may be needed to be effective. The detection probability was ~0.81 at 66 m, but ~0.41 and ~0.01 at 24 and 55 m respectively, supporting the possibility of CPDI or some detectability issue at specific receiver–transmitter combinations. Unfortunately, we did not have the resources to record sound levels, salinity gradients between areas, or other environmental covariates, nor could we deploy transmitters with different power output or coding system (e.g. Binary Phase-Shift Keying; Leander *et al.* 2020), which may have improved performance in this area. Irrespective of the cause, the low and variable detection range in the outer rocky reef habitat is concerning and warrants further investigation.

The covariates selected to test for factors that influenced DP at 6-h intervals were not correlated (VIF <3), therefore, all were considered in candidate GAMM models. Environmental variables fluctuated throughout the study (Fig. 3) with the lowest temperature occurring between 13 and 14 October in all habitats (transitional estuary: 26.1°C, mangrove: 25.6°C, rocky reef: 22.0°C) and the highest temperature occurring between October 10 and 11 in the estuary and mangrove (29.7°C for both) and on 5 October in the rocky reef (28.8°C) (Fig. 3*a*). The optimal models for each habitat are presented in Table 2. The model for mangrove habitat had the best fit ($R_{adj}^2 = 0.785$), followed by estuary ($R_{adj}^2 = 0.606$), and rocky reef ($R_{adj}^2 = 0.274$). At all three habitats, water temperature had a significant interaction with the distance away from a receiver (Table 2). Each habitat followed similar trends in which lower temperatures had higher detection probabilities compared to warmer temperatures at the same receiver–transmitter distance (Fig. 4). This pattern continued at all distances in the transitional estuary and mangrove (although less pronounced), and was particularly evident at distances <100 m in the rocky reef habitat (although model fit was low). The effect of temperature on detectability of acoustic transmitters is typically associated with deflecting soundwaves as they travel across thermal gradients due to changes in speed of sound at different temperatures (Medwin and Clay 1998). Therefore, changes in detection probability relative to distance and water temperature should be driven by thermal gradient changes (e.g. thermocline, depth), as opposed to

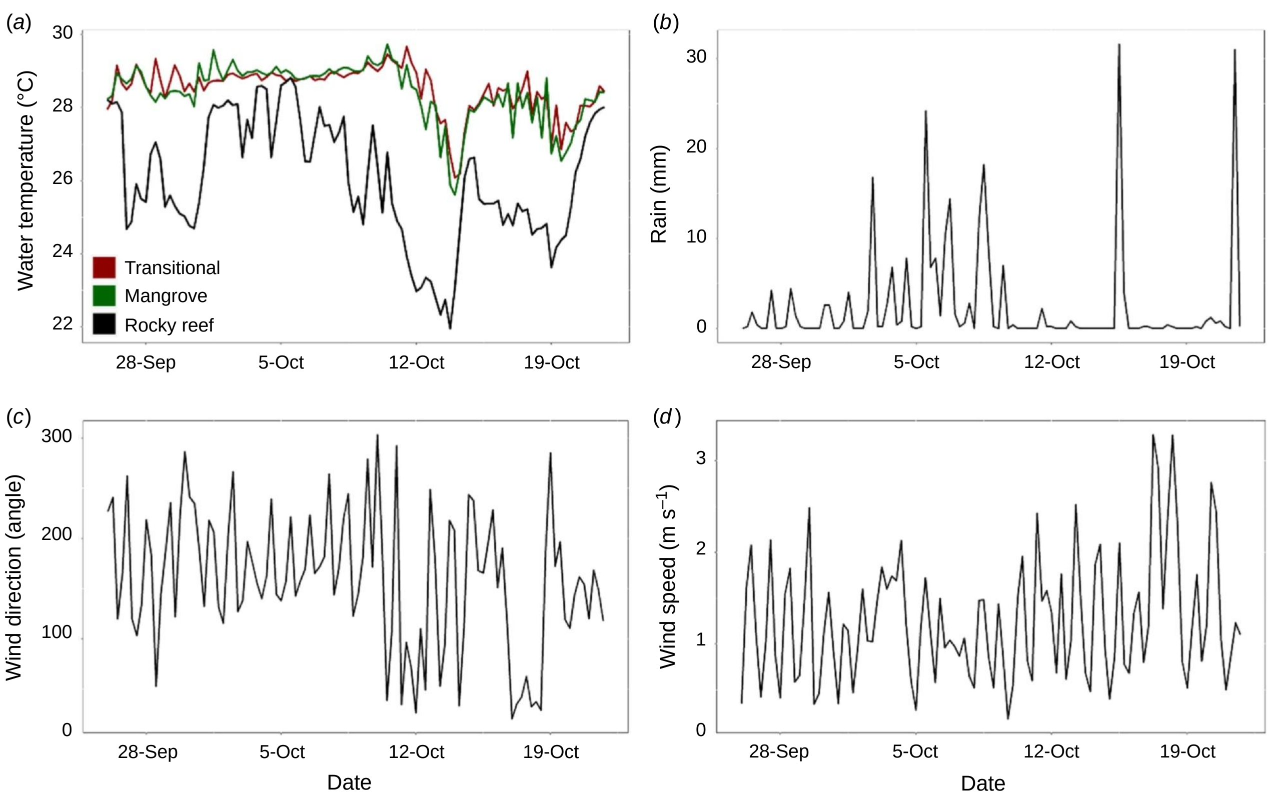

Fig. 3. Environmental measurements collected within or near the study area grouped in 6-h intervals.

Table 2. Generalised additive mixed model (GAMM) output for optimally fitted models among the three habitats in Santa Elena Bay, Costa Rica.

(1) Transitional estuary			
Nonlinear terms	**Degrees of freedom (effective)**	***F***	***P***
s(Distance)	1.00	22.18	**<0.001**
s(Temperature)	3.28	12.86	**<0.001**
s(Wind direction)	0.82	0.16	0.193
s(Rain)	1.00	0.00	0.980
ti(Distance, temperature)	1.00	9.65	**0.002**
ti(Distance, wind direction)	<0.01	<0.01	0.454
ti(Distance, rain)	1.00	0.92	0.339
n = 1248, AIC = −2131.7, R^2 = 0.606			
(2) Mangrove			
Nonlinear terms	**Degrees of freedom (effective)**	***F***	***P***
s(Distance)	1.00	47.96	**<0.001**
s(Temperature)	2.67	25.47	**<0.001**
ti(Distance, temperature)	3.51	5.58	**<0.001**
Parametric terms	**Estimate ± error**	***t***	***P***
(Intercept)	0.457 ± 0.055	8.31	<0.001
Diel category: morning (0600–1200 hours)	−0.012 ± 0.005	−2.66	**0.008**
Diel category: afternoon (1200–1800 hours)	−0.013 ± 0.006	−2.41	**0.016**
Diel category: evening (1800–2400 hours)	0.001 ± 0.005	0.29	0.773
n = 1248, AIC = −2724.5, R^2 = 0.785			
(3) Rocky reef			
Nonlinear terms	**Degrees of freedom (effective)**	***F***	***P***
s(Distance)	1.00	4.34	0.038
s(Temperature)	1.00	12.69	<0.001
s(Wind speed)	1.00	0.70	0.404
ti(Distance, temperature)	1.62	7.96	0.001
ti(Distance, wind speed)	3.68	11.25	<0.001
Parametric terms	**Estimate ± error**	***t***	***P***
(Intercept)	0.105 ± 0.061	1.73	0.084
Diel category: morning (0600–1200 hours)	0.021 ± 0.005	4.26	**<0.001**
Diel category: afternoon (1200–1800 hours)	0.011 ± 0.006	1.88	0.060
Diel category: evening (1800–2400 hours)	−0.017 ± 0.004	−4.34	**<0.001**
n = 1248, AIC = −3234.4, R^2 = 0.274			

(Continued on next column)

Nonlinear terms used in models are identified with an 's' and interactions between distance and each variable are identified with 'ti'. Probabilities that are statistically significant at $P < 0.5$ are represented in bold.

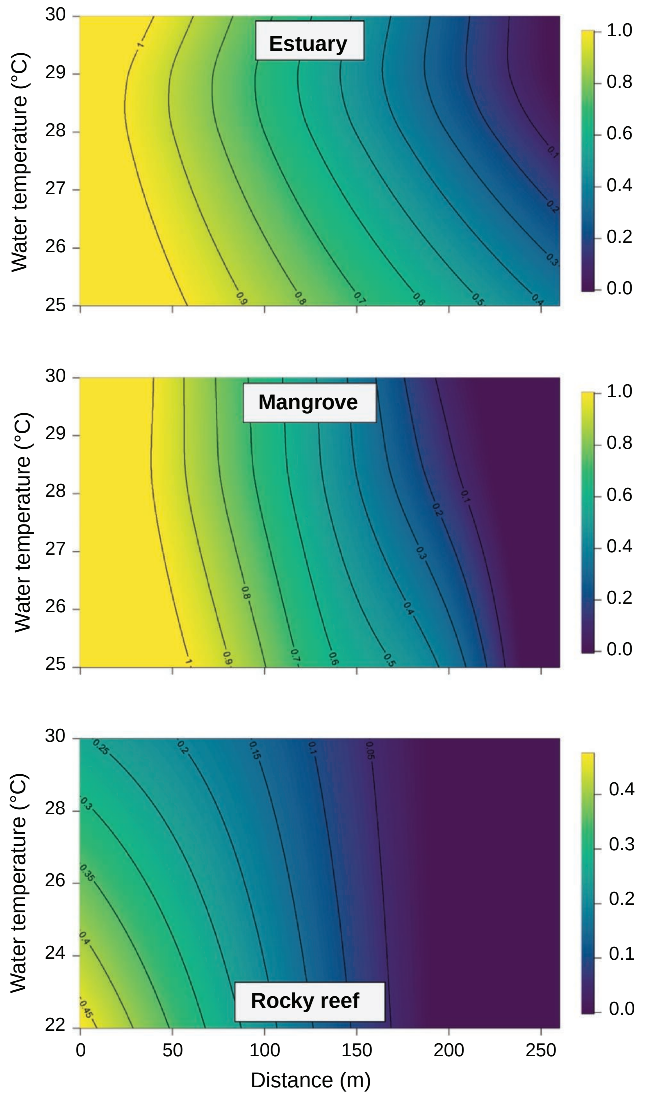

Fig. 4. Interaction plot of predicted 6-h detection probabilities (DP) varying with both water temperature and receiver–transmitter distance based on generalised additive mixed models (GAMM) for each habitat.

the specific effect of different water temperatures throughout the study (Gjelland and Hedger 2013). For example, the greater range of depth differences between receiver and transmitters in the rocky reef habitat (Table 1) could help explain the decreased detection range there compared to the other habitats (i.e. greater likelihood of signals being distorted across thermal layers). However, our results are somewhat confounding because receiver depth and receiver–transmitter depth differences were not significant for any habitat as would be expected. It may be that temperature sampling across a greater depth range would have helped elucidate these trends, but it also should be noted that the relationship between sound propagation and environmental variables is complex (Gjelland and Hedger 2013) and sampling all possible factors was beyond the scope of this study.

Diel period had a significant relationship with detection probability at both the mangrove (detection probability was lowest during the day: 0600–1800 hours; Supplementary Fig. S2, Table 2) and rocky reef (detection probability was lowest during the night: 1800–0600 hours; Supplementary Fig. S3*a*, Table 2). Differences between diel categories may relate to biological noise caused by animals (Heupel *et al.* 2006), human activity (Selby *et al.* 2016), or an unmeasured environmental variable. Regardless, the effect sizes of diel categories were small, typically only contributing to $<5\%$ differences in detection probability; therefore, the effect on interpreting animal behaviour (e.g. Payne *et al.* 2010) is likely marginal. Finally, increasing wind speed was related to higher detection efficiencies at distances <50 m (Supplementary Fig. S3*b*), which contrasts the expected negative effect of wind speed on detectability (e.g. Klinard *et al.* 2019). However, as noted by Cagua *et al.* (2013), a positive relationship between detection probability and wind speed could occur due to confounding effects with other predictor variables, dynamic acoustic interactions in shallow environments, or negative effects of wind on biological noise. As stated above, model fit at the rocky reef was low, so discretion is also needed when deciphering significant patterns.

Conclusion

This study investigated spatiotemporal variability in the detection of high-frequency acoustic transmitters in three distinct habitats within a large tropical estuary. Detection patterns in the transitional area and mangrove habitat were well supported by predictor variables and consisted of relatively high detection ranges that confirm the utility of using high-frequency transmitters to track small animals in these habitats. The finding that the rocky reef resulted in low (and highly variable) detection range provides cautionary information if working with small animals that may occupy this habitat. More comprehensive testing with transmitters of different power levels is required to confirm the occurrence of close proximity detection interference and other contributory factors in the reef habitat. Nevertheless, these findings reiterate the need for study- or region-specific range testing to help interpret detection data from tagged animals. For instance, the information garnered from this study will be used to optimise receiver configuration for future fish tracking in Santa Elena Bay (and other tropical marine embayments) using the same type of transmitters. Furthermore, knowledge of habitat-specific detection probabilities, for example, will help delineate activity space estimates and habitat use patterns (e.g. Matley *et al.* 2019). Additional tools to incorporate detection limitations in the rocky reef habitat will also be considered (e.g. Brownscombe *et al.* 2020). As acoustic telemetry continues to target smaller animals, the use of high-frequency transmitters in the marine environment will become increasingly popular, requiring case-specific information, such as presented here, to conduct animal tracking research effectively.

Supplementary material

Supplementary material is available online.

References

Ainslie MA, McColm JG (1998) A simplified formula for viscous and chemical absorption in sea water. *The Journal of the Acoustical Society of America* **103**, 1671–1672. doi:10.1121/1.421258

Amador JA, Alfaro EJ, Lizano OG, Magaña VO (2006) Atmospheric forcing of the eastern tropical Pacific: A review. *Progress in Oceanography* **69**, 101–142. doi:10.1016/j.pocean.2006.03.007

Aspillaga E, Arlinghaus R, Martorell-Barceló M, Follana-Berná G, Lana A, Campos-Candela A, Alós J (2021) Performance of a novel system for high-resolution tracking of marine fish societies. *Animal Biotelemetry* **9**, 1–14. doi:10.1186/s40317-020-00224-w

Brownscombe JW, Griffin LP, Chapman JM, Morley D, Acosta A, Crossin GT, Iverson SJ, Adams AJ, Cooke SJ, Danylchuk AJ (2020) A practical method to account for variation in detection range in acoustic telemetry arrays to accurately quantify the spatial ecology of aquatic animals. *Methods in Ecology and Evolution* **11**, 82–94. doi:10.1111/2041-210X.13322

Burnham KP, Anderson DR (2002) 'Model Selection and Multi-model Inference: A Practical Information Theoretic Approach.', 2nd edn. (Springer: New York, NY, USA)

Cagua EF, Berumen ML, Tyler EHM (2013) Topography and biological noise determine acoustic detectability on coral reefs. *Coral Reefs* **32**, 1123–1134. doi:10.1007/s00338-013-1069-2

Fox J, Weisberg S (2011) 'An R companion to Applied Regression', 2nd edn. (Sage: Thousand Oaks, CA, USA)

Gjelland KØ, Hedger RD (2013) Environmental influence on transmitter detection probability in biotelemetry: developing a general model of acoustic transmission. *Methods in Ecology and Evolution* **4**, 665–674. doi:10.1111/2041-210X.12057

Heupel MR, Semmens JM, Hobday AJ (2006) Automated acoustic tracking of aquatic animals: scales, design and deployment of listening station arrays. *Marine and Freshwater Research* **57**, 1–13. doi:10.1071/MF05091

Huveneers C, Simpfendorfer CA, Kim S, Semmens JM, Hobday AJ, Pederson H, Stieglitz T, Vallee R, Webber D, Heupel MR, Peddemors V, Harcourt RG (2016) The influence of environmental parameters on the performance and detection range of acoustic receivers. *Methods in Ecology and Evolution* **7**, 825–835. doi:10.1111/2041-210X.12520

Instituto Meteorológico Nacional (2020) 'Base de datos meteorológicos.' (IMN: San José, Costa Rica)

Kessel ST, Cooke SJ, Heupel MR, Hussey NE, Simpfendorfer CA, Vagle S, Fisk AT (2014) A review of detection range testing in aquatic passive acoustic telemetry studies. *Reviews in Fish Biology and Fisheries* **24**, 199–218. doi:10.1007/s11160-013-9328-4

Kessel ST, Hussey NE, Webber DM, Gruber SH, Young JM, Smale MJ, Fisk AT (2015) Close proximity detection interference with acoustic telemetry: The importance of considering tag power output in low ambient noise environments. *Animal Biotelemetry* **3**, 5. doi:10.1186/s40317-015-0023-1

Kessel ST, Hussey NE, Crawford RE, Yurkowski DJ, O'Neill CV, Fisk AT (2016) Distinct patterns of Arctic cod (*Boreogadus saida*) presence and absence in a shallow high Arctic embayment, revealed across open-water and ice-covered periods through acoustic telemetry. *Polar Biology* **39**, 1057–1068. doi:10.1007/s00300-015-1723-y

Klinard NV, Matley JK (2020) Living until proven dead: addressing mortality in acoustic telemetry research. *Reviews in Fish Biology and Fisheries* **30**, 485–499. doi:10.1007/s11160-020-09613-z

Klinard NV, Halfyard EA, Matley JK, Fisk AT, Johnson TB (2019) The influence of dynamic environmental interactions on detection efficiency of acoustic transmitters in a large, deep, freshwater lake. *Animal Biotelemetry* **7**, 17. doi:10.1186/s40317-019-0179-1

Larocque SM, Johnson TB, Fisk AT (2020) Survival and migration patterns of naturally and hatchery-reared Atlantic salmon (*Salmo salar*) smolts in a Lake Ontario tributary using acoustic telemetry. *Freshwater Biology* **65**, 835–848. doi:10.1111/fwb.13467

Leander J, Klaminder J, Jonsson M, Brodin T, Leonardsson K, Hellström G (2020) The old and the new: evaluating performance of acoustic telemetry systems in tracking migrating Atlantic salmon (*Salmo salar*) smolt and European eel (*Anguilla anguilla*) around hydropower facilities. *Canadian Journal of Fisheries and Aquatic Sciences* **77**, 177–187. doi:10.1139/cjfas-2019-0058

Matley JK, Eanes S, Nemeth RS, Jobsis PD (2019) Vulnerability of sea turtles and fishes in response to two catastrophic Caribbean hurricanes, Irma and Maria. *Scientific Reports* **9**, 14254. doi:10.1038/s41598-019-50523-3

Matley JK, Klinard NV, Martins APB, Aarestrup K, Aspillaga E, Cooke SJ, Cowley PD, Heupel MR, Lowe CG, Lowerre-Barbieri SK, Mitamura H, Moore JS, Simpfendorfer CS, Stokesbury MJW, Taylor MD, Thorstad EB, Vandergoot CS, Fisk AT (2022) Global trends in aquatic animal tracking with acoustic telemetry. *Trends in Ecology & Evolution* **37**, 79–94. doi:10.1016/j.tree.2021.09.001

Medwin H, Clay CS (1998) 'Fundamentals of acoustical oceanography.' (Academic Press: New York, NY, USA)

Melnychuk MC (2012) Detection efficiency in telemetry studies: definitions and evaluation methods. In 'Telemetry Techniques: A User Guide for Fisheries Research'. (Eds NS Adams, JW Beeman, JH Eiler) pp. 339–357. (American Fisheries Society: Bethesda, MD, USA)

Payne N, Gillanders B, Webber D, Semmens J (2010) Interpreting diel activity patterns from acoustic telemetry: the need for controls. *Marine Ecology Progress Series* **419**, 295–301. doi:10.3354/meps08864

Rechisky EL, Porter AD, Winchell PM, Welch DW (2020) Performance of a high-frequency (180 kHz) acoustic array for tracking juvenile Pacific salmon in the coastal ocean. *Animal Biotelemetry* **8**, 18. doi:10.1186/s40317-020-00205-z

Selby TH, Hart KM, Fujisaki I, Smith BJ, Pollock CJ, Hillis-Starr Z, Lundgren I, Oli MK (2016) Can you hear me now? Range-testing a submerged passive acoustic receiver array in a Caribbean coral reef habitat. *Ecology and Evolution* **6**, 4823–4835. doi:10.1002/ece3.2228

Sherman CH, Butler JL (2007) 'Transducers and Arrays for Underwater Sound.' (Springer: New York, NY, USA)

Simpfendorfer CA, Heupel MR, Hueter RE (2002) Estimation of short-term centers of activity from an array of omnidirectional hydrophones and its use in studying animal movements. *Canadian Journal of Fisheries and Aquatic Sciences* **59**, 23–32. doi:10.1139/f01-191

Simpfendorfer CA, Heupel MR, Collins AB, Legare B, Nemeth R, Kendall M, Poti M, Clark R, Wedding L, Caldow C (2008) Variation in the performance of acoustic receivers and its implication for positioning algorithms in a riverine setting. *Canadian Journal of Fisheries and Aquatic Sciences* **65**, 482–492. doi:10.1139/f07-180

Sistema Nacional de Áreas de Conservación (2017). 'Plan General de Manejo del Sitio de Importancia para la Conservación Bahía.' (SINAC report 69: Costa Rica).

Venables WN, Ripley BD (2002) 'Modern Applied Statistics with S', 4th edn. (Springer: New York, NY, USA)

Weinz AA, Matley JK, Klinard NV, Fisk AT, Colborne SF (2021) Performance of acoustic telemetry in relation to submerged aquatic vegetation in a nearshore freshwater habitat. *Marine and Freshwater Research* **72**, 1033–1044. doi:10.1071/MF20245

Wood SN (2011) Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society. Series B. Methodological* **73**, 3–36. doi:10.1111/j.1467-9868.2010.00749.x

Data availability. The data that support this study will be shared upon reasonable request to the corresponding author.

Conflicts of interest. The authors declare that they have no conflicts of interest.

Declaration of funding. This project was financially supported by A. Fisk at the University of Windsor.

Acknowledgements. We thank Verónica Valverde-Cantillo who helped during fieldwork. Fieldwork would have not been possible without the support from Minor and Steven Lara (Diving Center Cuajiniquil), Anibal Lara (Cuajiniquil Snorkeling Tours) and Area de Conservación Guanacaste (ACG-Costa Rica).

Author affiliations

[A]Great Lakes Institute for Environmental Research, University of Windsor, Windsor, ON, N9B 3P4, Canada.

[B]Centro de Investigación en Ciencias del Mar y Limnología, Universidad de Costa Rica, 2060-11501 San José, Costa Rica.

[C]Posgrado en Gestión Integrada de Áreas Costeras Tropicales, Universidad de Costa Rica, 2060-11501 San José, Costa Rica.

[D]Escuela de Biología, Universidad de Costa Rica, 2060-11501 San José, Costa Rica.

[E]Present address: Department of Aquatic Resources, St Francis Xavier University, Antigonish, NS, B2G 2W5, Canada.