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ORIGINAL PAPER

Determining effective acoustic array design for monitoring presence of white sharks *Carcharodon carcharias* in nearshore habitats

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Abstract

Inferences regarding animal presence from passive acoustic receiver arrays are driven by the spatial configuration of receivers. Large, dense arrays provide more information, but maintenance of multiple receivers is costly. Configuring acoustic receiver arrays to maximise coverage while minimising cost is therefore paramount. This study used data from a dense acoustic receiver array within a white shark *Carcharodon carcharias* nursery area on the east coast of Australia to assess how detection data of tagged white sharks in the area was affected by reducing the array size. Receivers were sub-sampled post hoc by simple random sampling, clustered random sampling, and sampling of the top performing receivers. Using the top performing receivers, array size could be reduced by 60% (10 out of 25 receivers) while still detecting a median of 100% of white sharks detected with the full array. With random and clustered sampling methods, a 40% reduction in array size (15 out of 25 receivers) detected a median of 100% of sharks. Reducing the array size by 60% using the top performing receivers resulted in a 35% decrease in the median number of detections per visit of the tagged sharks (67 out of 102.5 detections). In comparison, reducing the array by the same amount with random and clustered sampling methods resulted in a 57% decrease (44 out of 102.5 detections). The post hoc sampling methods used in this study are an empirical approach for optimising placement of limited receiver resources with broad application for establishing cost-effective monitoring.

Introduction

Passive acoustic telemetry is a highly utilised method for long-term tracking of aquatic animals (Voegeli et al. 2001; Heupel et al. 2006a; Sims 2010; Hussey et al. 2015), whereby acoustic receivers record the presence of an animal carrying a coded acoustic transmitter within the detection range of the receiver (Sundström et al. 2001; Voegeli et al. 2001; Sims 2010). Using tags with a lifespan of up to 10 years, researchers and managers are able to monitor animals over ontogenetically meaningful time scales for both large-scale (Udyawer et al. 2018) and small-scale (Klimley et al. 2001; Heupel et al. 2006b; Espinoza et al. 2011a; Pillans et al. 2014) ranges of movement. However, because the presence of an animal is only recorded when the individual is within a receiver's detection radius (typically < 500 m), an array's monitoring effectiveness is heavily influenced by the density and spatial arrangement of receivers (e.g., Welsh et al. 2012; Steel et al. 2014; Huveneers et al. 2016; Patterson and Pillans 2019).

Array designs vary considerably according to study constraints and specific goals. However, two common

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approaches defined by Heupel et al. (2006a) are (1) receiver grids, which are suited for the examination of home range and habitat utilisation within a particular site (e.g., Heupel et al. 2004, 2006b; Espinoza et al. 2011a; Pillans et al. 2014), and (2) receiver lines, or gates, which are often employed to monitor migrations and movements to or from areas of interest such as marine parks, spawning grounds or habitat types within an area (e.g., Andrews et al. 2010; Heupel et al. 2010; Carlisle et al. 2019). Within these two categories of array design, there is the further consideration of whether to attempt near complete coverage, which involves placing acoustic receivers close enough to each other that their detection ranges overlap allowing for better estimation of animal position based on simultaneous detection by multiple receivers (e.g., Klimley et al. 2001; Simpfendorfer et al. 2002; Heupel et al. 2004; Espinoza et al. 2011b), or a 'leaky' configuration, which maximises the total area that can be covered by the receivers but leaves gaps between the detection ranges of the individual receivers and therefore provides less detailed location information (e.g., Bruce and Bradford 2011b; Pillans et al. 2014; Harasti et al. 2017).

Array design should primarily be driven by the study objectives; however, constraints on cost and logistics of servicing the array are unavoidable. Acoustic receivers themselves, and the costs associated with deploying them, can be one of the greatest financial imposts for a study (Simpfendorfer and Heupel 2004; Heupel et al. 2006a; Espinoza et al. 2011b; Steel et al. 2014). Therefore, understanding the benefits and drawbacks of various array configurations (both number and spatial distribution of receivers) is essential to optimise data collection within the financial constraints of a given research project. Stemming from the widespread use of acoustic arrays and the necessity to optimise array configurations, a few papers have outlined steps in designing an effective passive acoustic telemetry study (Heupel et al. 2006a; Brownscombe et al. 2019; Patterson and Pillans 2019). While several papers have investigated the idea of iteratively refining the design of acoustic arrays using environmental (Welsh et al. 2012; Steel et al. 2014; Huveneers et al. 2016) or model-based approaches (Hobday and Pincock 2011; Patterson and Pillans 2019), there are few studies investigating an empirical approach to reducing the size of acoustic arrays by subsampling data from an existing dense array (e.g., Cowley et al. 2017; Steckenreuter et al. 2017; Carlisle et al. 2019). The similarities and differences of these studies with our study are discussed in more detail in Discussion.

Acoustic receiver arrays are increasingly being deployed in coastal waters where there is a high potential for negative interactions between water users and potentially dangerous sharks (Johnson et al. 2009; Bradford et al. 2012; Kock et al. 2013; Spaet et al. 2020a, b). For example, Port Stephens, New South Wales (NSW), on the east coast of Australia, is a coastal beach region which is intensively used for human water activities; it is also a popular region for white sharks. Juvenile (1.75–3.0 m total length (TL)) and sub-adult (3.0–3.6 m TL males; 3.0–5.0 m TL females, see Bruce and Bradford 2008) white sharks *Carcharodon carcharias* have been observed in the region year-round (Bruce et al. 2013), with increased usage and residency during the late austral spring and early summer months (Bruce and Bradford 2008; Harasti et al. 2017; Spaet et al. 2020b). White sharks have been a focus of research not just to inform beach safety measures (Tate et al. 2019; Colefax et al. 2020), but also to inform conservation measures for this species, which is globally listed as Vulnerable by the International Union for Conservation of Nature (IUCN) Red List criteria (Rigby et al. 2019) and listed as threatened in Australia under the Environment Protection and Biodiversity Conservation Act of 1999. A relatively dense acoustic array was deployed at Bennett's Beach, Hawks Nest (hereafter referred to as HN) near Port Stephens from 2010–2016 to monitor white shark presence and movements. Understanding array effectiveness is paramount under these circumstances to ensure that the presence of acoustically tagged sharks is being adequately and accurately assessed (Spaet et al. 2020b). Whether for conducting ecological research or to monitor for the presence of an animal for management reasons, it is necessary to understand what level of acoustic receiver coverage is necessary to reliably detect the presence of tagged animals.

In this study, we use white shark detection data from the HN acoustic array to investigate the number and spatial coverage of receivers required to reliably detect tagged shark presence. Our aim was to assess whether a reduced array could minimise cost and maintenance effort while maintaining effective observing power. This study does not investigate questions around designing deployments of acoustic tags on a study species, but instead focuses on the detection probability of a tagged individual present within the study area given a particular array design. Our approach involved analysing data from the full array before removing data from various subsets of receivers post hoc to determine what level of spatial coverage could effectively record the presence of acoustically tagged sharks relative to the full array. While the array utilised in this study was not designed specifically for the analysis conducted here, the density of the array makes it well suited for such an analysis. Moreover, monitoring white shark presence in regions where they are likely to overlap with intensive water usage by humans is of interest in various places throughout the global range of this species (e.g., Bruce et al. 2013; Kock et al. 2013). The analyses presented here provide valuable information for implementing cost-effective monitoring strategies to inform management efforts for both the safety of beach users and the conservation of this threatened species.

Methods

Study site and array design

Bennett's Beach, HN (32.6742° S, 152.1859° E) (see Fig. 1), is a known nursery area for juvenile white sharks near Port Stephens, NSW, on the eastern coast of Australia (Bruce and Bradford 2008; Bradford et al. 2012; Spaet et al. 2020b). In this area, internal tagging of white sharks with coded acoustic transmitters was initiated in 2007 (Bruce et al. 2013), and continued until 2015. At the same time, acoustic receiver arrays were deployed at several beaches around the Port Stephens area. From 2010–2016, a relatively dense array was deployed across 12.8 km^2 off HN (estimated total detection envelope of 24 km^2). The maximum number of acoustic receivers deployed at any one time was 25 receivers, in October

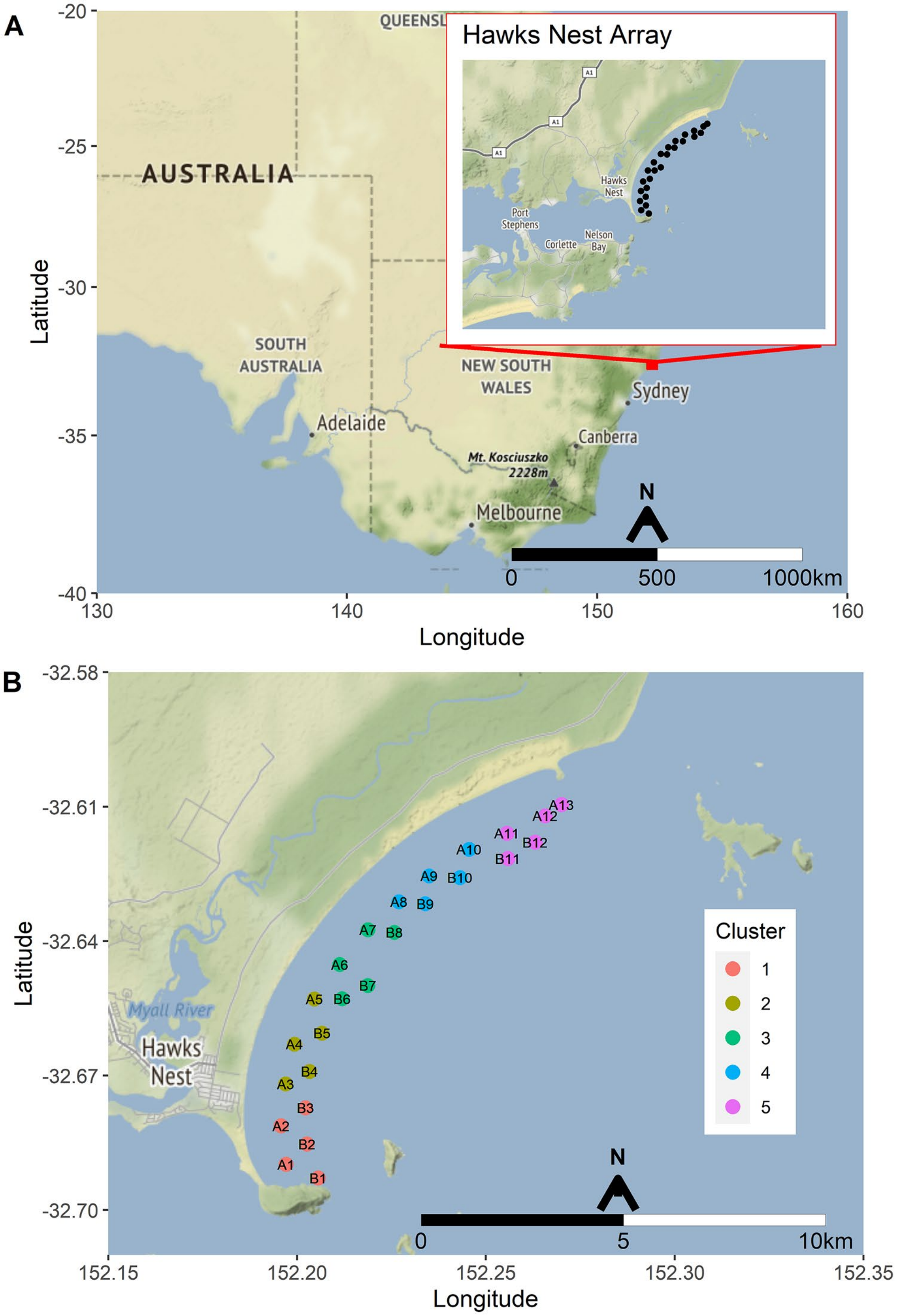

Fig. 1 Maps of the Hawks Nest Array. **a** Map of eastern Australia with an inset regional map of the study region showing receiver locations of the full Hawks Nest array in 2010 (black dots). **b** Fine-scale map of the 2010 Hawks Nest receiver array with receivers labelled and coloured by cluster group. Receivers were placed in clusters based on their relative position, with cluster 1 being the southern-most receivers and cluster 5 being the northernmost receivers in the array. Maps were created using the ggmap function from the ggplot2 package in R (Kahle and Wickham 2013)

2010 through March 2011 and August 2013 through February 2015. From December 2011 through April 2013, the array ranged from 4 to 17 receivers, and in February 2015, the array was reduced to 5 receivers until final retrieval in May 2016 (see Supplementary Table S1). The study used Vemco (now Innovasea, Nova Scotia, Canada) VR2W acoustic receivers, which are widely used for passive acoustic telemetry (Heupel et al. 2008; Simpfendorfer et al. 2008, 2015; Espinoza et al. 2011b). The coded acoustic transmitters used to tag the sharks (V-16 RCODE R64k, 16 × 92 mm, Vemco/Innovasea, Bedford, Nova Scotia, Canada) emit a sequence of sonic "pings" at 69 kHz encoding unique identification codes that are recorded by the acoustic receivers along with the date and time of detection. These time-stamped detections were downloaded from the VR2W receivers annually throughout the array deployment from 2010 through 2016. Biofouling did occur on some of the receivers and may have impacted detection numbers over the deployment time. The spatial configuration of the acoustic array was chosen to maximise assessment of shark presence along the length of the coastline (13.5 km), which was accomplished by deploying two lines of acoustic receivers extending along the length of the beach (Fig. 1b, Supplementary Fig. S1). Receivers within each line were spaced equally with non-overlapping detection envelopes (detection ranges were approximately 750–900 m based on field tests run in March 2011; Bruce and Bradford 2011b), and the two lines were staggered to minimise leaks in detection capability within the array (Fig. 1b, Supplementary Table S1 & Fig. S1).

Throughout the full deployment of the HN array from 2010 to 2016, 26 individual white sharks (19 female, 7 male) out of a total of 56 sharks that were internally tagged off the coast of New South Wales between 2007 and 2015 (Bruce and Bradford 2008; Bruce et al. 2013) were detected by the HN array, resulting in a total of 159,660 detections. Detected sharks ranged in total length (TL) from 1.9 to 2.8 m (Supplementary Table S2) with an average TL of 2.2 ± 0.22 (SD) m. Across all years, sharks were detected most frequently in the southern-most cluster of the array (Supplementary Fig. S2), and in the late spring/summer (Supplementary Fig. S3-S5).

Metrics for evaluating array performance

To evaluate how a reduced array would have performed compared to the full HN array, it was necessary to define quantitative measures of an array's ability to characterise tagged shark behaviour. We hence partitioned the data for each shark into periods termed "visits". A visit was defined as the period during which an individual shark was detected within the array as a whole for which the time between detections did not exceed a specified time interval, referred to as the inter-visit cut-off time (Bruce and Bradford 2011a). To determine an appropriate inter-visit cut-off time, time cut-offs from one to 24 h between detections of individual sharks were used to group detections into visits using data collected during the entire 2010–2016 deployment period. The resulting number of visits, median visit durations, and median inter-visit periods were compared visually. No clear signal was seen in these three metrics for determining the most appropriate threshold cut-off time (Supplementary Fig. S6). Therefore, a cut-off time of 5 h was selected. While this is somewhat subjective, the rationale for this was that for cut-off times greater than 5 h, an individual shark may well have left the HN array and travelled to other areas within that time. Moreover, cut-off times less than 5 h appeared to result in an over-calculation of visits, with a high likelihood that sharks were still present but simply not detected during that time. The detection envelope of the HN array extends to less than 1 km from the shoreline; however, in the Port Stephens region, the nursery area extends offshore about 25–30 km (Bruce and Bradford 2012). Therefore, sharks may remain in the immediate area but be outside of the detection envelope of the array for a significant proportion of their time in the vicinity of the array, thereby leading to over-calculations of visits to the area with shorter cut-off times.

Using the five hour inter-visit cut-off, the following summary statistics were extracted from the entire detection data set for each shark detected: total number of visits per shark, total number of visits across all sharks, visit durations (hours), number of detections recorded per visit, and inter-visit periods (hours) (reported in Supplementary Fig. S7). Based on these summary statistics, four visit metrics were chosen for comparing detection data between the full and reduced arrays: total number of individual sharks detected, total number of visits across all sharks, median number of detections per visit across all sharks, and median visit duration (in hours) across all sharks. Median values were chosen to be more robust to right skew in the metric data.

To make comparison of the reduced and full arrays unbiased, only data from time periods with the full array (25 receivers) deployed were used to calculate the four visit metrics (October 2010–March 2011, and August 2013–February 2015) (Supplementary Table S1).

Evaluating effectiveness of reduced arrays

To determine how a less dense array of acoustic receivers would have performed, three approaches were used to sample smaller numbers of receivers from the full array and evaluate their typical performance: simple random sampling, spatially clustered sampling, and top receiver sampling.

Simple random sampling

Random samples of 5, 10, 15, and 20 receivers were taken from the periods with full receiver arrays. These results were used as the base-case scenario as this sampling scheme assumes no factor other than the total number of receivers is applied to determine which receivers should be kept. One would typically have more insight into the placement of acoustic receivers (e.g., based on prior information such as tracking data, presence only data from surveys, etc.) or in the absence of such information, design the array to meet some goal such as having broad spatial coverage. Nonetheless, evaluating a totally random array design is useful for comparison with the other more-nuanced approaches described below. We resampled the full array dataset 500 times for each array size (5, 10, 15, and 20 receivers) using a bootstrapping method coded in R (R Core Team 2019). Each sample of receivers was taken without replacement to avoid data from a given receiver appearing more than once in each iteration of the bootstrap. The summary metrics defined in the previous section were calculated using each bootstrapped dataset.

Spatially clustered sampling

Often researchers might attempt to maintain spatial coverage despite reducing the number of acoustic receivers. Thus, in this scenario, the HN array was divided into five clusters, each containing five receivers, based on north–south position within the array (Fig. 1b). Random samples of 1, 2, 3, and 4 receivers were then taken from each of the five clusters to provide overall array sizes of 5, 10, 15, and 20 receivers, with the sample arrays bootstrapped 500 times for each number of receivers. Again, the summary metrics defined in the previous section were calculated using each bootstrapped dataset.

Top receiver sampling

The final approach was designed to replicate the situation where a dense array is employed for an initial period of a study and early results are used to select receivers for the ongoing study based on those that provided the most detections. Under this scenario, the top-detecting 1, 5, 10, 15, and 20 receivers (i.e., receivers with the greatest number of detections) were selected for the period of each year when the full array was deployed and data from all 25 receivers were recovered (i.e., Oct–Dec 2010, Jan–Mar 2011, Aug–Dec 2013, and Jan–Jun 2014) (Fig. 2, Supplementary Table S3). In reality, only the initial period would be used for determining the top-detecting receivers; however, to determine the potential impact of annual variation in tagged shark movement on the results, each of these four periods were used as a reference. The total number of detections recorded was used as the metric for determining the top performing receivers rather than number of individual sharks detected, because the receivers with the highest total detections and those with the highest number of individual sharks detected were mostly the same, and there was not a large variation in the number of individual sharks detected by the different receivers overall. Visit metrics were then calculated using detection data from all periods with the full array using the subset of receivers chosen for each reference period. For example, using Oct–Dec 2010 as the reference period, the top-detecting 5 receivers in that period were determined, and the visit metrics were calculated using the detection data collected from those 5 receivers during all periods when the full array was deployed.

For the random and clustered sampling methods, summary statistics consisting of median, inter-quartile range (IQR), and coefficient of variation (CV = standard deviation / mean) were calculated for each visit metric across the 500 bootstrapped datasets for each array size (5, 10, 15, or 20 receivers). The CV was used to assess whether an array reduction method is highly influenced by the randomly chosen receiver set. A CV less than 0.2 is a useful guide indicating sufficiently small variation for robust inference (Hilborn and Mangel 1997). Here, this would indicate that a reduced array yields consistent visit metrics despite the variability introduced by bootstrap samples and, therefore, we could be confident that most of the signal gathered by the full array was retained in the reduced array. For the top receiver sampling method, only four datasets were generated for each array size (one for each of the four reference periods); therefore, only the median and IQR values of the metrics for these four years were calculated (not the CV). The median values of the metrics were compared graphically between the random, clustered, and top receiver sampling methods for each array size. In addition, the visit metrics for the top performing receiver method were compared graphically between the four reference periods to look for potential changes in white shark detections over time.

Results

The four visit metrics (total number of individual sharks detected, total number of visits across all sharks, median number of detections per visit, and median visit duration in hours) were first calculated using the data from the full array to allow for subsequent comparison with the visit metric values for the reduced array sizes. With the full array of 25 receivers during Oct 2010–Mar 2011 and Aug 2013–Feb 2015, a total of 18 individual sharks were detected in the HN array (sharks 1–12, sharks 14–18, and shark 20; Supplementary Table S2). Using an inter-visit cut-off time of 5 h, the

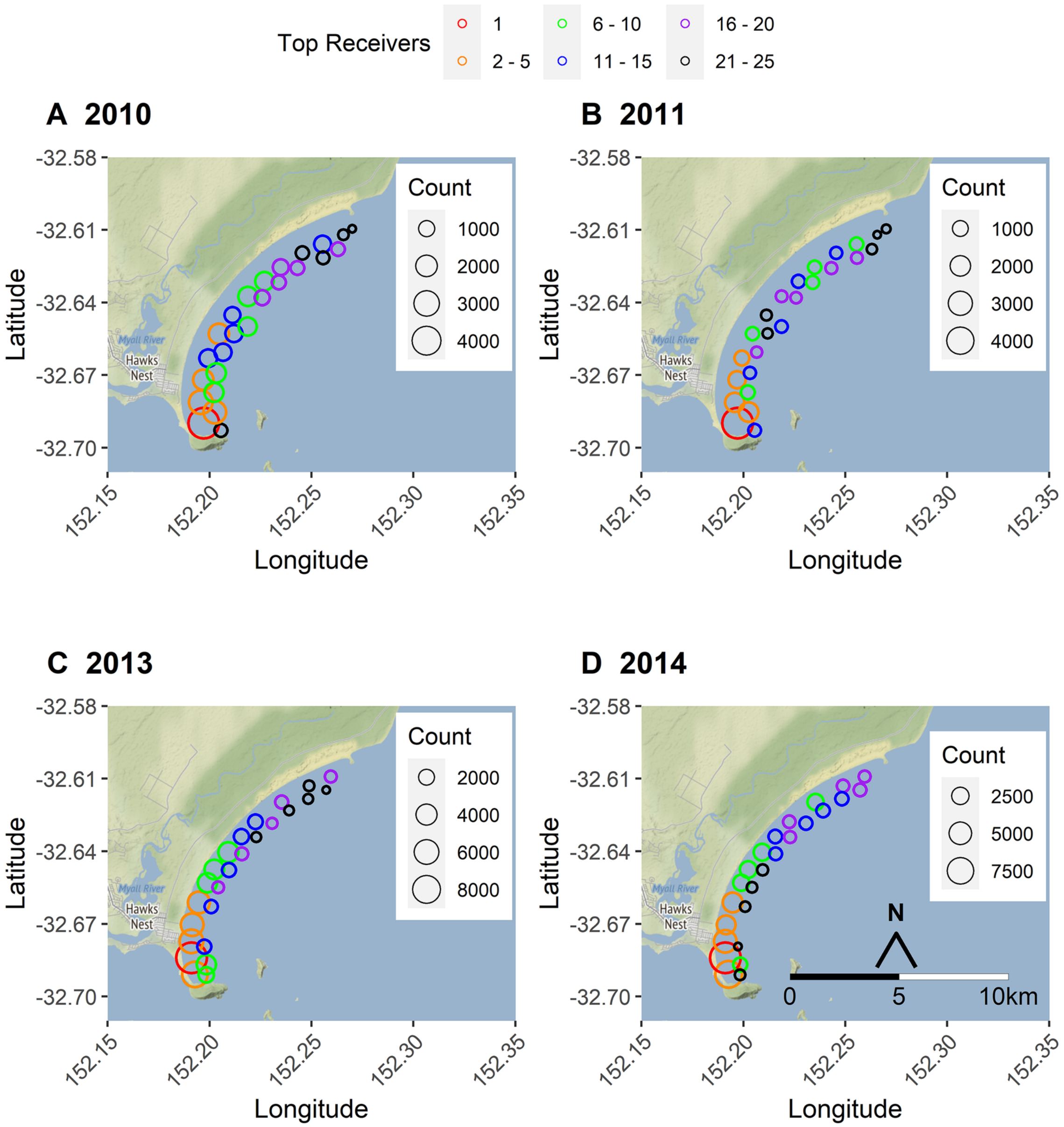

Fig. 2 Fine-scale map of Hawks Nest showing all shark detections (count) by receiver location for each reference period— **a** Oct–Dec 2010, **b** Jan–Mar 2011, **c** Aug–Dec 2013, and **d** Jan–Jun 2014 — with the top 1 (red), 2–5 (orange), 6–10 (light green), 11–15 (blue), and 16–20 (purple) receivers from each reference period indicated by colour

18 sharks detected visited the HN array a total of 488 times. There was high variability in visit duration and number of shark detections per visit, with highly right-skewed distributions for both these visit metrics (Fig. 3). Across all sharks, the median (IQR) visit duration was 7.8 (2.5–16.8) h, with a maximum visit duration of 331.9 h (about 14 days) (Fig. 3a). The median (IQR) number of detections per visit was 102.5 (31.0–281.0) detections, with a maximum of 11,703 detections in a visit (Fig. 3b).

In general, across all four visit metrics and array sizes, the clustered and random samples had very similar median values (Fig. 4), but the clustered samples had slightly but consistently lower CVs (Fig. 5). CVs on both total number of sharks and total number of visits were less than 0.2 for the random and clustered samples across all array sizes, suggesting a reliable signal on these two metrics (Fig. 5a, b). CVs for median number of detections per visit increased above 0.2 with 5 receivers for both the random and clustered samples, and CVs for median number of detections per visit increased above 0.2 with 5 receivers for the random samples, suggesting that an array with less than 10 receivers is too sparse to be robust to individual array placement (Fig. 5c, d).

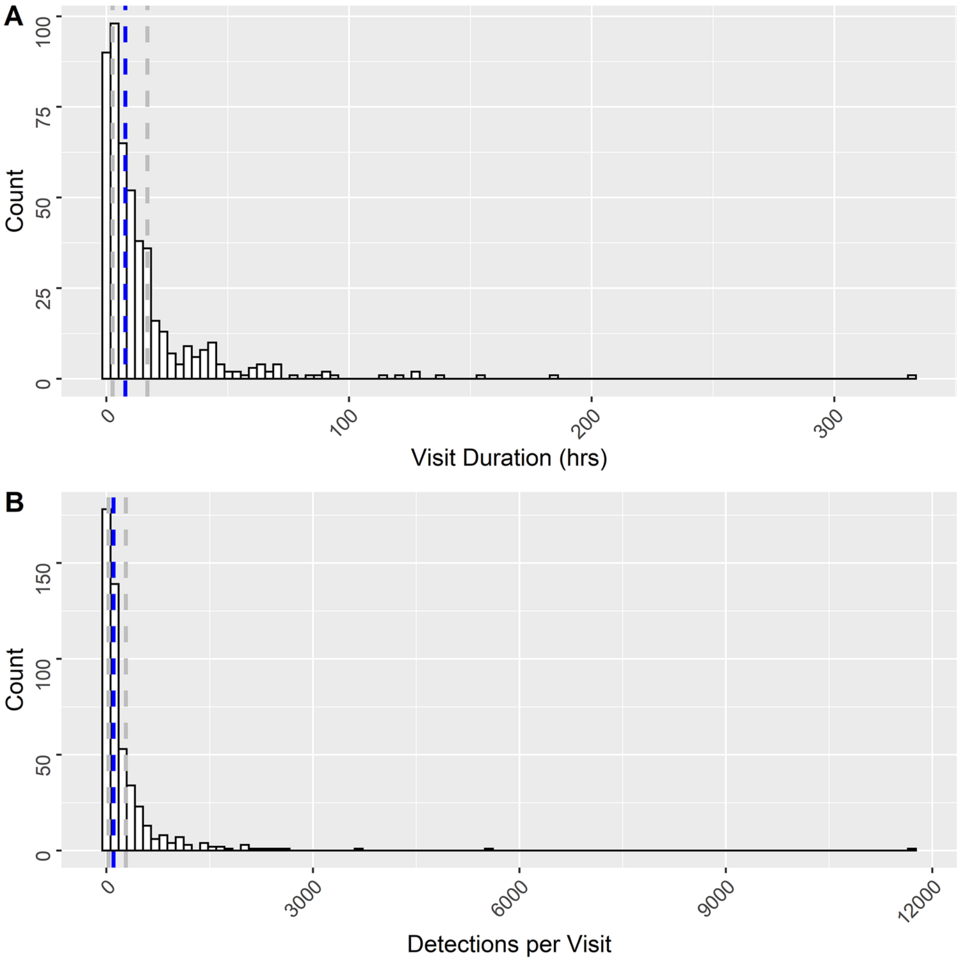

Fig. 3 Histograms for the visit metrics: **a** visit duration in hours, and **b** number of detections per visit, calculated using an inter-visit cut-off time of 5 h. Only data from when the full array of 25 receivers was deployed are included (i.e., from Oct 2010–Mar 2011, and Aug 2013–Feb 2015). The dashed lines depict the median (blue) and inter-quartile ranges (grey)

As expected, the variability in visit metrics decreased with larger array sizes (Fig. 5). Note that these same general patterns were observed when inter-visit cut-off times of 1 and 10 h were tried instead of the chosen 5 h (Supplementary Fig.'s S8-S12). Due to the similarity in the results between the random and clustered sampling methods, for the rest of this paper, we will focus on comparison of the clustered and top receiver sampling methods.

For both the clustered sampling and top receiver sampling methods, the number of sharks detected, the median visit duration, and the median number of detections per visit increased with an increasing number of receivers sampled (Fig. 4a, b, c). For arrays of 5–20 receivers, the number of detected sharks was consistent between the two sampling methods, with median number of sharks detected being the same across the sampling methods for all array sizes except the array size of 10 receivers, where the difference in median number of sharks detected by the different sampling methods was one shark. A reduction of the full array to only 10 receivers using the top receiver sampling method resulted in a median of 18 sharks (the total possible). Sampling of the single top receiver from each reference period resulted in a median of 16.5 out of the total 18 sharks. Although the clustered sampling method did not reach a median of 18 detected sharks until the array was increased to 15 receivers, the difference between the median numbers of sharks detected with the clustered and top receiver sampling methods was never greater than one shark (Fig. 4a).

For the visit metrics of median visit duration and median number of detections per visit, the top receiver sampling method displayed higher median values than the clustered sampling method at each array size (Fig. 4c, d). This was particularly true for the median number of detections per visit, with sampling of the single top receiver resulting in higher median detections per visit than sampling of 5 receivers with the clustered sampling method (Fig. 4d). When the array size was reduced by 60% (10 out of 25 receivers), both sampling methods were able to detect all 18 sharks detected by the full array, but there was only a 35% decrease in the median number of detections per visit with the top receiver sampling method (67 out of 102.5 detections) compared to a 57% decrease with the clustered sampling method (44 out of 102.5 detections) (Fig. 4).

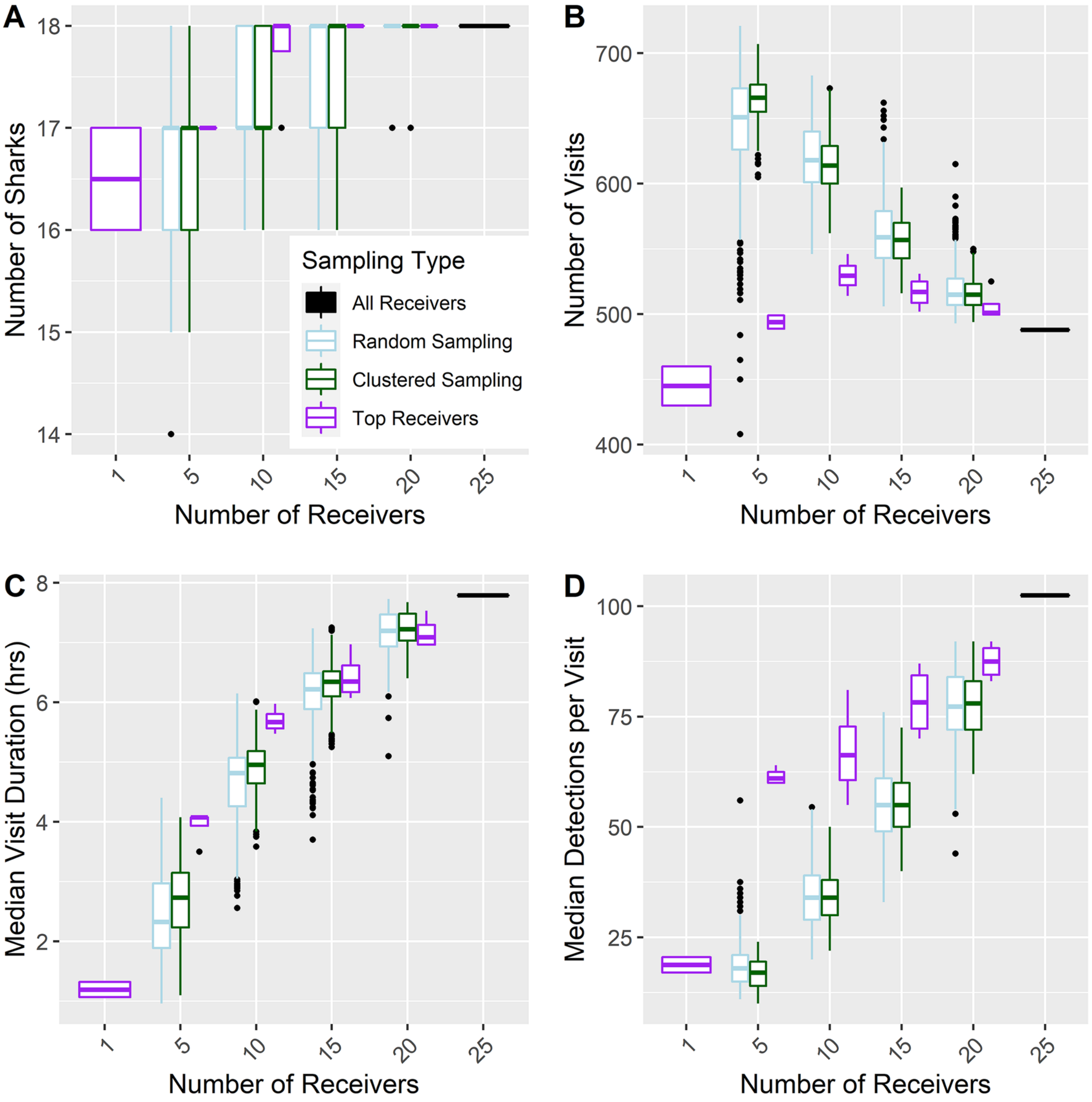

Fig. 4 Visit metric data resulting from receiver sampling of 1, 5, 10, 15, and 20 receivers compared to the full array of 25 receivers, using data from all periods during 2010–2015 for which the full array was deployed. Visit metrics were calculated with an inter-visit cut-off time of 5 h. **a** Number of sharks detected by number of receivers. **b** Number of white shark visits by number of receivers. **c** Median visit duration in hours by number of receivers. **d** Median detections per visit by number of receivers. The boxplots display the median (middle line) and inter-quartile range (IQR) (box), with whiskers extending to the largest and smallest values no further than 1.5*IQR, and all data points beyond that range depicted as outlying dot points. Light blue denotes visit metrics based on random sampling (n = 500), dark green denotes the visit metrics based on clustered receiver sampling (n = 500), and purple denotes the visit metrics based on sampling the top receivers from each reference period (n = 4)

Looking at the visit metric of total number of visits recorded, for the clustered sampling method, the number of visits decreased as the number of receivers increased, which is opposite to the median visit duration and median number of detections per visit (Fig. 4b). With fewer receivers, a shark that stays within the array will not always be detected during what is actually (using the 5-h cut-off rule) a single continuous visit; thus, more visits with shorter durations are identified. Conversely, with more receivers available to detect shark presence, there are fewer periods of more than 5 h between detections, and therefore, overall fewer visits identified with longer durations. Similarly, the number of visits is lower for the top receiver method compared to the clustered sampling method across all array sizes (Fig. 4b); top receivers consistently record higher detections per visit (Fig. 4d), meaning that single visits are less likely to be split into multiple visits. The pattern in the number of visits across the array sizes is different for the top receivers

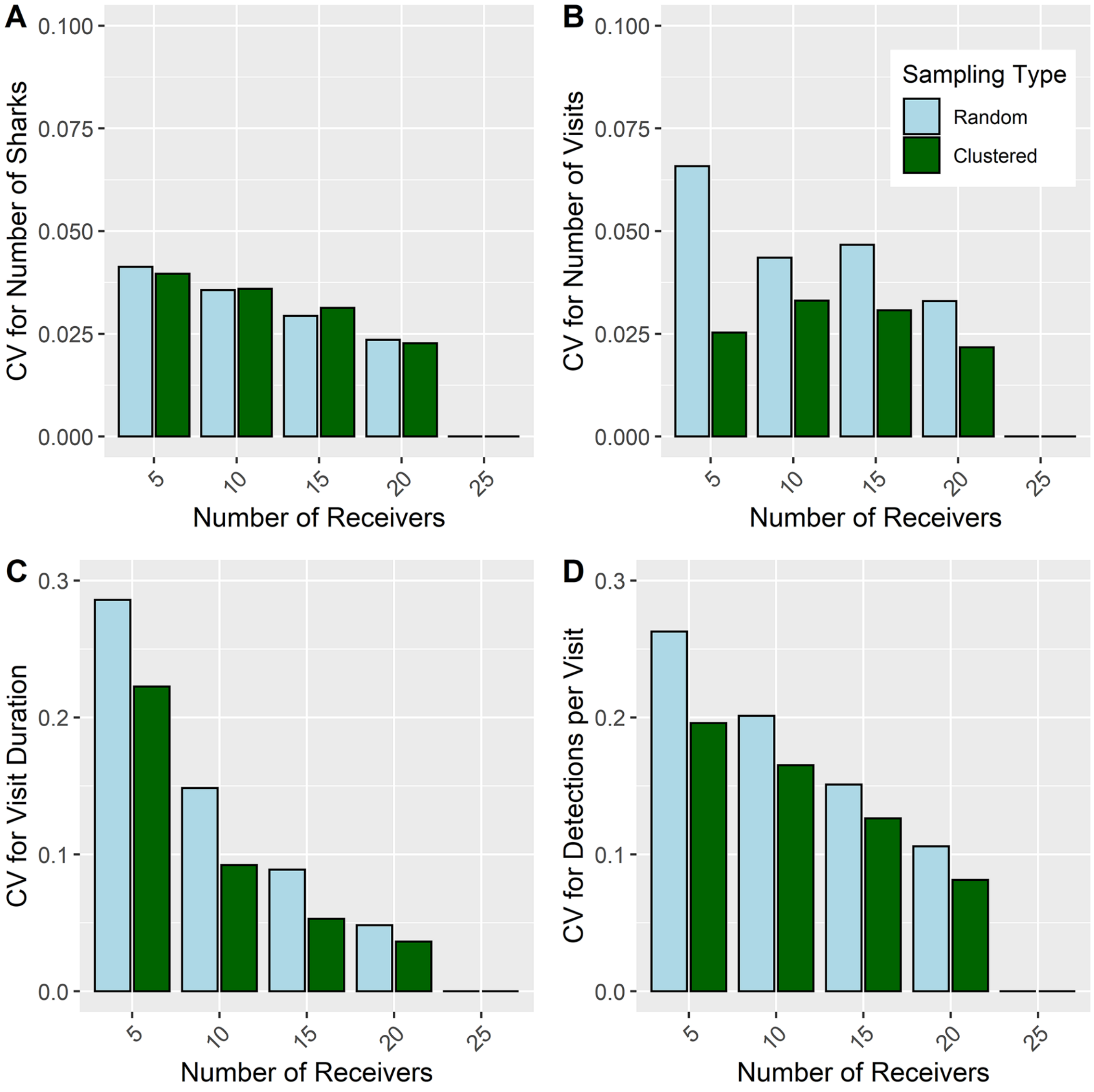

Fig. 5 Coefficients of variation (CVs) for: **a** the number of sharks detected, **b** the number of shark visits, **c** the median visit duration, and **d** the median number of detections per visit, calculated with random sampling (light blue) and clustered receiver sampling (green). CV values less than 0.2 were considered to allow a meaningful data signal without too much impact of random variation in the receivers sampled. It should be noted the y-axes are different in (**a**) and (**b**) compared to (**c**) and (**d**)

compared to the clustered sampling, with the number of visits increasing up to 10 receivers, and then decreasing from 10 to 20 receivers (Fig. 4b). With the top 1 and 5 receivers, slightly fewer sharks were detected than with the full array (Fig. 4a), but the average number of detections recorded per visit was relatively high (Fig. 4d). Therefore, fewer total instances of shark presence were detected, but these were less likely to be split into multiple separate visits as the collection of data through time was more consistent on the top receivers. More intermittent data collection causes a greater drop in total detections, as seen with the clustered sampling method. Therefore, number of visits only increased as the number of sharks detected increased, from the top 1 to the top 10 receivers. From the top 10 to the top 20 receivers, the number of sharks detected had reached the maximum and remained constant (Fig. 4a); however, as the number of receivers increased, the number of detections per visit also increased (Fig. 4d). Due to the more numerous and continuous detections, the visits of those sharks were less frequently split into separate visits, resulting in fewer total visits with longer durations (Fig. 4b, c).

While there was some inter-year variation in individual receiver efficiency, in general, the top-detecting 20 receivers from each year were either the same receivers across the years or were from similar areas/clusters of the array (Fig. 2, Supplementary Table S2). For example, the top receiver across all years was either HN A1 or HN A2 (Fig. 2, Supplementary Table S2). In addition, there was very limited inter-annual variation in all the visit metrics resulting from the top receivers from different reference periods (Supplementary Fig. S13). Across the reference periods, receivers from the southern-most area of the beach (clusters 1 and 2) were generally the most efficient based on total number of detections, as was expected based on mapping of the total numbers of detections across all years (Fig. 2, Supplementary Table S2).

Discussion

This study presents the first examination of the minimum number of receivers required to adequately detect white shark presence at a coastal aggregation site. Comparison of the presence and detection data recorded by a dense array of 25 receivers off the Australian east coast to that recorded at reduced sizes showed that similar presence data could be collected using as few as 10 acoustic receivers, or 40% of the full array. Across the sampling methods employed to subsample the full array, the most reduced arrays (1 and 5 receivers, or 4% and 20% of the full array, respectively) were likely too small to reliably detect the presence of all the tagged sharks detected by the full array. Although the differences in visit metrics between sampling methods were generally small, retaining the top receivers provided the best detection results. While the median visit metric values between the clustered and random sample arrays matched closely, the clustered samples displayed lower levels of variation (CVs). Smaller array sizes across the sampling methods did result in lower overall detections and therefore shorter inferred visit durations. This would not, however, be concerning from a management perspective if the importance is on detecting presence of sharks near shore, and once a shark has been detected other forms of monitoring efforts take over. Even though the effectiveness of reduced array sizes in this study may not be directly applicable to arrays in other areas, the sampling designs used provide an empirical method by which the spatial configuration and number of receivers needed for monitoring arrays could be designed and assessed.

For marine predators such as white sharks, the ability to monitor areas effectively is important not only for increasing understanding and conservation of the species, but also to inform beach safety measures in areas where human and shark use overlap (Simmons and Mehmet 2018; Spaet et al. 2020b). Reduction of array costs can have substantial benefits for management agencies, such as freeing up funding for monitoring in other coastal areas within the range of the species of interest or for other management and research efforts (Cowley et al. 2017; Steckenreuter et al. 2017). Where funding is particularly limited, reduction of array costs might also be the deciding factor for whether monitoring in an area is feasible. There are often many factors that impact where receivers can be placed in an area, e.g., limitations due to other uses of the marine environment such as shipping lanes, how many receivers can be deployed, and how many can be retrieved (Lowe et al. 2006; Chin et al. 2016).

The importance of receiver spatial configuration for the detection effectiveness of an acoustic receiver array has been demonstrated by many previous studies (e.g., Welsh et al. 2012; Steel et al. 2014; Simpfendorfer et al. 2015; Huveneers et al. 2016). These studies indicated that the depth, placement, and orientation of receivers within an array are important factors in determining receiver detection rates and performance across a variety of aquatic habitats, from rivers and coastal bays to coral reefs and the open ocean. Acoustic receiver spatial configuration has also been found to be an important factor in position estimate accuracy for animals within dense arrays (Steel et al. 2014), and receiver configurations can impact the number of false detections recorded by an array (Simpfendorfer et al. 2015).

It is well accepted that receiver array configuration is an important consideration in designing an effective telemetry study (Heupel et al. 2006a; Brownscombe et al. 2019), and several papers have focussed on finding empirical or experimental approaches for determining optimal array configuration when approaching a novel study site (Hobday and Pincock 2011; Welsh et al. 2012; Huveneers et al. 2016; Carlisle et al. 2019; Patterson and Pillans 2019). Welsh et al. (2012) and Huveneers et al. (2016) both utilised experimental methods by deploying receiver arrays specifically aimed at assessing the detection efficiency of receivers in different spatial configurations in two different habitats (coral reef habitat, and deep pelagic habitat, respectively). Both studies used the results from those receiver arrays to provide recommendations on how acoustic receiver arrays should be configured in similar habitats in future studies. However, neither of these studies relate to habitats such as the coastal beach area monitored in this study, and they did not address variation in array effectiveness with reduced numbers of receivers.

Carlisle et al. (2019) presented a similar study method to this current study, by subsampling arrays of varying sizes from a full array data set to investigate the effect of array design on subsequent analysis of residency, detection rate, and estimates of movement for two shark species in a Marine Protected Area based on passive acoustic array data. While their methods were similar to the methods in this study, their aims were very different. Rather than looking for the minimum number of receivers required to adequately monitor an area for the presence of marine species, Carlisle et al. (2019) were interested in quantifying the impact of array size and density on the subsequent estimates of animal movement and habitat use within an area.

Simulation models have been previously developed and assessed, with Patterson and Pillans (2019) examining how array design affected estimation of survival rates. Hobday and Pincock (2011) modelled the effect of various detection ranges, spatial configurations, and environmental factors on detection probability in a linear array design. These studies presented modelling processes that could be used to design and assess spatial configurations of novel acoustic arrays in similar habitats. Patterson and Pillans (2019) used simulations to compare varying array sizes and concluded that increasing the spatial coverage and number of receivers increases the ability to determine the life history and survival rate of tagged species. Neither of these studies compared real detection data from a reduced array with a dense array in the same area. However, use of modelling approaches (Patterson and Pillans 2019) to simulate movements of the study species could be used to investigate array design prior to deployment in instances where experimental initial deployment of a dense array is not financially or logistically possible.

Even in situations where an initial dense array cannot be deployed, our results indicate that it could still be beneficial to consider adaptive reconfiguration of arrays throughout a study. Doing so could decrease array costs, and allow reallocation of conservation and management agency funds to other areas of study while maintaining effective monitoring in that region. For instance, as long as there is more than a single receiver within an area of interest, it is possible to determine whether receivers are to some degree redundant in terms of the aims of the monitoring. This is supported by a similar study conducted by Steckenreuter et al. (2017) which used detection data from acoustic receiver curtains maintained by the Integrated Marine Observing System's Animal Tracking Facility around Australia to determine how many receivers could be removed while still maintaining full detection of the migratory species that cross the array. Steckenreuter et al. (2017) were able to reduce the number of receivers by 36% while maintaining detection of all the monitored species and 84% of the total detections.

Reduction of array size based on total number of detections at different receivers within a dense array has been utilised for effectively reducing the cost of maintenance while maximising detection efficiency in the large-scale South African Acoustic Tracking Array Platform (ATAP) (Cowley et al. 2017). As described by Cowley et al. (2017), in 2014, the ATAP monitoring array programme encountered a major loss of array equipment due to environmental conditions and difficulty retrieving receivers. As a result, the array size was subsequently reduced by removing receivers with the least total numbers of detections, to reduce maintenance costs and increase likelihood of successful deployment and retrieval each year. Similarly, the top receiver sampling used in this study to reduce array size could be used to improve monitoring for white shark presence at coastal beaches in the broader NSW area. For example, in 2015, the NSW Government deployed 21 VR4G shark tracking buoys across 1200 km of coastline (including HN) to inform the public about tagged sharks adjacent to coastal beaches (Spaet et al. 2020b). These receivers send information in real time to the public via apps and social media when a shark is detected. At around that same time in 2015, the HN array was decreased down to five receivers, and has since been reduced to just a single VR4G receiver in the southern end of the beach. Using a design study like the top receiver sampling method to initially determine the best location for this VR4G receiver array would optimise the long-term efficiency of the receivers for both bather protection and research purposes (Spaet et al. 2020b).

One limitation of a minimal optimal array is that monitoring variation in fine-scale movement would be difficult. In the present study, the objective was monitoring presence rather than fine-scale movement and habitat use of white sharks, although the array itself was deployed to determine spatial usage. Regardless of the study objective, understanding variation in annual shark movement is necessary for assessing if the initial reference period is a reliable predictor of the movement of the species being studied. Despite some inter-annual variation, in general, the 20 receivers with the highest total numbers of detections from each reference period were either the same or came from similar areas of the array. All white sharks in this study were observed most frequently at the southern-most area of the beach consistently across the years. These observations of shark spatial distribution are in line with previous analyses of juvenile and sub-adult white shark movements in the area conducted by Bruce et al. (2013), which found that acoustically tagged white sharks spent a higher percentage of time (mean ± SD of 55.1 ± 14.8% of time detected in the array) in the 'Southern' (receivers HN1–HN4) part of the array, compared to 28.1 ± 11.6% and 16.8 ± 4.6% of time spent in the 'Central' (receivers HN5–HN8) and 'Northern' (receivers HN9–HN13) parts of the array, respectively.

If researchers can start with a high number of receivers in an area, with the intention to reduce the array for longer term monitoring, the top receiver sampling method described in this study would be appropriate to assess and compare the monitoring effectiveness of varying array sizes within an area. This would allow for more accurate temporal comparisons with varying receiver numbers. Maintaining the same number of receivers consistently at a site is not always possible, due to financial reasons and variation in ability to deploy receivers due to weather conditions, or loss of receivers after deployment. Since 2015, the number of receivers along HN has progressively been decreased partly due to resources, environmental conditions, and time restrictions. However, the removal of receivers was based on informal consideration of accumulating data streams rather than an analysis similar to that presented here. If the approach outlined in this study had been employed from the start, time and financial savings would have been achieved while maintaining a robust data stream.

Though the specific numerical results of this case study cannot be directly applied to the reduction of arrays in other areas and for the monitoring of other species, this study shows that arrays for monitoring purposes can be successfully reduced while maintaining detections using experimental methods. While it may not always be possible to run an initial assessment of habitat use, other methods such as simulations of animal movement and detection data can be used to inform initial placement, after which the subsampling methods presented here could be used for adaptive re-designing of arrays as a monitoring study is conducted. With consideration for the study area and species, these methods could be fruitfully employed in future studies using acoustic arrays to monitor not just white sharks but also other marine species of interest.

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Author contributions Data collection was conducted by Russ Bradford, David Harasti, and Paul Butcher; Sofia Gabriel, Toby Patterson, Paige Eveson, and Russ Bradford conceived the study idea, conducted the data analyses, and wrote the manuscript, with assistance and commentary from Julia Spaet and Jayson Semmens.

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Data availability The data analysed during the current study are available from the Commonwealth Scientific and Industrial Research Organisation of Australia (CSIRO), but restrictions apply to the availability of these data, which were used under licence for the current study, and so, the data are not publicly available. Data are however available from the authors upon reasonable request and with permission of CSIRO.

Code availability All coding was conducted in R, and relevant packages are noted in the methods section. The custom code used for sampling of the receivers is available from the corresponding author upon request.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval ACEC 14/07; Scientific Collection permit P07/0099; Scientific Research Permit P01/0059(A); Marine Parks Research Permit P16/0145- 1.1 and Commonwealth Scientific and Industrial Research Organisation (CSIRO) Tasmanian Department of Primary Industries, Parks, Water and the Environment (DPIPWE): AEC Permit 22/2015–16, and its predecessors; DPIPWE Living Marine Resources Management Act 1995 Permit 15,008 (and previous derivations), DPIPWE Threatened Fauna for Scientific Purposes permit 14,239; Victorian Department of Environment and Primary Industries (VDPI) Research permit 10,006,912, VDPI Protected Aquatic Biota permit PA38. All tagging was carried out in accordance with the CSIRO Code of Practice for tagging marine animals, with protocols used approved by the Tasmanian DPIPWE Animal Ethics and NSW DPI Animal Care and Ethics Research Authority.

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References

Andrews KS, Williams GD, Levin PS (2010) Seasonal and ontogenetic changes in movement patterns of sixgill sharks. PLoS ONE 5:e12549. https://doi.org/10.1371/journal.pone.0012549

Bradford RW, Hobday AJ, Bruce BD (2012) Identifying juvenile white shark behavior from electronic tag data. In: Domeier ML (ed) Global perspectives on the biology and life history of the white shark. CRC Press, Boca Raton, FL, pp 255–270

Brownscombe JW, Lédée EJI, Raby GD, Struthers DP, Gutowsky LFG, Nguyen VM, Young N, Stokesbury MJW, Holbrook CM, Brenden TO, Vandergoot CS, Murchie KJ, Whoriskey K, Mills Flemming J, Kessel ST, Krueger CC, Cooke SJ (2019) Conducting and interpreting fish telemetry studies: considerations for researchers and resource managers. Rev Fish Biol Fisheries 29:369–400. https://doi.org/10.1007/s11160-019-09560-4

Bruce BD, Bradford R (2008) Spatial dynamics and habitat preferences of juvenile white sharks—identifying critical habitat and options for monitoring recruitment. Final report to the department of the environment, water, heritage and the arts. CSIRO, Hobart, Tasmania, AUS

Bruce BD, Bradford RW (2011a) The effects of berleying on the distribution and behaviour of white sharks, *Carcharodon carcharias*, at the Neptune Islands, South Australia. Final report to the Department of Environment and Natural Resources, South Australia. CSIRO, Hobart, Tasmania, AUS

Bruce BD, Bradford RW (2011b) Near-shore habitat use by juvenile white sharks in coastal waters off Port Stephens. Final Report, CSIRO, Hobart, Tasmania, AUS

Bruce BD, Bradford RW (2012) Habitat use and spatial dynamics of juvenile white sharks, *Carcharodon carcharias*, in eastern Australia. In: Domeier ML (ed) Global perspectives on the biology and life history of the white shark. CRC Press, Boca Raton, FL, pp 225–254

Bruce BD, Bradford RW, Hughes B, Carraro R, Gallen C, Harasti D, Gladstone W (2013) Acoustic tracking and aerial surveys of juvenile white sharks in the Hunter Catchment Management Authority region. Final Report, CSIRO, Hobart, Tasmania, AUS

Carlisle AB, Tickler D, Dale JJ, Ferretti F, Curnick DJ, Chapple TK, Schallert RJ, Castleton M, Block BA (2019) Estimating space use of mobile fishes in a large marine protected area with methodological considerations in acoustic array design. Front Mar Sci 6:1–17. https://doi.org/10.3389/fmars.2019.00256/full

Chin A, Heupel M, Simpfendorfer C, Tobin A (2016) Population organisation in reef sharks: new variations in coastal habitat use by mobile marine predators. Mar Ecol Prog Ser 544:197–211. https://doi.org/10.3354/meps11545

Colefax AP, Kelaher BP, Pagendam DE, Butcher PA (2020) Assessing white shark (*Carcharodon carcharias*) behavior along coastal beaches for conservation-focused shark mitigation. Front Mar Sci 7:1–10. https://doi.org/10.3389/fmars.2020.00268/full

Cowley P, Bennett R, Childs AR, Murray T (2017) Reflection on the first five years of South Africa's Acoustic Tracking Array Platform (ATAP): status, challenges and opportunities. Afr J Mar Sci 39:363–372. https://doi.org/10.2989/1814232x.2017.1399927

Espinoza M, Farrugia TJ, Lowe CG (2011a) Habitat use, movements and site fidelity of the gray smooth-hound shark (*Mustelus californicus* Gill 1863) in a newly restored southern California estuary. J Exp Mar Biol Ecol 401:63–74. https://doi.org/10.1016/j.jembe.2011.03.001

Espinoza M, Farrugia TJ, Webber DM, Smith F, Lowe CG (2011b) Testing a new acoustic telemetry technique to quantify long-term, fine-scale movements of aquatic animals. Fish Res 108:364–371. https://doi.org/10.1016/j.fishres.2011.01.011

Harasti D, Lee K, Bruce B, Gallen C, Bradford R (2017) Juvenile white sharks *Carcharodon carcharias* use estuarine environments in south-eastern Australia. Mar Biol 164:58. https://doi.org/10.1007/s00227-017-3087-z

Heupel MR, Simpfendorfer CA, Hueter RE (2004) Estimation of shark home ranges using passive monitoring techniques. Environ Biol Fishes 71:135–142. https://doi.org/10.1023/b:ebfi.0000045710.18997.f7

Heupel MR, Semmens JM, Hobday AJ (2006a) Automated acoustic tracking of aquatic animals: scales, design and deployment of listening station arrays. Mar Freshw Res 57:1–13. https://doi.org/10.1071/mf05091

Heupel MR, Simpfendorfer CA, Collins AB, Tyminski JP (2006b) Residency and movement patterns of bonnethead sharks, *Sphyrna tiburo*, in a large Florida estuary. Environ Biol Fishes 76:47–67. https://doi.org/10.1007/s10641-006-9007-6

Heupel MR, Reiss KL, Yeiser BG, Simpfendorfer CA (2008) Effects of biofouling on performance of moored data logging acoustic receivers. Limnol Oceanogr 6:327–335. https://doi.org/10.4319/lom.2008.6.327

Heupel MR, Yeiser BG, Collins AB, Ortega L, Simpfendorfer CA (2010) Long-term presence and movement patterns of juvenile bull sharks, *Carcharhinus leucas*, in an estuarine river system. Mar Freshw Res 61:1–10. https://doi.org/10.1071/MF09019

Hilborn R, Mangel M (1997) Probability and probability models: know your data The ecological detective: Confronting models with data. Princeton University Press, Princeton, New Jersey, pp 39–93

Hobday AJ, Pincock D (2011) Estimating detection probabilities for linear acoustic monitoring arrays American Fisheries Society Symposium, pp 1–22

Hussey NE, Kessel ST, Aarestrup K, Cooke SJ, Cowley PD, Fisk AT, Harcourt RG, Holland KN, Iverson SJ, Kocik JF, Mills Flemming JE, Whoriskey FG (2015) Aquatic animal telemetry: a panoramic window into the underwater world. Science 348:1255642. https://doi.org/10.1126/science.1255642

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 Ecol Evol 7:825–835. https://doi.org/10.1111/2041-210x.12520

Johnson R, Bester MN, Dudley SFJ, Oosthuizen WH, Meÿer M, Hancke L, Gennari E (2009) Coastal swimming patterns of white sharks (*Carcharodon carcharias*) at Mossel Bay, South Africa. Environ Biol Fishes 85:189–200. https://doi.org/10.1007/s10641-009-9477-4

Kahle D, Wickham H (2013) ggmap: spatial visualization with ggplot2. The R Journal 5:144–161

Klimley AP, Le Boeuf BJ, Cantara KM, Richert JE, Davis SF, Van Sommeran S (2001) Radio-acoustic positioning as a tool for studying site-specific behavior of the white shark and other large marine species. Mar Biol 138:429–446. https://doi.org/10.1007/s002270000394

Kock A, O'Riain MJ, Mauff K, Meyer M, Kotze D, Griffiths C (2013) Residency, habitat use and sexual segregation of white sharks, *Carcharodon carcharias* in False Bay. South Africa PLoS One 8:e55048. https://doi.org/10.1371/journal.pone.0055048

Lowe CG, Wetherbee BM, Meyer CG (2006) Using acoustic telemetry monitoring techniques to quantify movement patterns and site fidelity of sharks and giant trevally around French Frigate Shoals and Midway Atoll. Atoll Res Bull 543:281–304

Patterson TA, Pillans RD (2019) Designing acoustic arrays for estimation of mortality rates in riverine and estuarine systems. Can J Fish Aquat Sci 76:1471–1479. https://doi.org/10.1139/cjfas-2018-0090

Pillans RD, Bearham D, Boomer A, Downie RA, Patterson TA, Thomson DP, Babcock RC (2014) Multi year observations reveal variability in residence of a tropical Demersal Fish, *Lethrinus nebulosus*: implications for spatial management. PLoS ONE 9:e105507. https://doi.org/10.1371/journal.pone.0105507

R Core Team (2019) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Rigby CL, Barreto R, Carlson J, Fernando D, Fordham S, Francis MP, Herman K, Jabado RW, Liu KM, Lowe CG, Marshall A, Pacoureau N, Romanov E, Sherley RB, Winker H (2019) *Carcharodon carcharias*. The IUCN Red List of Threatened Species 2019 e.T3855A2878674. https://doi.org/10.2305/IUCN.UK.2019-3.RLTS.T3855A2878674.en

Simmons P, Mehmet MI (2018) Shark management strategy policy considerations: community preferences, reasoning and speculations. Marine Policy 96:111–119. https://doi.org/10.1016/j.marpol.2018.08.010

Simpfendorfer CA, Heupel M (2004) Assessing habitat use and movement. In: Carrier JC, Musick JA, Heithaus MR (eds) Biology of sharks and their relatives. CRC Press, Boca Raton, FL, pp 553–572

Simpfendorfer CA, Heupel MR, Collins AB (2008) Variation in the performance of acoustic receivers and its implication for positioning algorithms in a riverine setting. Can J Fish Aquat Sci 65:482–492. https://doi.org/10.1139/f07-180

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. Can J Fish Aquat Sci 59:23–32. https://doi.org/10.1139/f01-191

Simpfendorfer CA, Huveneers C, Steckenreuter A, Tattersall K, Hoenner X, Harcourt R, Heupel MR (2015) Ghosts in the data: false detections in VEMCO pulse position modulation acoustic telemetry monitoring equipment. Animal Biotelemetry 3:55. https://doi.org/10.1186/s40317-015-0094-z

Sims DW (2010) Tracking and analysis techniques for understanding free-ranging shark movements and behavior Sharks and their relatives II. CRC Press, Boca Raton, FL, pp 367–408

Spaet JLY, Manica A, Brand CP, Gallen C, Butcher PA (2020a) Environmental conditions are poor predictors of immature white shark (*Carcharodon carcharias*) occurrences on coastal beaches of eastern Australia. Mar Ecol Prog Ser 653:167–179. https://doi.org/10.3354/meps13488

Spaet JLY, Patterson TA, Bradford RW, Butcher PA (2020b) Spatiotemporal distribution patterns of immature Australasian white sharks (*Carcharodon carcharias*). Sci Rep 10:1–13. https://doi.org/10.1038/s41598-020-66876-z

Steckenreuter A, Hoenner X, Huveneers C, Simpfendorfer C, Buscot MJ, Tattersall K, Babcock R, Heupel M, Meekan M, van den Broek J, McDowall P, Peddemors V, Harcourt R (2017) Optimising the design of large-scale acoustic telemetry curtains. Mar Freshw Res 68:1403–1413. https://doi.org/10.1071/mf16126

Steel AE, Coates JH, Hearn AR, Klimley AP (2014) Performance of an ultrasonic telemetry positioning system under varied environmental conditions. Anim Biotelemet 2:15. https://doi.org/10.1186/2050-3385-2-15

Sundström LF, Gruber SH, Clermont SM, Correia JP, De Marignac JR, Morrissey JF, Lowrance CR, Thomassen L, Oliveira MT (2001) Review of elasmobranch behavioral studies using ultrasonic telemetry with special reference to the lemon shark, *Negaprion brevirostris*, around Bimini Islands, Bahamas. Environ Biol Fishes 60:225–250. https://doi.org/10.1023/A:1007657505099

Tate RD, Cullis BR, Smith SDA, Kelaher BP, Brand CP, Gallen CR, Mandelman JW, Butcher PA (2019) The acute physiological status of white sharks (*Carcharodon carcharias*) exhibits minimal variation after capture on SMART drumlines. Conserv Physiol. https://doi.org/10.1093/conphys/coz042

Udyawer V, Dwyer RG, Hoenner X, Babcock RC, Brodie S, Campbell HA, Harcourt RG, Huveneers C, Jaine FRA, Simpfendorfer CA, Taylor MD, Heupel MR (2018) A standardised framework for analysing animal detections from automated tracking arrays. Animal Biotelemetry 6:17. https://doi.org/10.1186/s40317-018-0162-2

Voegeli FA, Smale MJ, Webber DM, Andrade Y, O'Dor RK (2001) Ultrasonic telemetry, tracking and automated monitoring technology for sharks. Environ Biol Fishes 60:267–282. https://doi.org/10.1023/a:1007682304720

Welsh JQ, Fox RJ, Webber DM, Bellwood DR (2012) Performance of remote acoustic receivers within a coral reef habitat: implications for array design. Coral Reefs 31:693–702. https://doi.org/10.1007/s00338-012-0892-1