Animal Biotelemetry

RESEARCH

Open Access

Seagrass canopies and the performance of acoustic telemetry: implications for the interpretation of fish movements

Daniel S. Swadling[1*], Nathan A. Knott[2], Matthew J. Rees[2], Hugh Pederson[3], Kye R. Adams[1], Matthew D. Taylor[4] and Andrew R. Davis[1]

Abstract

Background: Acoustic telemetry has been used with great success to quantify the movements of marine fishes in open habitats, however research has begun to focus on patterns of movement and habitat usage within more structurally complex habitats. To date, there has been no detailed assessment of the performance of acoustic telemetry within seagrass, which forms a crucial nursery and foraging habitat for many fish species globally. Information on the detection range of acoustic receivers within seagrass is essential to guide receiver array design, particularly positioning systems. Here, we compare detection ranges for transmitters (Vemco V7) within and above the seagrass to determine impacts on the performance of a Vemco Positioning System (VPS). We also investigate the influence of environmental conditions (i.e. wind, time of day, background noise, atmospheric pressure and depth) on detection probability.

Results: The performance of the VPS declined dramatically when the transmitters were positioned within the seagrass (positional accuracy = 2.69 m, precision = 0.9 m, system efficiency (i.e. the proportion of successful positions) = 5.9%) compared to above the canopy (positional accuracy = 2.21 m, precision = 0.45 m, system efficiency = 30.9%). The reduction in VPS efficiency when transmitters were within seagrass was caused by a decline in the detection range of receivers (range of 50% detections) from 85 to 40 m, as this limited the ability of the three receivers to simultaneously detect transmissions. Additionally, no detections were recorded for the transmitters within seagrass at a distance greater than 150 m from the receiver. Increasing wind speed from 0 to 50 km h^{-1} correlated with a 15% reduction in detections while detection probability decreased from 0.8 during the day to 0.55 at night, due to higher in-band noise (69 kHz).

Conclusions: Our findings demonstrate that tagged fish ensconced within seagrass are unlikely to be detected by receivers or positioned by a VPS. Further, we demonstrate that wind conditions and the time of day create temporal variation in detection probability. These findings highlight the need for telemetry studies to perform in situ range testing and consider how fish use vegetated habitats such as seagrasses when positioning receivers and interpreting data.

Keywords: Acoustic telemetry, Range testing, Seagrass meadows, Passive monitoring, Detection range, VEMCO Positioning System (VPS), *Posidonia australis*, Detection probability

*Correspondence: dss999@uowmail.edu.au
[1] School of Earth, Atmospheric and Life Sciences, University of Wollongong, Wollongong, NSW, Australia
Full list of author information is available at the end of the article

Background

Acoustic telemetry is used to quantify the movement patterns of marine fauna [1–3], however assessments on the performance of telemetry among different habitats is limited [4–7]. A key factor affecting the performance of acoustic telemetry is the detection range of a receiver [5]. The 'detection range' is defined as the maximum distance where a certain proportion of transmissions, generally 50%, are detected by a receiver [5]. Quantifying the factors affecting the detection range in various systems is essential to guide the spatial arrangement of receiver arrays and help interpret the movement and behaviour of tagged individuals [5, 8–10]. Further, information on detection ranges can prevent studies drawing inaccurate conclusions on fish movements that would misinform management [5, 10]. The detection range of receivers is sometimes assumed, and not all studies have conducted in situ range tests of acoustic equipment. Consequently, there is a paucity of data available for the performance of acoustic equipment in many habitats or environmental conditions.

Understanding detection range is particularly relevant when arrays are designed as positioning systems (e.g. Vemco Positioning System—hereafter called VPS). Positioning systems allow for the fine-scale movements of tagged individuals to be determined within metres. These systems are becoming a popular tool in both marine and freshwater systems to elucidate activity and patterns of habitat use [11–13]. In a VPS, positions are triangulated through measuring the differential time of arrival of transmissions from a transmitter detected simultaneously by three or more receivers with overlapping detection ranges [11, 14, 15]. The successful application of positioning systems is dependent on receivers being spaced to maximise the likelihood of multiple receivers detecting a transmitter and the speed of sound being relatively consistent throughout the habitat. Therefore, information on the detection range of receivers a priori is critical for determining the geometry to be employed in positioning systems.

Determining the detection range can be difficult, and it is temporally variable and dependent on several factors including attenuation and refraction of acoustic signals and spreading losses with increasing distance [5, 7, 16, 17]. Further, environmental variables such as water properties (e.g. temperature and salinity) and physical barriers can increase attenuation or obstruct the transmission of acoustic signals [4, 6, 7, 17–19]. Noise from anthropogenic and natural sources, for example snapping shrimp, wind-generated waves, boats or depth sounders can interactively contribute to variation in detection range and create background noise which disrupts the decoding of signals by receivers [4, 9, 10]. The behavioural traits of tagged individuals can also contribute to variation in detection ranges, such as animals sheltering within refugia (e.g. rock crevices or aquatic vegetation) at regular diurnal intervals [20]. These factors have contributed to the variable performance of acoustic telemetry reported in the literature [5, 7]. This creates a need to conduct acoustic range testing prior to commencing research in specific habitats or systems, and to account for this variation in array design and data analyses [7, 10].

One common habitat where the relationships between the performance of acoustic telemetry and environmental variables are poorly understood is seagrass meadows. Seagrasses are structurally complex and productive habitats containing high levels of biodiversity and play an important role in ecosystem functioning [21–23]. The spatial distributions of numerous fish species captured in both recreational and commercial fisheries are linked to seagrass meadows as fish use the habitat for foraging, shelter or as nurseries [13, 24–26]. Seagrass meadows, however, are under increasing pressure from anthropogenic activities and have been declining at alarming rates [27, 28]. Protecting seagrass meadows is therefore a focus of conservation strategies and fisheries management [29], making them an important system in which to study the movement and behaviour of organisms. This has undoubtedly contributed to the increasing number of studies investigating the movement of fishes within seagrass [13, 30–33], but no studies have quantitatively assessed the performance of a VPS or acoustic receivers in this habitat. Seagrass meadows contain a suite of unique conditions that pose challenges for the performance of acoustic telemetry. Most notably, the oxygen produced in photosynthesis by the plants and either stored in aerenchyma or emitted as bubbles can attenuate acoustic signals and alter sound wave velocity, thereby affecting VPS performance and error [34, 35]. Furthermore, many fish species are known to regularly position themselves within the seagrass canopy to rest, shelter from predators or stalk prey [36]. The consequence of these behaviours could include attenuation or obstruction of acoustic transmissions by seagrass leaves.

This study quantitatively evaluates the performance of acoustic telemetry within seagrass habitats. Specifically, we compare detection ranges for transmitters within and above the seagrass to determine impacts on the performance of a VPS. We also assess the effects of a number of environmental factors commonly measured in range tests on the performance of acoustic receivers, such as meteorological conditions (i.e. wind, rain and atmospheric pressure), depth, time of day, ambient noise (69 kHz) and water temperature.

The overarching goal of this research was to determine how the performance of acoustic telemetry is affected by fish moving amongst *Posidonia australis,* a large, robust seagrass species similar to *Posidonia oceanica*, that grows to a width of 2 cm and a length of 60 cm. These tests were performed to ascertain the appropriate spatial configuration of receivers forming a VPS and arrays in seagrass.

Results

VPS performance was substantially reduced when transmitters were positioned within the seagrass (Fig. 1). The positional accuracy of the VPS significantly improved when transmitters were positioned above the seagrass (2.2 m) compared to when transmitters were within seagrass (2.7 m) ($P < 0.01$; Fig. 1a). There was also substantially more variation in the positional accuracy of transmitters within the seagrass (1.7–5.26 m) than above it (1.7–2.74 m). Transmitters located above seagrass were positioned with significantly better precision (0.45 m) in contrast to those within seagrass (0.9 m) ($P < 0.001$; Fig. 1b). The greatest impact of a transmitters position relative to the seagrass canopy on VPS performance was on the proportion of successful number of positions per day (i.e. daily system efficiency), which significantly decreased from 30.9% for transmitters above the canopy to 5.9% when they were within seagrass ($P < 0.01$; Fig. 1c).

Detection probability was significantly reduced when transmitters were positioned within the seagrass compared to above ($t_{125} = 12.56$, $P < 0.001$). The distance at which 50% of transmissions were detected more than halved from ~ 85 m for transmitters above the seagrass to ~ 40 m when they were located amongst the seagrass (Fig. 2). For transmitters within seagrass, 10% of detections were recorded at ~ 90 m from the receiver and the detection probability decreased to 0 at 150 m (Fig. 2). In comparison, transmitters above seagrass had a 10% probability of detection at ~ 200 m from the receiver (Fig. 2). We therefore estimate the maximum detection range to be 90 m and 200 m for the transmitters located within and above the seagrass, respectively. However, fish implanted with V7 transmitters with a fixed delay of 180 s would have to be resident within these distances for an average of 30 min to be recorded (i.e. one in every 10 transmissions are detected on average at these distances ((180 s × 10)/60)).

Variation in the detection probability of the internal transmitters in the VR2Tx receivers was best explained by the distance to receiver, average wind speed and hour of day ($R^2 = 0.45$; Fig. 3). Considering that acoustic signals attenuate over distance, it was expected that distance from the receiver would be an important variable for predicting detection probability. The detection probability of the internal transmitters was high (> 0.8) up to 200 m but declined beyond this distance (Fig. 3). The distance at which 50% of transmissions were detected for the internal transmitters was ~ 260 m (Fig. 3). Detection probability was found to negatively correlate with average wind speed, decreasing from 0.9 in conditions of no wind to 0.75 when wind gusts reached 50 km h^{-1} (Fig. 3). A strong diurnal pattern in detection probability was also observed, increasing from 0.55 at midnight to 0.80 in the middle of the day (Fig. 3). It was notable that a strong diurnal pattern was also found for the mean environmental noise at 69 kHz which peaked at 710 mV at night and decreased to 520 mV at 1500 h (Fig. 4).

Discussion

This study provides clear evidence that the seagrass canopy represents an obstacle to the transmission of acoustic signals and can substantially reduce the performance of a VPS and acoustic receivers. The positional accuracy, precision and the system efficiency of the VPS was significantly poorer when transmitters were within the seagrass compared to those positioned above the canopy. The reduced VPS performance was ascribed to a decrease in detection range for transmitters amongst seagrass, with the distance at which 50% of detections were recorded declining from 85 to ~ 40 m. Further, detection probability varied temporally, with fewer detections found in high wind conditions and at night. Other range testing studies have reported similar temporal variations in response to wind and time of day [4, 6, 10, 18], however these were performed in reefs, lakes and open habitats such as soft sediments and not in seagrass meadows. Overall, our findings highlight that VPS performance and detection range may be significantly reduced for fish residing in seagrass habitats, particularly if they are routinely sheltered amongst seagrass such as juveniles or cryptic species. These results demonstrate the importance of performing in situ acoustic range tests that consider how fish use habitats for creating effective receiver arrays and interpreting movement data.

Previous research has highlighted that topographic features and vegetation obstructing the line of sight between a receiver and transmitter can reduce the performance of acoustic telemetry [5, 19, 37–39]. For instance, in coral reef systems the topography of the substrate has been reported to reduce the detection range of acoustic receivers by up to 70% [38]. In the present study, seagrass leaves obstructing the line of sight of receivers were observed to reduce detection range. For transmitters positioned in the water column above seagrass, the 50% detection range of receivers was 85 m which is comparable to previous studies using the same model transmitter (i.e. V7) in coral reef habitats (60–120 m) [18, 40]. When

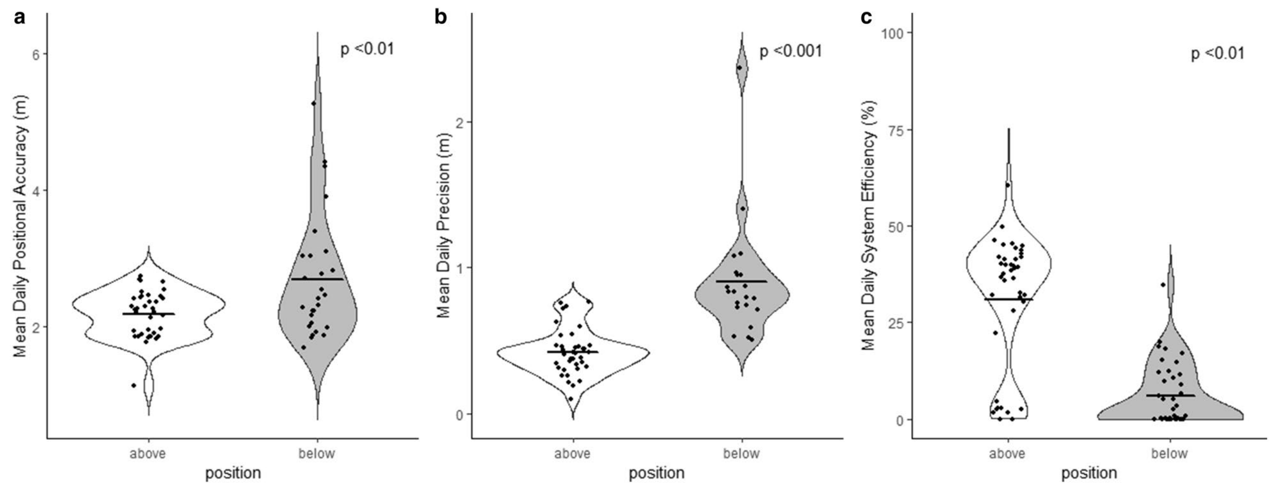

Fig. 1 Distributions of the mean daily **a** positional accuracy (*m*), **b** precision and **c** system efficiency (%) for the transmitters above and within seagrass (*x*-axis). Data points represent the raw values, violin plots illustrate the probability density and the black line is the mean

transmitters were placed within the seagrass canopy, however, the distance at which 50% of detections were recorded decreased by over half to 40 m and no detections were recorded beyond 150 m. The blades of *Posidonia australis* are large and robust and therefore present a substantial obstacle that impedes or absorbs the acoustic signals reaching receivers.

The ability of the VPS to position a transmitter is dependent on at least three receivers simultaneously detecting an acoustic signal travelling at a known speed. Given that the probability of detecting a transmitter decreased when it was amongst the seagrass, it is unsurprising that the daily system efficiency of the VPS was significantly lower for transmitters within (5.9%) compared to above (30.9%) the seagrass. It is also notable that no positions could be calculated for transmitters outside of the VPS boundary. The relatively low percentage of positions by the VPS for both the above and within seagrass transmitters could also result from the high levels of 'in-band' noise recorded in the system. The noise levels during the day were high enough to impact the ability of a receiver to detect an acoustic signal (i.e. 450–650 mV) and the extreme noise levels at night would drastically decrease receiver performance (>650 mV). The accuracy of positions was reasonable (2–3 m) for both the transmitters above and within seagrass and corroborates estimates reported in marine and freshwater systems (<5 m) [14, 15, 37]. The positional accuracy and precision of the VPS, however, were significantly different when transmitters were within seagrass. Furthermore, the positional accuracy of the VPS for transmitters within seagrass had a much higher variance than those above seagrass. It is possible that the poorer accuracy and precision recorded for transmitters within seagrass was caused by the acoustic signal being refracted by seagrass leaves and therefore taking a longer time to travel between receivers [41]. Alternatively, the acoustic signal may be attenuated or change speed as it travels through the plant tissue, the gas contained within the seagrass and the oxygen bubbles collected on the leaves. Overall, our findings suggest that a VPS in seagrass will provide a low system efficiency, particularly if fish ensconce in seagrass for periods of time, although any positions should have a reasonable accuracy and precision.

Detection probability of the internal VR2Tx transmitters was lower in high wind conditions and at night. Wind speed has previously been reported to negatively affect detection range, particularly in shallow water habitats [4, 42]. Wind influences sound propagation as it generates surface waves which create noise and air bubbles that penetrate the upper water column [4–6]. We also observed a strong diel pattern, with detection probability increasing during the day and declining at night. Similar observations have been made in previous studies in reef systems and attributed to biological noise [6, 10, 18, 38]. Although we cannot explicitly state the exact mechanism behind the observed diurnal patterns, noise at the 69 kHz frequency was exceptionally loud (>650 mV) at night and likely originates from biological sources. For example, invertebrates commonly found in seagrass such as snapping shrimp (*Alpheus* spp.) are nocturnally active and create background noise [43, 44]. This background noise has been suggested to mask acoustic signals and interfere with a receiver's ability to translate pings to detections [9, 10, 45]. These findings highlight the importance

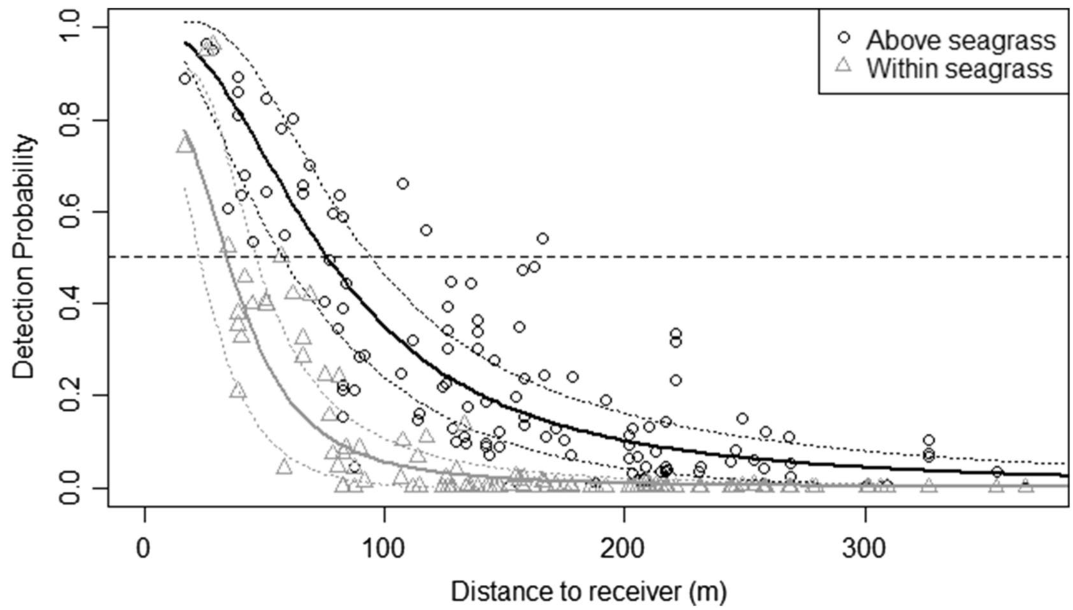

Fig. 2 Modelled detection probability for each deployment period at varying distance between transmitters and receivers. Black dots represent transmitters above seagrass and grey triangles illustrate transmitters within seagrass. Solid lines illustrate the prediction of the model and dashed lines define the standard error. The horizontal dashed line indicates the distance at which 50% of transmissions were detected

of considering environmental conditions when designing arrays and analysing movement patterns from detection data [10].

While studying acoustic telemetry performance under varying abiotic and biotic conditions is important, it is equally relevant to recognise how to address confounding factors when implementing telemetry research [4, 42]. The findings of this study emphasise the importance of considering the effects of how fish use structurally complex vegetated habitats on VPS and receiver performance when designing telemetry studies. For instance, tracking fish species known to move regularly within the water column will require a different receiver configuration when compared to tracking species that regularly shelter amongst seagrass. Our results suggest that receivers must be tightly spaced in our system when using V7 transmitters, ~ 40 m for a VPS and 80 m in receiver arrays to ensure that fish moving within seagrass have a 50% chance of being detected. However, detection ranges will vary with location and are dependent on local environmental conditions. We therefore strongly advocate that all telemetry studies perform in situ range tests rather than infer detection ranges to determine the adequate spacing of receivers. In addition, studies should include multiple sentinel transmitters in receiver arrays placed within and above the seagrass to quantify variations in detection probability through time [4, 5, 7, 10]. This information on the spatiotemporal variation of detection probabilities can be incorporated into statistical analyses to improve confidence in the interpretation of fish movement patterns and behaviour [7, 10]. Furthermore, understanding detection range over spatiotemporal scales can guide the positioning of receivers to maximise coverage over habitats or areas relevant to scientific questions and therefore increase the economic efficiency of research [6]. The performance of acoustic telemetry in seagrass habitat will also vary with the model of transmitter selected. For example, in the current study the internal VR2Tx transmitters were equivalent to a low-powered V16 transmitter and increased the 50% detection range of receivers to ~ 260 m when above seagrass (compared to 85 m for the lower powered V7 transmitters). It is likely that higher-powered transmitters would also have an increased detection range when amongst the seagrass compared to low-powered transmitters. However, the attenuation rate of acoustic signals emitted by high-powered transmitters within seagrass remains unclear and the influence of this on detection ranges should be explored in future acoustic range tests. It is noteworthy that higher output transmitters are intrinsically large due to increased battery size and would not be as appropriate as the V7 model for tracking the smaller cryptic species or juveniles commonly found in seagrass meadows (e.g. the 2% rule; [46]).

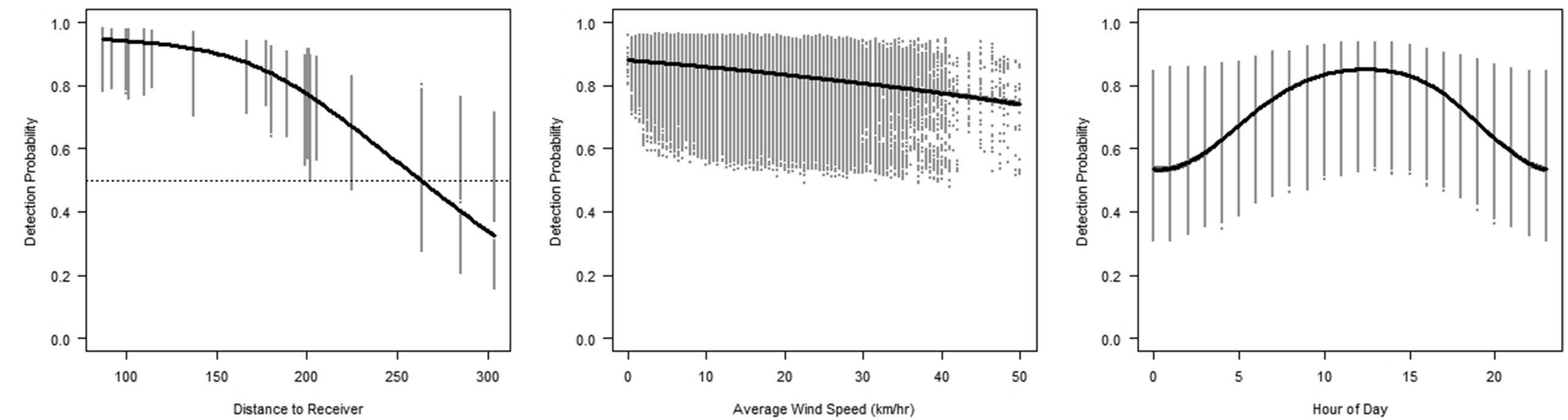

Fig. 3 Relationships for the model of environmental variables found to predict the detection probability of the internal VR2Tx transmitters from a GAMM. Solid lines illustrate the prediction of the model and the dashed areas define the 95% confidence intervals around the fitted values. The horizontal dashed line in the distance to receiver plot represents the distance at which 50% of transmissions were detected

Conclusion

In conclusion, we have provided the first evidence that the performance of a VPS and acoustic receivers is greatly reduced when transmitters are within the seagrass. The reduced performance observed in the VPS can be attributed to declines in detection range when transmitters are amongst seagrass. In addition, detection probability was found to decrease in high wind conditions and at night, which corroborates previous range testing studies in other habitats. We strongly support recommendations for performing acoustic range tests as a prerequisite for acoustic telemetry studies and the incorporation of multiple sentinel transmitters (i.e. stationary transmitters) within arrays to quantify temporal changes in detection probability [4, 5, 7, 10]. Incorporating range testing and sentinel transmitters into studies will allow researchers to better understand any assumptions made when estimating the home ranges or habitat associations of fishes [6]. Future research is necessary to explore if similar patterns in detection probability occur for transmitters within other seagrass species possessing different morphologies to *P. australis*, such as those with smaller leaves (e.g. *Zostera* spp.) as these may represent less of an obstacle to acoustic signals. Future range testing studies should also consider the effect of a fish's behaviour on the performance of acoustic telemetry in other habitat types, such as fish sheltering within reef crevasses or being buried within soft sediments [47].

Methods

Study area

The study was conducted in Jervis Bay Marine Park (JBMP; 35.06203° S, 150.73419° E) on the south coast of New South Wales (NSW), Australia (Fig. 5). JBMP incorporates a large acoustic array consisting of approximately 60 receivers which has been used to track a range of fish species over the past ~ 10 years [48, 49]. The seascape of JBMP is dominated by rocky intertidal and subtidal reefs, seagrass meadows and soft sediments. The seagrass selected for this study was *Posidonia australis* (Hook.f.), a species endemic to temperate Australia that forms large meadows within JBMP. *P. australis* is a long leaved, slow-growing seagrass of high conservation significance due to population declines and has been listed as endangered at six locations in NSW [28, 50].

Experimental design

In November 2017, three VR2Tx acoustic receivers (VEMCO Ltd Canada, Nova Scotia) were deployed to form a VPS within a large seagrass bed at Plantation Point in JBMP (Fig. 5). The three receivers were placed in a triangular formation and separated by 150 m on fixed moorings (Fig. 5). An additional six VR2W acoustic receivers (VEMCO Ltd Canada, Nova Scotia) were deployed in a cross formation 150 m apart to allow for a range of distances between the receivers and transmitters placed within the array (Fig. 5). The nine receiver moorings were deployed at depths ranging from 2.4 to 9 m and were comprised of a section of railway line (50 kg) and

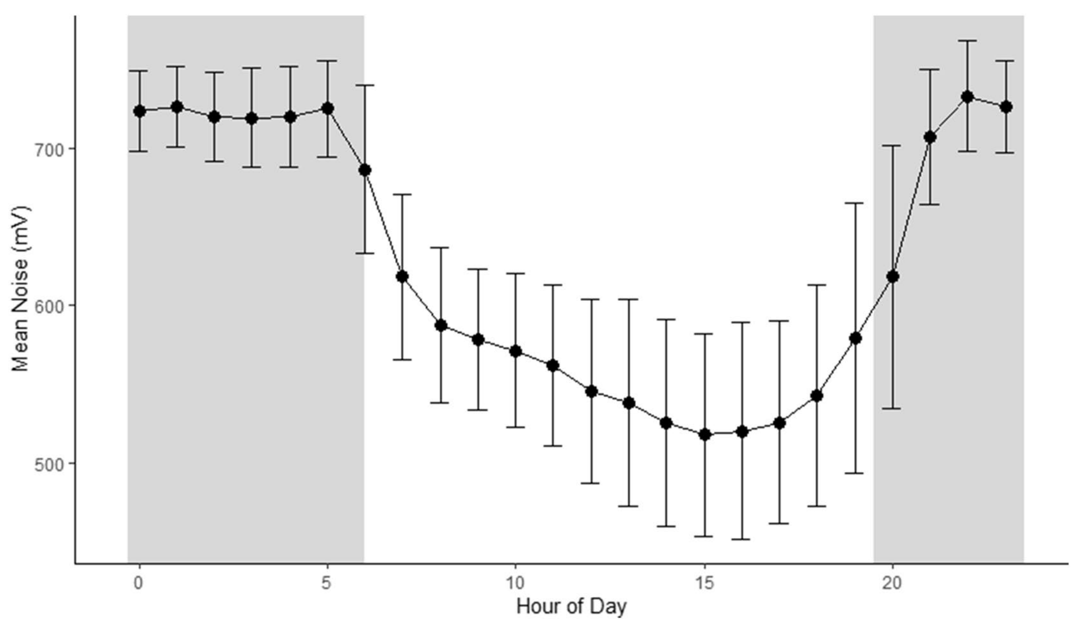

Fig. 4 Noise (mV) at 69 kHz calculated at all three VR2Tx receivers for each hour of the day. Solid dots represent the mean hourly value and error bars are ± standard deviation. Shading indicates nocturnal hours between 1930 and 06:00

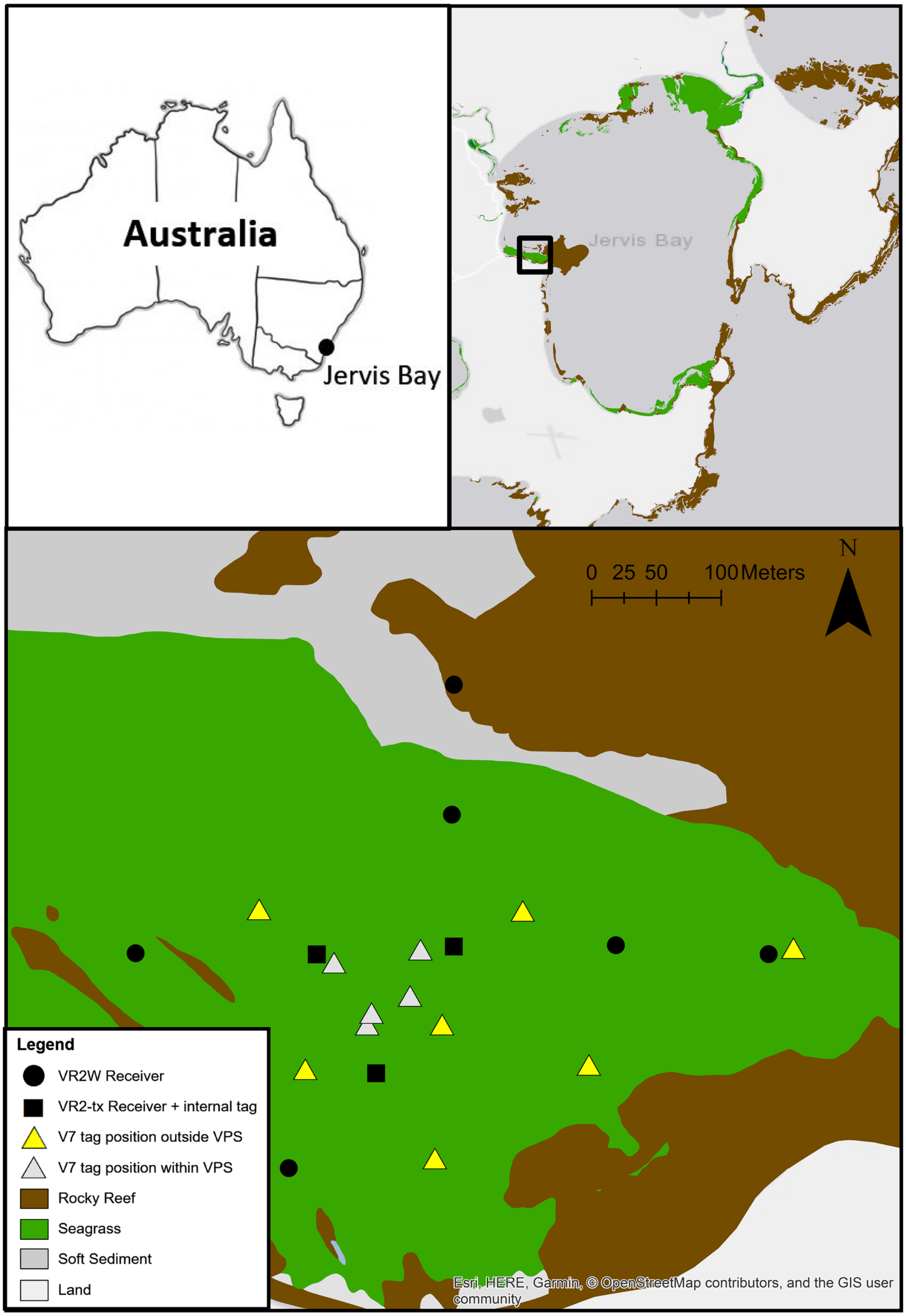

Fig. 5 Map of the location of Jervis Bay, NSW, Australia, showing the major habitats and the positions of the VPS, additional receivers and transmitters

a subsurface polystyrene buoy attached to a rope which maintained receivers in an upright position (hydrophones oriented to the surface). Receivers were fixed to the mooring a minimum of 1 m below the buoy to avoid blocking the hydrophone.

Range testing was performed using two different models of acoustic transmitters. First, four VEMCO V7-4x 69 kHz range test transmitters (power output 136 dB, fixed delay 180 s) were used to test the effect of submersion within seagrass on the performance of the VPS and acoustic receivers. These four V7-4x range testing transmitters were attached to two transportable moorings, respectively. These moorings were 2 m in height and comprised a six-pound dive weight with a subsurface polystyrene buoy attached to polypropylene rope. The V7-4x transmitters were placed either 15 cm or 145 cm from the base of the mooring to ensure that one transmitter was within the seagrass while the other was above the canopy (Fig. 6). Each pair of transmitters were located either within or outside of the VPS (Fig. 5). The transmitters within the VPS were relocated to five positions across two 4-week periods. The transmitters outside of the VPS were relocated to different positions generally every 7 days over two 4-week periods during November–December 2017 and March 2018 (one deployment was for a 2-week period due to poor weather). The locations of each V7 transmitter pair within and outside the VPS were spatially balanced using ArcGIS version v. 10 and ranged from 2.3 to 6 m in depth. Second, the three VR2Tx receivers each had an internal transmitter set to high power (154 dB) and a 300-s fixed delay, which is comparable to the output of a V16-4L transmitter (150–162 dB). These internal VR2Tx transmitters were deployed from November 2017 to April 2018 at depths ranging between 3.5 and 5 m and were used to investigate the influence of environmental variables on array performance over a broader temporal scale.

The distance between each transmitter location and receiver was calculated in R using the GPS locations and the ComputeDistance function in the package VTrack [51]. Meteorological conditions were recorded by the Australian Bureau of Meteorology (BOM) at the Point Perpendicular meteorological station 10.5 km from the study site. Four meteorological variables were included in our analyses; wind speed and direction, precipitation and air pressure. Each meteorological variable was recorded every 30 min and averaged to get an hourly value. The VR2Tx receivers recorded water temperature, receiver tilt and the ambient noise levels at 69 kHz (the operational frequency of the acoustic transmitters) every 10 min (Table 1). Each metric recorded by the VR2Tx receivers was averaged to provide an hourly mean. A variety of environmental conditions were encountered during the study period (Table 1), but as variation in receiver tilt was found to be negligible it was excluded from subsequent analyses.

Statistical analyses

The detection probability for each receiver and V7 transmitter combination was calculated as the total number of recorded detections for each deployment period over the number of expected detections. The detection probability of the internal VR2Tx transmitters was calculated as the number of recorded detections for each transmitter per hour divided by the number of expected detections (i.e. 12 detections). Days when the transmitters were relocated or deployed were excluded from the analyses. The influence of distance on the detection probability of transmitters above and within seagrass was estimated by fitting a logistic regression. A paired-sample t test was used to evaluate differences in the number of detections for transmitters “above” versus “within” seagrass over the entire deployment period.

The VPS used three acoustic receivers (VR2Tx) to triangulate the x–y positions of transmitters [52]. Positions calculated by the VPS were based on the differential time of arrival of acoustic transmissions travelling at a known speed that were simultaneously detected by all three receivers [11, 15]. The speed of sound was quantified from the temperature and salinity of the water [8]. The internal clocks of the VPS receivers were synchronised using the internal VR2Tx sync transmitters that emitted pings at known times [11, 15]. Time synchronisation of the receivers is necessary to accurately calculate differences in the time of arrival and account for time drift in the receiver’s clocks. Differences in the time of arrival of transmissions between receivers were then converted to differences in range and used in a hyperbolic positioning algorithm to generate an x–y position [52].

Three metrics for VPS performance were calculated: (1) positional accuracy, (2) precision, and (3) system efficiency [37]. Positional accuracy was measured as the Euclidean distance between the position estimated by the VPS and the GPS position of the transmitters. Precision represented the variability of positional accuracy and was the standard deviation of the mean daily positional accuracy. System efficiency was calculated as the proportion of successful estimated positions (i.e. number of positions/expected number of positions) by the VPS. These metrics were calculated and averaged to give a daily value for each day the transmitters were in the water, excluding the days during which transmitters were relocated. Generalised linear models (GLMs) were used to test the influence of a transmitter’s position

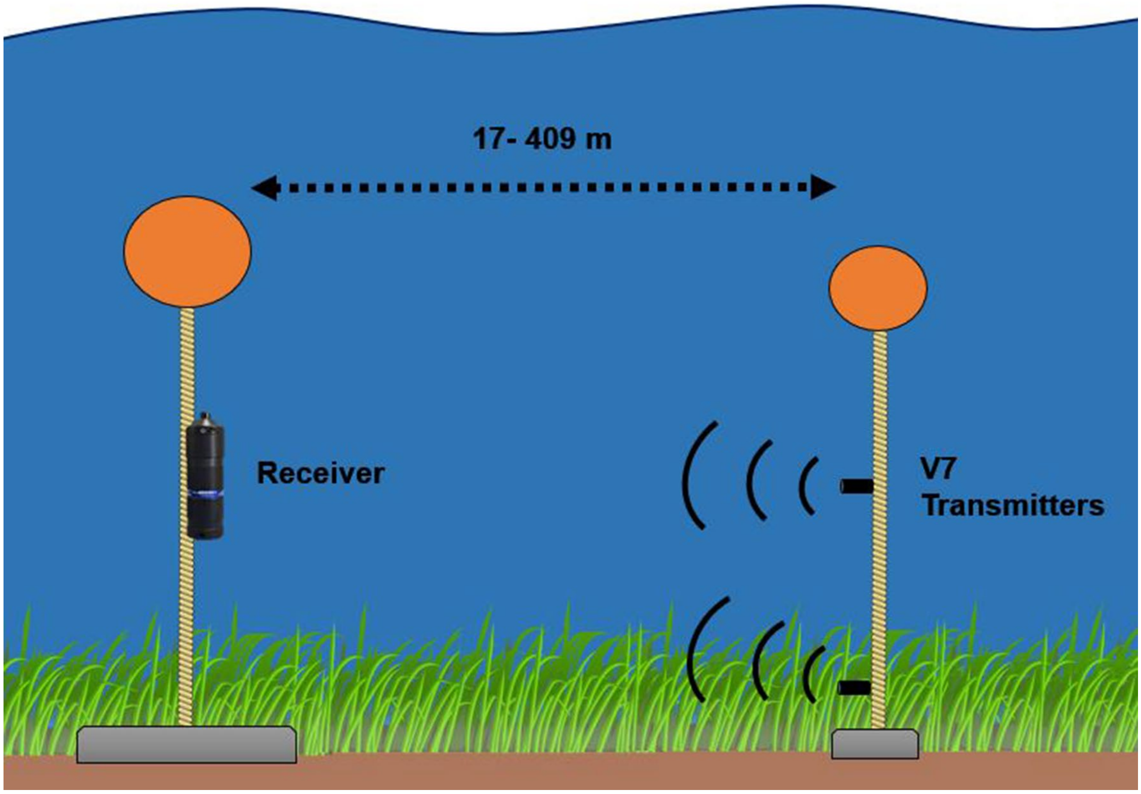

Fig. 6 Schematic of a VR2W acoustic receiver station (left) and two transmitters (V7-4x) suspended either above (145 cm) and within (15 cm) the seagrass

Table 1 The minimum and maximum values of environmental conditions

Variable	Source	Min. value	Max. value
Precipitation (mm)	BOM	0	8.7
Wind speed (km/h)	BOM	0	50
Wind direction (°)	BOM	0.5	359.5
Atmospheric pressure (Pa)	BOM	996.95	1030.25
Depth of receivers (m)	Depth sounder	2.4	9
Temperature (°C)	VR2Tx sensor	13.4	25
Noise 69 kHz (mV)	VR2Tx sensor	290	803.3

above or within the seagrass canopy on the mean daily positional accuracy, precision and system efficiency. GLMs for daily system efficiency were fitted with a binomial distribution and a gamma distribution was used for daily accuracy and precision.

Relationships between the detection probability of the internal VR2Tx transmitters and environmental variables were examined using generalised additive mixed models (GAMMs) [53, 54]. Prior to analysis, collinearity between explanatory variables was assessed using Pearson's pairwise correlation coefficients and Variance Inflation Factor (VIF). GAMMs were constructed using a full-subset approach to provide all possible model combinations [55]. GAMMs were fitted using a beta distribution with receiver ID as a random effect to account for the lack of independence between receivers. Models were restricted to a maximum of three explanatory variables and excluded variables with a Pearson's correlation greater than 0.28 to avoid issues with collinearity [55, 56]. These parameters were selected to prevent over-fitting and develop conservative, interpretable models. Average wind direction and hour of day were fitted using cyclic smooths to account for their circular nature [55]. Akaike Information Criterion corrected for small sample sizes (AICc) was used to compare models, with the best fitting model containing the lowest AICc [57]. No alternate candidate models were within ± 2 AICc of the best model. All statistical analyses and plots were developed using the statistical computing program R [58] and the functions; FSSGAM 1.11 [55], mgcv [59], ggplot2 [60], visreg [61] and gamm4 [62].

Abbreviations

VPS: Vemco Positioning System; BOM: Bureau of Meteorology; GPS: Global Positioning System; JBMP: Jervis Bay Marine Park; NSW: New South Wales; ID: Identification; GLM: Generalised linear models; GAMM: Generalised additive mixed models; AICc: Akaike Information Criterion corrected for small sample sizes.

Acknowledgements

We thank D. Ruiz-Garcia, C. O'Connor, C. Ahls, K. Swadling and C. De Mestre for field assistance. We acknowledge the support of Jervis Bay Marine Park staff, Mark Fackerell and Eddie Douglas.

Authors' contributions

DS, NK, HP, AD and KA conceived the study and designed the methodology. DS, KA, NK and AD performed fieldwork and collected data. DS, HP, MT and MR analysed the data. DS led the writing of the manuscript. All authors read and approved the final manuscript.

Funding

This research was funded by the NSW DPI, Sea World Research and Rescue Foundation Inc. (Grant No. SWR/2/2018), Winifred Scott Charitable Trust and the Australian Government Research Training Program.

Availability of data and materials

The datasets used and/or analysed in this study can be accessed through the AATAMS data base (https://animaltracking.aodn.org.au/) under the NSW DPI Jervis Bay project. Alternatively, the datasets used and/or analysed during the current study are available from the corresponding author upon reasonable request.

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

HP is currently employed by Vemco, a division of InnovaSea who manufacture the acoustic equipment used in this study.

Author details

[1] School of Earth, Atmospheric and Life Sciences, University of Wollongong, Wollongong, NSW, Australia. [2] NSW Department of Primary Industries, Fisheries Research, 4 Woollamia Road, Huskisson, NSW, Australia. [3] Vemco, A Division of InnovaSea, Bedford, NS, Canada. [4] New South Wales Department of Primary Industries, Port Stephens Fisheries Institute, Taylors Beach Rd, Taylors Beach, NSW, Australia.

Received: 18 December 2019 Accepted: 27 February 2020
Published online: 14 March 2020

References

1. Donaldson MR, Hinch SG, Suski CD, Fisk AT, Heupel MR, Cooke SJ. Making connections in aquatic ecosystems with acoustic telemetry monitoring. Front Ecol Environ. 2014;12:565–73.
2. Hussey NE, Kessel ST, Aarestrup K, Cooke SJ, Cowley PD, Fisk AT, et al. Aquatic animal telemetry: A panoramic window into the underwater world. Science. 2015. https://doi.org/10.1126/science.1255642.
3. Taylor MD, Babcock RC, Simpfendorfer CA, Crook DA. Where technology meets ecology: acoustic telemetry in contemporary Australian aquatic research and management. Mar Freshw Res. 2017;68:1397–402.
4. Gjelland KØ, Hedger RD. Environmental influence on transmitter detection probability in biotelemetry: developing a general model of acoustic transmission. Methods Ecol Evol. 2013;4:665–74.
5. Kessel ST, Cooke SJ, Heupel MR, Hussey NE, Simpfendorfer CA, Vagle S, et al. A review of detection range testing in aquatic passive acoustic telemetry studies. Rev Fish Biol Fisher. 2014;24:199–218.
6. Stocks JR, Gray CA, Taylor MD. Testing the effects of near-shore environmental variables on acoustic detections: implications on telemetry array design and data interpretation. Mar Technol Soc J. 2014;48:28–35.
7. Huveneers C, Simpfendorfer CA, Kim S, Semmens JM, Hobday AJ, Pederson H, et al. The influence of environmental parameters on the performance and detection range of acoustic receivers. Methods Ecol Evol. 2016;7:825–35.
8. Klimley AP, Voegeli F, Beavers SC, Le Boeuf BJ. Automated listening stations for tagged marine fishes. Mar Technol Soc J. 1998;32:94–101.
9. Heupel MR, Semmens JM, Hobday A. Automated acoustic tracking of aquatic animals: scales, design and deployment of listening station arrays. Mar Freshw Res. 2006;57:1–13.
10. Payne NL, Gillanders BM, Webber DM, Semmens JM. Interpreting diel activity patterns from acoustic telemetry: the need for controls. Mar Ecol Prog Ser. 2010;419:295–301.
11. Andrews KS, Tolimieri N, Williams GD, Samhouri JF, Harvey CJ, Levin PS. Comparison of fine-scale acoustic monitoring systems using home range size of a demersal fish. Mar Biol. 2011;158:2377–87.
12. Binder TR, Farha SA, Thompson HT, Holbrook CM, Bergstedt RA, Riley SC, et al. Fine-scale acoustic telemetry reveals unexpected lake trout, Salvelinus namaycush, spawning habitats in northern Lake Huron, North America. Ecol Freshw Fish. 2018;27:594–605.
13. Taylor MD, Becker A, Lowry MB. Investigating the Functional Role of an Artificial Reef Within an Estuarine Seascape: a Case Study of Yellowfin Bream (Acanthopagrus australis). Estuar Coast. 2018;41:1782–92.
14. Espinoza M, Farrugia TJ, Webber DM, Smith F, Lowe CG. Testing a new acoustic telemetry technique to quantify long-term, fine-scale movements of aquatic animals. Fish Res. 2011;108:364–71.
15. Roy R, Beguin J, Argillier C, Tissot L, Smith F, Smedbol S, et al. Testing the VEMCO Positioning System: spatial distribution of the probability of location and the positioning error in a reservoir. Anim Biotelemetry. 2014;2:1–6.
16. Medwin H, Clay CS. Fundamentals of acoustical oceanography. New York: Academic press; 1997.
17. Mathies NH, Ogburn MB, McFall G, Fangman S. Environmental interference factors affecting detection range in acoustic telemetry studies using fixed receiver arrays. Mar Ecol Prog Ser. 2014;495:27–38.
18. How JR, de Lestang S. Acoustic tracking: issues affecting design, analysis and interpretation of data from movement studies. Mar Freshw Res. 2012;63:312–24.
19. Welsh J, Fox R, Webber D, Bellwood D. Performance of remote acoustic receivers within a coral reef habitat: implications for array design. Coral Reefs. 2012;31:693–702.
20. Hedger RD, Dodson JJ, Hatin D, Caron F, Fournier D. River and estuary movements of yellow-stage American eels Anguilla rostrata, using a hydrophone array. J Fish Biol. 2010;76:1294–311.
21. Jackson EL, Rowden AA, Attrill MJ, Bossey SJ, Jones MB. The importance of seagrass beds as a habitat for fishery species. Oceanogr Mar Biol. 2001;39:269–304.
22. Boström C, Jackson EL, Simenstad CA. Seagrass landscapes and their effects on associated fauna: a review. Estuar Coast Shelf Sci. 2006;68:383–403.
23. Gillanders BM. Seagrasses, fish, and fisheries. In: Larkum AWD, Orth RJ, Duarte CM, editors. Seagrasses: biology, ecology and conservation. Springer: Dordrecht; 2006. p. 503–36.
24. Rees MJ, Knott NA, Davis AR. Habitat and seascape patterns drive spatial variability in temperate fish assemblages: implications for marine protected areas. Mar Ecol Prog Ser. 2018;607:171–86.
25. Sambrook K, Hoey AS, Andréfouët S, Cumming GS, Duce S, Bonin MC. Beyond the reef: the widespread use of non-reef habitats by coral reef fishes. Fish Fisher. 2019;20:903–20.
26. Swadling DS, Knott NA, Rees MJ, Davis AR. Temperate zone coastal seascapes: seascape patterning and adjacent seagrass habitat shape the distribution of rocky reef fish assemblages. Landsc Ecol. 2019;34:2337–52.
27. Orth RJ, Carruthers TJ, Dennison WC, Duarte CM, Fourqurean JW, Heck KL, et al. A global crisis for seagrass ecosystems. Bioscience. 2006;56:987–96.
28. Evans SM, Griffin KJ, Blick RA, Poore AG, Vergés A. Seagrass on the brink: decline of threatened seagrass *Posidonia australis* continues following protection. PLoS ONE. 2018;13:e0190370.
29. Adams MP, Saunders MI, Maxwell PS, Tuazon D, Roelfsema CM, Callaghan DP, et al. Prioritizing localized management actions for seagrass

conservation and restoration using a species distribution model. Aquat Conserv. 2016;26:639–59.
30. Hitt S, Pittman SJ, Nemeth RS. Diel movements of fishes linked to benthic seascape structure in a Caribbean coral reef ecosystem. Mar Ecol Prog Ser. 2011;427:275–91.
31. Dance MA, Rooker JR. Habitat- and bay-scale connectivity of sympatric fishes in an estuarine nursery. Estuar Coast Shelf Sci. 2015;167:447–57.
32. Papastamatiou YP, Dean Grubbs R, Imhoff JL, Gulak SJB, Carlson JK, Burgess GH. A subtropical embayment serves as essential habitat for sub-adults and adults of the critically endangered smalltooth sawfish. Glob Ecol Conserv. 2015;3:764–75.
33. Moulton DL, Dance MA, Williams JA, Sluis MZ, Stunz GW, Rooker JR. Habitat partitioning and seasonal movement of red drum and spotted seatrout. Estuar Coast. 2017;40:905–16.
34. Lee KM, Ballard MS, Venegas GR, Sagers JD, McNeese AR, Johnson JR, et al. Broadband sound propagation in a seagrass meadow throughout a diurnal cycle. J Acoust Soc Am. 2019;146:335–41.
35. Felisberto P, Rodriguez O, Santos P, Zabel F, Jesus S. Variability of the ambient noise in a seagrass bed. In: Proceedings of the IEEE 2014 Oceans: 14-19 September 2014; St. John's, NL, USA. 2014:1-6.
36. Heck Jnr K, Orth R. Seagrass habitats: The roles of habitat complexity, competition and predation in structuring associated fish and motile macroinvertebrate assemblages. In: Kennedy VS, editor. Estuarine perspectives. New York: Academic Press; 1980. p. 449–64.
37. Baktoft H, Zajicek P, Klefoth T, Svendsen JC, Jacobsen L, Pedersen MW, et al. Performance assessment of two whole-lake acoustic positional telemetry systems—is reality mining of free-ranging aquatic animals technologically possible? PLoS ONE. 2015;10:e0126534.
38. Cagua EF, Berumen ML, Tyler EHM. Topography and biological noise determine acoustic detectability on coral reefs. Coral Reefs. 2013;32:1123–34.
39. Selby TH, Hart KM, Fujisaki I, Smith BJ, Pollock CJ, Hillis-Starr Z, et al. Can you hear me now? Range-testing a submerged passive acoustic receiver array in a Caribbean coral reef habitat. Ecol Evol. 2016;6:4823–35.
40. Marshell A, Mills JS, Rhodes KL, McIlwain J. Passive acoustic telemetry reveals highly variable home range and movement patterns among unicornfish within a marine reserve. Coral Reefs. 2011;30:631–42.
41. Miksis-Olds JL, Miller JH. Transmission loss in manatee habitats. J Acoust Soc Am. 2006;120:2320–7.
42. Reubens J, Verhelst P, van der Knaap I, Deneudt K, Moens T, Hernandez F. Environmental factors influence the detection probability in acoustic telemetry in a marine environment: results from a new setup. Hydrobiologia. 2018;845:81–94.
43. Radford CA, Jeffs AG, Tindle CT, Montgomery JC. Temporal patterns in ambient noise of biological origin from a shallow water temperate reef. Oecologia. 2008;156:921–9.
44. Felisberto P, Rodriguez O, Santos P, Zabel F, Jesus S. Using passive acoustics for monitoring seagrass beds. In: Proceedings of the Oceans 2016 MTS/IEEE Monterey: 19–23 September 2016; Monterey, CA, USA. 2016. p. 1–6.
45. Jossart J, Nemeth R, Primack A, Stolz R. Extreme passive acoustic telemetry detection variability on a mesophotic coral reef, United States Virgin Islands. Mar Biol. 2017;164:180.
46. Jepsen N, Schreck C, Clements S, Thorstad E. A brief discussion on the 2% tag/Bodymass rule of thumb. In: Spedicato MT, Lembo G, Marmulla G, editors. Aquatic telemetry: advances and applications—proceedings of the fifth conference on fish telemetry: 9-13 June 2005; Ustica, Italy. Rome: FAO; 2005. p. 255–9.
47. Grothues TM, Able KW, Pravatiner JH. Winter flounder (*Pseudopleuronectes americanus* Walbaum) burial in estuaries: acoustic telemetry triumph and tribulation. J Exp Mar Biol Ecol. 2012;438:125–36.
48. Ferguson AM, Harvey ES, Taylor MD, Knott NA. A herbivore knows its patch: luderick, girella tricuspidata, exhibit strong site fidelity on shallow subtidal reefs in a temperate marine park. PLoS ONE. 2013;8:e65838.
49. Bass NC, Mourier J, Knott NA, Day J, Guttridge T, Brown C. Long-term migration patterns and bisexual philopatry in a benthic shark species. Mar Freshw Res. 2017;68:1414–21.
50. Larkum A. Ecology of Botany Bay. I. Growth of Posidonia australis (Brown) Hook. f. in Botany Bay and other bays of the Sydney basin. Mar Freshw Res. 1976;27:117–27.
51. Campbell HA, Watts ME, Dwyer RG, Franklin CE. V-Track: software for analysing and visualising animal movement from acoustic telemetry detections. Mar Freshw Res. 2012;63:815–20.
52. Smith F. Understanding HPE in the VEMCO positioning system (VPS). Vemco Inc. 2013. http://vemco.com/wp-content/uploads/2013/09/understanding-hpe-vps.pdf. Accessed 02 Dec 2019.
53. Hastie T, Tibshirani R. Generalized additive models: some applications. J Am Stat Assoc. 1987;82:371–86.
54. Hastie TJ. Generalized additive models. In: Statistical models in S. Routledge; 2017, p. 249–307.
55. Fisher R, Wilson SK, Sin TM, Lee AC, Langlois TJ. A simple function for full-subsets multiple regression in ecology with R. Ecol Evol. 2018;8:6104–13.
56. Graham MH. Confronting multicollinearity in ecological multiple regression. Ecology. 2003;84:2809–15.
57. Burnham KP, Anderson D. Model selection and multi-model inference: a practical information-theoretic approach. New York: Springer; 2004.
58. R Development Core Team. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. 2018. https://www.R-projectorg/.
59. Wood S, Wood MS. Package 'mgcv'. R Package Version. 2015;1:29.
60. Wickham H. ggplot2: elegant graphics for data analysis. New York: Springer; 2016.
61. Breheny P, Burchett W. Visualization of regression models using visreg. R J. 2017;9:56–71.
62. Wood S, Scheipl F. gamm4: generalized additive mixed models using mgcv and lme4. R package version. 2014;02–3:45–339.

Publisher's Note

Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.