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REPORT

Performance of remote acoustic receivers within a coral reef habitat: implications for array design

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Abstract Remote monitoring technologies are increasingly being implemented in the marine environment to better understand the movement patterns of taxa. Coral reefs are no exception. However, there is a paucity of information relating to the performance of acoustic receivers on coral reefs. Our results suggest that the detection performance of acoustic receivers may be significantly impacted by the unique nature of the reef environment. This study assessed the performance of passive acoustic receivers on a typical inner-shelf fringing reef, Orpheus Island, on the Great Barrier Reef, Australia. The detection range and diel performance variability of acoustic receivers was assessed using two parallel lines of 5 VR2W receivers spanning 125 m, deployed on the reef base and reef crest. Two 9-mm acoustic transmitters were moored at opposite ends of each receiver line. The working detection range for receivers was found to be approximately 90 m for the transmitter moored on the reef base and just 60 m for the transmitter moored on the reef crest. However, the detection range on the reef crest increased to 90 m when just the reef crest receivers were considered, highlighting importance of optimal receiver deployment. No diel patterns in receiver performance or detection capacities were detected, suggesting that no corrections are required when interpreting nocturnal versus diurnal activity patterns. We suggest that studies aiming for complete coverage of a site within a reef environment will require receivers in close (<100 m) proximity, and that the placement depth of receivers must be a major consideration, with shallow receivers exhibiting a greater detection range than those on the reef slope. Our results highlight the challenges imposed by coral reefs for acoustic telemetry and the importance of receiver placement for studies conducted within these habitats.

Keywords Acoustic telemetry · Passive monitoring · Detection range · Detection efficiency · Coral reef

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Introduction

Investigations of the movement patterns and site fidelity of aquatic species are now increasingly being carried out using passive (remote) acoustic monitoring, where focal individuals are tagged with coded transmitters and are monitored at automated listening stations (receivers) (Afonso et al. 2009; Semmens et al. 2010; Simpfendorfer et al. 2011). Of all peer-reviewed studies carried out using remote acoustic telemetry, more than one-third have been published in the last 3 years. Passive acoustic monitoring, therefore, represents a burgeoning field, presenting the opportunity to track the movement of individuals over periods of months (Egli and Babcock 2004; March et al. 2010) or years (Afonso et al. 2008; Meyer et al. 2010), and giving researchers the opportunity to test hypotheses relating to long-term habitat usage and site fidelity. The technology has been most frequently employed within estuarine (e.g., Hartill et al. 2003; Heupel et al. 2006), riverine (e.g., Winter et al. 2006) or deep-water oceanic habitats (e.g., Clements et al. 2005). Increasingly, however, the methodology is being utilized within the coral reef environment, particularly to answer important questions relating to the site fidelity and habitat use of harvested reef fish species (e.g., Meyer et al. 2010; O'Toole et al. 2011).

Despite the remarkable technological advances that have facilitated the increased ease and flexibility of use of remote acoustic monitoring, the interpretation of data collected by automated listening stations is still a developing area of research (Lacroix and Voegeli 2000; Clements et al. 2005; Simpfendorfer et al. 2008). Critical to the interpretation of detections made by an acoustic array is an understanding of both the detection range (Klimley et al. 1998) and the performance (sensu Simpfendorfer et al. 2008) of receivers within that array. Ultimately, the coverage yielded by the array at any given time will determine whether the data collected represents either a minimum or complete estimate of the animal's movement range. Detection ranges are all too frequently assumed, rather than tested. Where range tests are undertaken and reported for individual studies, detection ranges can deviate from the value reported in manufacturers' product specifications, highlighting the discrepancy in listening range for receivers within different aquatic habitats (Voegeli and Pincock 1996; Heupel et al. 2006). Both the detection range and performance of individual monitoring stations have been shown to be highly variable on temporal and spatial scales (Simpfendorfer et al. 2008; Payne et al. 2010). Without a full understanding of this variability in performance, the behaviour of the organisms being studied can be grossly misinterpreted (e.g., Payne et al. 2010).

The constraints of the technology, and the potential for variability in the detection performance of monitoring stations highlights the importance of properly evaluating receiver performance prior to and during each individual study (Heupel et al. 2006). However, there is currently a paucity of studies focusing on the acoustic equipment and its performance, especially on coral reefs (Heupel et al. 2008). As information on equipment performance in any given environment is integral to understanding telemetry results, variability in detection ranges between different environments should be a consideration in data analysis and interpretation. This is particularly important on coral reefs, which represent a relatively new and potentially difficult environment for the acoustic technology. Coral reefs are extremely noisy environments with a plethora of reef noise generated by the feeding, mating and territorial displays of invertebrates and fish taxa (e.g., Cato 1978; McCauley and Cato 2000; Simpson et al. 2008a, b). Reef noise, coupled with the high topographic complexity of coral reefs, may result in a highly variable acoustic receiver detection range, unique to the reef environment. The synergistic effects of the aforementioned obstacles when working on coral reefs stand to significantly affect the performance of acoustic receivers, with median detection ranges being reported as low as 108 m with a minimum value of 55 m (Meyer et al. 2010), well below manufacturer's specifications.

Recently, several performance metrics such as code detection efficiency, rejection coefficients, and noise quotients have become available, making it possible to evaluate the performance of receivers individually. The availability of performance metrics at the scale of the individual receiver has created the potential to better understand how the complexity and acoustic environment of coral reefs are influencing the receiver's capacity to detect acoustic transmitters, ultimately leading to an ameliorated capacity to interpret telemetry data (Simpfendorfer et al. 2008).

The goals of the current study were: first, to investigate the detection range and performance of ultrasonic acoustic receivers within a specific shallow coral reef environment and, second, to provide data to inform the design of listening arrays and interpretation of animal movement patterns within coral reef habitats more generally. The specific aims of the study were to determine (1) the effective working detection range of 9-mm acoustic transmitters within a coral reef environment, and (2) the extent of diel variability in acoustic receiver performance on a coral reef.

Methods

Study site

The study site was a 1.5-km stretch of fringing reef within Pioneer Bay, Orpheus Island, a granitic island in the inner-shelf region of the Great Barrier Reef lagoon (Fig. 1a). The leeward stretch of reef within Pioneer Bay is a low-energy environment composed of an extensive reef flat that reaches up to 400 m from the shoreline (details in Fox and Bellwood 2007). The reef flat has little topographic complexity and is frequently exposed at low tide. The reef crest is not sharply defined and is composed of many bare patches of consolidated substratum. The crest gives way to a gentle slope that displays high topographic complexity in many places near the crest created by large colonies of *Porites* spp. and *Acropora* spp. interspersed with sand and coral rubble areas, which create gullies and channels in many areas. At a depth of approximately 5 m (below chart datum) the topographic complexity decreases and the reef slope continues as a gently sloping sand substratum with occasional low patches of coral before flattening off at approximately 18 m. Due to its location on the inner part of

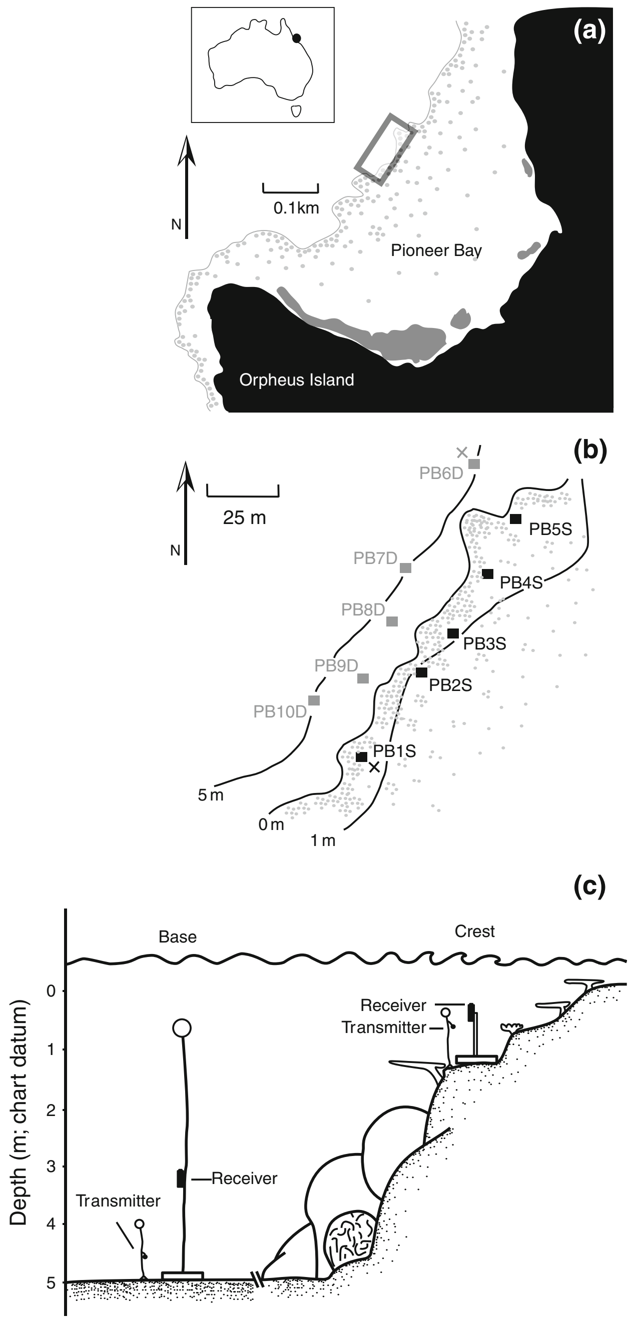

Fig. 1 Study site. Pioneer Bay, Orpheus Island, Great Barrier Reef. **a** Map showing location of range-testing array within Pioneer Bay, **b** locations of remote acoustic receivers along reef base contour (*grey squares*) and reef crest contour (*black squares*), fixed delay test transmitters (Vemco, V9-1L) were moored 0.5 m above the substratum at opposite ends of the array at deep (*grey cross*) and shallow (*black cross*) positions, and **c** an illustration of the depth at which the receivers were placed as well as the reef profile (please note, receivers and transmitters are not to scale, *horizontal axis* is truncated; receivers are 25 m apart)

the continental shelf and proximity to the mouth of the Herbert River, the reef on the leeward side of Orpheus Island is in a high sediment environment, with turbidity often resulting in visibility dropping to less than 2 m. Visibility is usually in the region of 4–10 m. Water turbidity was consistent throughout the study period, with visibility remaining at approximately 3 m.

Transmitter detection-range tests

Maximum detection range

Prior to the commencement of the study, preliminary tests were carried out to determine the maximum unobstructed detection range of 9-mm acoustic transmitters using fixed delay transmitters, which have a predictable, and constant, transmission interval (Vemco, V9-1L, 69 kHz, 5-s repeat rate, power output 146 dB re 1 μPa at 1 m). These data were then used to estimate effective distance increments between receivers for temporal detection range evaluations. In these initial tests, a single remote acoustic receiver (VR2W, Vemco. Ltd., NS, Canada) was moored at a depth of 2 m (approximately 5 m seaward off the reef crest). A fixed delay transmitter was then moored for approximately 15 min at a distance of 50 m from the receiver, a sufficient amount of time for the transmitter to produce more than 100 signal transmissions. After this time, the transmitter was moved parallel to the reef, maintaining the same depth, to a distance of 75 m where it was moored for an additional 15 min. The procedure was repeated at 100, 125 and 150 m fixed distances from the receiver. The detection efficiency of the receiver at each distance was then calculated based on the number of recorded detections divided by the number expected over the deployment period at each distance increment. The value for the expected number of detections could be calculated from preliminary laboratory tests of the transmitter run prior to the field deployment, as signals were produced by the transmitter at fixed, non-random time intervals. The transmission interval was determined to be 8 s as a result of the approximate 3 s it takes for the transmitter to emit a complete signal pulse train coupled with the 5-s fixed delay transmission interval, giving an expected detection rate of 7.5 signals min^{-1}.

Effective detection range and temporal variation in detection

Between 25th February and 3rd March 2011, 10 VR2W acoustic receivers were deployed in Pioneer Bay. Based on the results of preliminary tests to determine maximum detection range within the reef habitat (see above), the receivers were positioned in parallel lines following two distinct reef zones. Each line along the reef consisted of 5 VR2W receivers and was configured with the first two receivers spaced 50 m apart and the remaining 3 receivers spaced at 25 m increments (i.e., 0, 50, 75, 100 and 125 m from start point, respectively; Fig. 1b). This deployment configuration is designed to achieve high detection area coverage to estimate various spatial attributes of site attached fish such as their home range (e.g., Marshell et al. 2011) or the median distance travelled (Murchie et al. 2010). One line of receivers was positioned just shoreward of the reef crest while the other receiver line followed the reef base contour (Fig. 1b). Moorings for the receivers on the reef crest were placed at a depth of approximately 1 m (below chart datum) and consisted of a 50-cm metal pole, the base of which was sunk into a 30-kg concrete block. Receivers were fixed to the pole and oriented vertically upwards with the hydrophone extending 10 cm above the top of the metal pole in order to minimize interference between the mooring structure and hydrophone reception (Clements et al. 2005). The shallow crest receivers were, therefore, about 0.5 m below chart datum. Receivers along the reef base contour were attached to a simple rope mooring which was anchored to the sea floor at a depth of approximately 5 m. Receivers were fixed to the rope at least 1 m below a sub-surface float, which held the receiver vertical in the water column at a depth of about 3 m. While the receivers were deployed, climactic conditions remained consistent, with moderate winds (<15 km) and swell (<60 cm), overcast skies and <1 mm of rain.

Two coded transmitters (Vemco, V9-1L, 69 kHz, random delay interval 190–290 s, power output 146 dB re 1 μPa at 1 m) were moored at opposite ends of each receiver line, one adjacent to receiver PB1 (1 m from receiver; transmitter 1) and the other adjacent to receiver PB6 (transmitter 2) (Fig. 1b, c). The transmitters were held 0.5 m from the substratum, simulating the depth at which most medium to large (20–70 cm TL) benthic reef fish would be active while foraging or swimming. As a result of the long random delay interval of the transmitters used in the long-term range-testing experiment, the number of code transmissions produced cannot be calculated with the required precision over short time periods (hours) in the same manner as a transmitter with a fixed delay transmission interval. Therefore, the number of detections recorded by PB1 and PB6 for transmitters 1 and 2, respectively, were used for analysis as the number of transmissions made by each transmitter during the study period. The transmitters were left in place for a 7-day period, after which time they were removed from the study site and the detection data files downloaded from each VR2W receiver. Immediately after the 7-day data collection period, the transmitters used for the long-term deployment were assessed to determine if they were representative of typical V9 transmitters. To do this, both transmitters used in the study and an identical third transmitter (Vemco, V9-1L, 69 kHz, random delay interval 190–290 s, power output 146 dB re 1 μPa at 1 m) were moved to a mooring 50 m from a receiver, which was left in place for a 12-h period. Following this, the receiver was collected and data was downloaded to compare the average number of detections from each transmitter during five randomly selected 30-min time periods.

Data analysis

Overall detection probabilities and effective detection range

The average number of detections from the transmitters deployed on the array, and a third transmitter, were compared using a one-way ANOVA. The assumption of normality was inspected using residual plots, and homogeneity of variances was checked using Levene's test for homogeneity of variances. No transformations were required to meet the assumptions of ANOVA.

For each of the two test transmitters, detections recorded at individual receivers over the 7-day test period were grouped into 6-h bins and classified as either "day" (0601–1800 hours) or "night" (1801–0600 hours). Individual detection probabilities for each 6-h period at each receiver were calculated based on the total number of recorded detections expressed as a percentage of the known number of transmissions (derived from the number of detections from the receiver adjacent to the transmitter). Missed transmissions due to signal overlap from occasional visits of tagged taxa to the study site were factored into the analysis. Individual detection probabilities for each receiver were then plotted against the distance from the receiver to the transmitter for diurnal and nocturnal sampling periods. Detections were modelled using linear regressions and logistic regressions. For the reef base, a linear regression analysis was the best model for the data (distance to transmitter as independent variable). For the reef crest, the relationship between number of detections (number of signals per day present vs. absent across the array) and the distance from the transmitter was best modelled by a logistic regression.

Temporal (diel) variation in detection

Temporal variation in detection probabilities were examined by calculating the average number of detections for each of the 12-h diurnal and nocturnal sampling periods (average values per 12-h bin were treated as individual data points for analysis). Differences in the proportion of signals detected by each receiver in diurnal and nocturnal sampling periods were then compared using a repeated measures analysis of variance (RMANOVA).

To evaluate the effect of interference, which may occur on a regular diel basis (such as reef noise), diel detection densities (hourly detection frequencies) across the array as a whole were also examined. For each day during which the array was in place, detections from the two test transmitters were grouped into hourly bins to give a total number of detections hour^{-1} by the array. Hourly values were then averaged across the 7 days of the study to give a mean hourly detection frequency in each of the 24 hourly bins, and these hourly detection frequencies were compared using a Chi-squared goodness of fit test. To detect any fine-scale cyclical patterns in diel detection frequency, a Fast Fourier Transformation (FFT) (with Hamming window smoothing) was also applied to the data. Following Payne et al. (2010) the magnitude of variation of each hourly bin (the standardized detection frequency or SDF) around the overall mean daily detection frequency was then calculated as: $\mathrm{SDF_b} = B_b/\mu$, where B is the mean detection frequency in each of the hourly bins and μ is the overall mean detection frequency. Therefore, should acoustic interference be high at certain periods of the day, we would expect low SDF values for the hourly bins during that time period as the receiver would be detecting fewer than average detections. This provides an indication of the extent to which transmitter detections may have been under-represented during particular parts of the diel cycle due to environmental factors.

Acoustic receiver performance

Parameters recorded in the metadata file downloaded from each VR2W receiver were used to provide a quantitative metrics of the overall performance of the array. Metrics were based around four specific parameters relating to the 8-pulse train emitted by the coded transmitters used in this study: (1) the total number of pulses recorded each day by a receiver (P); (2) the number of recorded detections (D); (3) the number of valid synchs (where a synch is the interval between the first two pulses of the 8-pulse train that identifies the incoming code as belonging to a transmitter) (S) and; (4) the number of codes rejected due to invalid checksum periods between the final two pulses of the train (C). From these parameters the daily code detection efficiency ($\mathrm{D{\cdot}S^{-1}}$), daily rejection coefficient ($\mathrm{C{\cdot}S^{-1}}$) and daily noise quotient (P–S·# of pulses required to make a valid code) were calculated for each receiver (see Simpfendorfer et al. 2008 for further description of individual parameters and metrics). It is worth noting that the VR2W can also count non-synch periods (periods generated by transmission overlap and noise interpreted by the receiver as pings) as syncs, however, there was very little evidence of this factor herein. The effect of the receiver's distance from each of the moored transmitters on the aforementioned performance metrics was evaluated using Pearson's correlation analysis.

Results

Maximum detection range

The preliminary tests of maximum detection range revealed a rapid decline in detection probability for a 9-mm transmitter over short distances within the reef environment. At 50 m from the receiver only 62% of transmissions from a fixed delay range-testing transmitter were detected, decreasing to a probability of just 4% at a distance of 150 m. At a distance of 125 m from the receiver, 22% of transmissions were detected, beyond this distance, detection values fell to below 5% and, therefore, 125 m was taken to be the maximum workable detection range within the study reef environment. This means that, in the absence of other competing transmitters, a lone individual tagged with an acoustic transmitter must be resident, on average, for at least 1,090 s ([190 + 290]$\cdot 0.22^{-1}$) to be detected at a distance of 125 m.

Overall detection probabilities and detection range

For each transmitter a significant negative relationship existed between both diurnal and nocturnal detection probabilities and distance from receiver (Fig. 2). The slopes and intercepts for the regression equations for diurnal and nocturnal periods were similar on both the reef crest ($y = e^{4.91-0.08(x)}/(1 + e^{4.91-0.08(x)}$ and $y = e^{4.75-0.07(x)}/(1 + e^{4.91-0.08(x)}$, respectively) and on the base ($y = 94.56–0.52x$ and $y = 90.92–0.49x$, respectively). For the 9-mm transmitter (random delay interval transmitter) moored on the reef base (next to the deep receiver line), detection probabilities decreased gradually at increasing distance from the receiver (Fig. 2a). For practical purposes, a cut-off of 50% detection efficiency was deemed acceptable for biological interpretation (Payne et al. 2010), meaning that the effective working detection range for this deep transmitter was 90 m. However, an average 30% of detections were still being recorded at a distance of 125 m from the transmitter. For the 9-mm transmitter moored on the reef crest (next to the shallow receiver line), detections dropped off much more steeply, driven for the most part by the small probability of detection by receivers moored along the reef base (Fig. 2b). In this case, the working (50%) detection range was just 60 m (Fig. 2b), although this increased to approximately 90 m when considering only detections by the shallow line of receivers. In contrast to the results for the deep transmitter, virtually no detections were being recorded at a distance of 125 m from the shallow transmitter, even by the shallow line of receivers (Fig. 2b).

Differences in the number of detections from the transmitter deployed on the reef base and the one on the

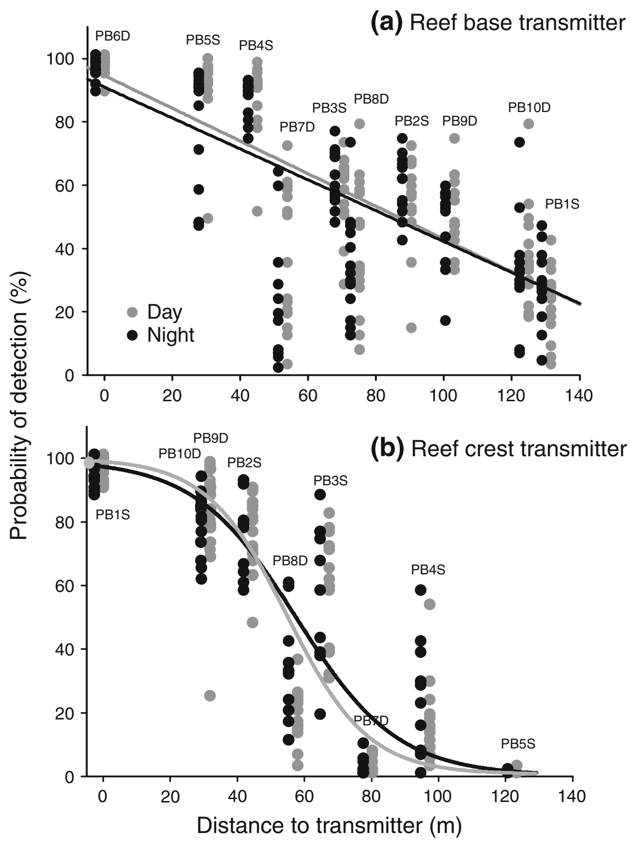

Fig. 2 **a** Relationship between the probability of detection and distance from the receiver for a transmitter moored on the reef base during diurnal hours (*grey line*, linear regression, slope = −0.516, constant = 94.56, $P < 0.000$, $R^2 = 0.516$) and nocturnal hours (*black line*, linear regression, slope = −0.488, constant = 90.92, $P < 0.000$, $R^2 = 0.482$) and **b** relationship between the number of successful versus unsuccessful detections and distance from the receiver for a transmitter moored on the reef crest during diurnal hours (*grey line*, logistic regression, slope = −0.084, constant = 2.35, $P < 0.000$, Nagelkerke $R^2 = 0.705$) and nocturnal hours (*black line*, logistic regression, slope = −0.067, constant = 4.08, $P <$ 0.000, Nagelkerke $R^2 = 0.635$). Detection probabilities are shown for each 6-h period of the 7-day test and are classified as diurnal (0601–1800 hours) (*grey circles*) or nocturnal (1801–0600 hours) (*black circles*). Nocturnal data points have been shifted slightly left on the *y* axis to eliminated significant overlap with diurnal data points

reef crest cannot be attributed to differences in transmitter performance. Post hoc tests revealed no significant difference between the number of transmissions made by either of the transmitters used over the 7-day trial period or a third transmitter used to compare transmitter performance ($F_{2,12} = 1.27$, $P > 0.05$).

Temporal (diel) variation in detection

The comparison of average detection probabilities for 12-h diurnal and nocturnal periods revealed no significant diel difference in signal detection probability for the deep receiver line ($F_{1,8} = 0.17$, $P = 0.69$) or the shallow receiver line ($F_{1,8} = 0.02$, $P = 0.88$). On an hour-by-hour basis there were some differences in detection frequencies over the course of the day ($\chi^2_{22} = 34.62$, $P = 0.042$). However, the overall diel pattern of detection densities did not reveal any distinct trend in over- or under-representation of detections during nocturnal or diurnal hours (Fig. 3). FFT analysis likewise revealed no prominent diel cycles of detection in the observed power spectrum (please see Electronic Supplemental Material, ESM for FFT output). Instead, several major peaks were found and those with the greatest spectral density occurred at 40, 10 and 16.7 h cycles (ESM Fig. 1). Standardization of detection frequencies to remove any artefacts of environment and varying distance to receiver on detection frequency confirmed that there was little diel variation in detection density, with the only discernable pattern being an under-representation of detections in the period around dawn (0500–0600 hours) (Fig. 3). Otherwise, both positive and negative variation around the mean daily detection frequency was observed in both diurnal and nocturnal periods (Fig. 3).

Receiver performance

The daily code detection efficiency of the receivers used in this study ranged from 0.268 to 0.816 detections synch^{-1}, with an overall average of 0.516 detections synch^{-1} (±0.01 SE). This meant that just over half the codes transmitted by the two transmitters were successfully recorded by the receiver array. The mean rate of code rejection was just 0.022 (±0.001), suggesting that, on average, only 2% of codes were rejected due to invalid checksum periods. The value of the noise quotient recorded by each receiver was almost universally negative in value and averaged −1067.8

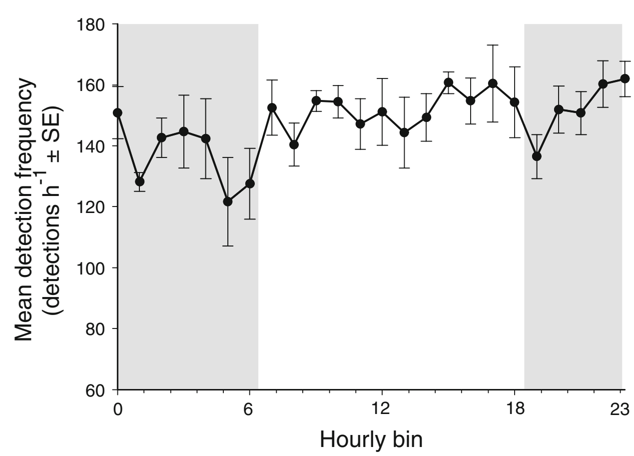

Fig. 3 Diel detection frequency (mean detections per hourly bin over the 7-day test period ± SE) across the entire array for the two test transmitters. *Shading* indicates nocturnal hours (1801–0600 hours)

($\pm$87.5). There was no relationship between the distance of receivers to transmitters and code detection efficiency ($r = -0.20$, $P > 0.05$), code rejection rate ($r = 0.23$, $P > 0.05$) or the noise quotient ($r = -0.16$, $P > 0.05$).

Discussion

Our results suggest that the working detection range for 9-mm transmitters (Vemco, V9-1L, 69 kHz, power output 146 dB re 1 μPa at 1 m), the size most suited for the majority of benthic reef fishes on coral reefs, may be as low as 60 m. While transmitters with higher power outputs may be detectable at a slightly greater range, this value is a fraction of the ranges previously reported in the literature for this size of transmitter within aquatic habitats. For example, a 450-m range was reported for 9-mm transmitters in the Caloosahatchee River (Simpfendorfer et al. 2008), and a 200-m detection range was reported for V9-2L transmitters (with a similar power output to those used herein) in temperate reef habitats of South Australia (Payne et al. 2010). Instead, the overall detection range found herein is most comparable to the minimum detection range of 60 m reported by Meyer et al. (2010) on Hawaiian reefs. Our results suggest that the detection performance of acoustic receivers may be significantly impacted by the unique nature of the reef environment and demonstrates the importance of testing the range of acoustic arrays across individual habitats and study sites.

In the case of Pioneer Bay, the receiver performance metrics may provide potential explanations for the reduced detection ranges reported. The low code rejection coefficients exhibited by receivers indicates that codes were not being rejected because of invalid checksum values (values that check the integrity of the code transmission used by the receiver to validate the code and confirm it is a recognizable transmitter). The reduced detection efficiencies recorded in this study, therefore, were driven by the receiver unit not receiving the full sequence of pulses emitted by the transmitter. For the coral reef environment, there are several possible explanations for the reception of incomplete code sequences by the receiver. These include (1) distortion of the acoustic pulse train (e.g., dampening of amplitude) via interference from environmental noise (acoustic waves) (both physical and biological sources and periodic or chronic); (2) the distortion of the code sequence via reflection off topographically complex substrata; (3) the distortion of the code sequence via absorption by particles in the water; (4) collision with pulses from other transmitters within the detection range of the receiver; (5) blockage of the transmission by a tagged individual moving behind an obstacle. In the case of the current study, the latter two explanations can be eliminated by virtue of the fact that detection performance was based on stationary transmitters operating in an environment with minimal transmitters present. This leaves background noise, suspended sediment and topography as likely explanations for the fact that transmitter code sequences attenuated over shorter than expected distances in the reef environment.

In terms of background noise, it has been suggested previously that the capacity of an acoustic receiver to detect a signal emitted by a transmitter is hindered in the presence of large amounts of background interference, such as the noise generated by snapping shrimp and other marine taxa (e.g., Voegeli and Pincock 1996; Clements et al. 2005; Simpfendorfer et al. 2008). Intermittent noise recorded as a ping during an actual transmitter's transmission can cause the receiver to reject the transmission, resulting in the receiver ignoring the actual transmitter's acoustic signal. Continuous noise can raise the threshold required to detect a transmission from a transmitter resulting in a lower detection range (with fewer pings likely to be detected). Reefs are notoriously noisy environments and, undeniably, there is a range of noises on coral reefs, mostly biological in origin, occurring over an extremely broad acoustic spectrum. Reef noise has been documented to reach frequencies as high as 200 kHz, in the case of the noise produced by snapping shrimp (Au and Banks 1998). The evidence from the negative noise quotient values in the present study suggests that, in the reef environment, the receivers are not hearing intermittent noise, which would contribute to a high noise quotient value, but are perhaps hearing continuous noise. Continuous background noise would cause the receivers to adjust their signal detection sensitivity to ignore consistent background noise, which may result in the occasional signal from the transmitter being ignored, thus contributing to a lower detection range than has been reported in other aquatic environments.

A further manner by which ambient noise may reduce the detection capacities of the receiver is by modifying the acoustic signal of the transmitter itself. The further the acoustic signal from a transmitter must travel, the more likely it becomes that the signal will collide with other noise and thus, be modified. In this sense, reef noise may cause an incomplete pulse train to reach the receiver. Ambient noise may therefore have both an indirect (interference with the transmitter) and direct (interference with the receiver) effect on acoustic signal detection.

Surprisingly, the current study did not detect a significant difference between the diurnal and nocturnal performance of acoustic receivers within the reef habitat, something which has been reported in other environments where testing of passive acoustic arrays has been undertaken (Payne et al. 2010). In temperate, shallow, marine environments and estuaries, the temporal variation in activity of invertebrates such as snapping shrimp have been suggested as the cause of these patterns in the detection range of acoustic receivers (Heupel et al. 2004, 2006). While the source of biological noise on reefs is highly variable, and possibly more intense at night (Bardyshev 2007), the acoustic characteristics of the noises produced are actually quite similar in diurnal and nocturnal periods (Leis et al. 2002). Choruses from fish schools (McCauley and Cato 2000) and invertebrates can be heard in both diurnal and nocturnal time periods (Radford et al. 2008). Therefore, should noise be capable of having a significant impact on the signal transmitted from a transmitter, it is likely to be having a similar impact in both nocturnal and diurnal sampling periods. Small, yet significant, declines in the number of detects were, however, recorded at dawn and dusk. These trends may arise as a result of an increased instance of reef noise documented to occur during these time periods on tropical reefs from fish choruses and invertebrates (Fish 1964; Cato 1978; Radford et al. 2008). However, the absence of a distinct peak in the spectral density of the FFT analysis herein suggests that these patterns are non-cyclic, and may be random noise. This is most apparent when our results are compared to the strong spectral peaks at 24 h, and secondary peaks at 6 and 12 h, described by Payne et al. (2010) using stationary control transmitters. Although we did not see the same degree of diel variation in the mean detection frequency of transmitters reported from previous studies (Payne et al. 2010), our results do suggest that, to at least some extent, background noise is contributing to lower detection ranges and small detection probabilities.

Within the reef environment at Pioneer Bay, several physical factors are also likely to have contributed to interference in signal detection by physically blocking the acoustic signal. High levels of suspended matter that are characteristic of turbid inshore reefs, such as Orpheus Island, may cause reflection of acoustic signals, interrupting acoustic pulse trains (Voegeli and Pincock 1996 cited in Simpfendorfer et al. 2008). Moreover, the natural topographic complexity of reefs mean that a clear line of sight between receiver and transmitter is likely to be more frequently breached than in a sandy or muddy-bottomed lagoonal or estuarine habitat. Even in the current study where receivers were detecting stationary transmitters, high topographic complexity may have an impact on detection ability. Receiver PB7D, which consistently performed below the level expected given its distance to the two transmitters, was in close proximity to significant benthic complexity, which is likely to have effectively and consistently blocked the acoustic signal. This result, even on a stationary transmitter, stresses the importance of both optimal receiver placement and assessment of the detection performance of individual receivers to the design of an effective remote monitoring array.

However, the precise causes of the strong signal attenuation are probably complex and may have several contributing factors. Intra-environmental variability in receiver detection capacities, both holistically and in terms of diel variation, as seen in temperate reefs (e.g., Payne et al. 2010), highlight the need to perform detailed range tests when utilizing acoustic telemetry to monitor movement biology. Moreover, the unique performance of acoustic telemetry in a variety of environments emphasizes the dangers of simply inferring detection ranges from previous studies. It is strongly recommended that simple range tests, such as those conducted herein, be undertaken to assess maximum detection ranges in arrays, to help avoid misinterpretation of results.

Knowledge of the study environment and careful selection of individual receiver placement is imperative to inferring the detection range not only of individual receivers, but also the area covered by the detection array. Similar to the reduced detection capacity of receiver PB7D, those receivers moored on the deep line detected a lower than expected proportion of the acoustic signals emitted from the shallow transmitter. This is likely to be due to the fact that pulses emitted from the transmitter would need to pass the reef slope, at which point they may reflect off the reef matrix and attenuate before reaching the receivers. Therefore, the deep line of receivers is likely to be more useful for the detection of off-reef movements and may not be effective for detecting within-reef movement of focal organisms. Other aquatic habitats such as rivers, estuaries and the open ocean are not likely to contain such pronounced drop-offs and receivers are therefore likely to exhibit a more uniform performance in all directions. For coral reefs, however, receivers are likely to have a more biased elliptical detection range, extending further into less complex areas. The use of multiple lines of receivers when designing arrays for the reef environment is therefore recommended for capturing the movement patterns of animals over different reef zones. In the current study, a shallow line was found to be most effective for the detection of organisms moving over the reef crest and flat, with the likely benefits of decreased acoustic shadow zones out-weighing the disadvantages of potential exposure during low tide. By virtue of the complexity to reefs, benthic organisms' movements through structurally complex areas may be under-represented in the data. It appears that specific care needs to be taken during receiver deployment to minimize the number of acoustic shadow zones in areas of high utilization by focal tagged individuals.

The results of the present study suggest that, for reef environments, maximum detection ranges and defined diel variability in detection range cannot be assumed. Moreover, they highlight the importance of receiver placement for passive monitoring studies on coral reefs. In this study both environmental and acoustic attributes of coral reefs which are likely to cause a lower detection range of acoustic transmitters were found to be more or less constant throughout the diel period and thus, it would not be necessary to correct for detection variability to infer activity levels across the diurnal-nocturnal cycle. Given the size of reef fishes, 9-mm transmitters are suitable for the majority of larger species on coral reefs. However, we suggest that studies aiming for complete coverage of a site inhabited by individuals tagged with 9-mm transmitters (or any transmitter with a similar power output) will require receivers in close (less than 100 m) proximity. Moreover, gated or curtain arrays may require double lines or some other form of redundancy in the array in order to confirm the movement of an individual past a particular point. The farther the acoustic signal must travel over the reef, reflecting off various substrates and colliding with any number of propagating acoustic signals, the more likely it is that the pulse will significantly attenuate before it reaches the receiver and not be detected. A combination of particulate matter, extreme topographic complexity and high ambient noise levels may, therefore, act in concert to create a reduced capacity for acoustic signals to propagate in reef habitats, compared to other aquatic environments. By their very nature, reefs create a challenge for working with acoustic technology, the result of which appears to be a reduction in the effective working range of 9-mm transmitters and receivers. Overall, estimates of animal movement in the coral reef environment as determined by passive acoustic monitoring must be interpreted with caution. In these systems, the old maxim that the absence of evidence does not represent evidence of absence is particularly important.

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