

What drives spatial and temporal patterns within the residential range of two commercially important *Carcharhinus* species, and can they be used to predict broad scale displacements?

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## *Declaration*

I declare that the data used in this project was collected and provided by my secondary supervisor Dr Matias Braccini, Western Australian Fisheries and Marine Laboratories, Government of Western Australia. I was provided with the raw dataset and carried out all processing, analysis and model development myself, with advice from Dr Matias Braccini and my primary supervisor, Dr David Jacoby, Institute of Zoology, Zoological Society of London. Dr Jacoby also provided training and R code for network analysis, which I adapted for the dataset used.



## 2 Introduction

The majority of sharks species are known to undertake large scale movements or regular migrations (Speed et al., 2010, Espinoza et al., 2016), on the scale of tens to thousands of kilometres (Braccini et al., 2016). These movements enable connectivity between populations, and can prevent genetic drift and ultimately species persistence (Olds et al., 2012, Espinoza et al., 2016). However, broad scale marine movements are difficult to track, especially in highly mobile species such as sharks, which exhibit complex life histories (Baeyaert et al., 2018). This limits our understanding of the role that species play within ecosystems, their habitat use and threats facing them (Espinoza et al., 2016).

A major threat to shark populations is overexploitation by commercial fisheries (Worm et al., 2013), both as targeted catch and as bycatch. Estimates of shark take ranged from 6.4 - 7.9% of the global population (Worm et al., 2013), with high proportions of catches going unreported (Clarke et al., 2006). Shark finning is widely acknowledged as a driver of shark mortality due to the high value of fins in Eastern Asia (Clarke et al., 2013). Despite regulations against shark finning by countries including Australia, Brazil, the USA and the European Union (Clarke et al., 2006, Benavides et al., 2011, Braccini et al., 2017a), unregulated catches within Chinese waters and illegal catches globally, lead to high error margins in estimates of decline (Worm et al., 2013).

Understanding movements is necessary for effective management and to mitigating against threats such as shark finning (Espinoza et al., 2016). One method of monitoring movements is the use of acoustic arrays and tags, which have traditionally be used over short spatial and temporal ranges (Braccini et al., 2017b), however recent studies have used long term acoustic telemetry to determine fine scale movements in several species of reef shark (Lea et al., 2016) and broader spatial scales in bull sharks, *Carcharhinus leucas*, (Espinoza et al., 2016). Network analysis is also now regularly used in spatial studies, as it allows the interpretation of complex movement behaviours (Lea et al., 2016). Spatial network analyses allow the incorporation of biotic and abiotic factors, to build models and make predictions regarding future movements, making it a useful tool in conservation management (Jacoby and Freeman, 2016).

Movements of dusky, *Carcharhinus obscurus*, and sandbar sharks, *Carcharhinus plumbeus*, have been monitored using acoustic telemetry (Braccini and Taylor, 2016) and fisheries catch logs along the coast of Western Australia (Braccini, 2017). Both species are of commercial importance to WA shark fisheries (Braccini, 2017) however both are also listed as Vulnerable by the IUCN Red List (Musick et al., 2009a,b), therefore understanding their movements is important economically and ecologically. As coastal species, they are at particularly high risk due to their close proximity to hu-

37 mans, leading to easier exploitation (Espinoza et al., 2015) and a higher risk of habitat destruction  
38 (Speed et al., 2010). Additionally, both species have been previously overfished (Benavides et al.,  
39 2011, Braccini, 2017) and sandbar sharks have a particularly high fin to body size ratio making them  
40 more vulnerable to finning, due to higher fin value (Braccini et al., 2017a).

41

42 Studies of *C. obscurus* and *C. plumbeus* have mainly examined large scale movements or move-  
43 ments of juveniles. The two species are often grouped as both are relatively long lived, late to mature  
44 and have long gestation periods (Cortés, 2000, Benavides et al., 2011, Braccini et al., 2017a, Junge  
45 et al., 2019) adults are more important for population stability. There is evidence that mature *C. obscu-*  
46 *rus* undertake periodic large scale migrations (Hussey et al., 2009, Braccini et al., 2017c), however  
47 there is little evidence of this in mature *C. plumbeus* individuals (Mcauley et al., 2005). Furthermore,  
48 network analyses have not been applied to either species in WA and have yet to consider individual  
49 behaviours in addition to population trends.

50

51 This study will examine the movements of mature dusky and sandbar sharks within their residential  
52 range, Ningaloo Reef, WA, comparing the two species spatially and temporally. Network analyses  
53 will be applied to long term acoustic monitoring data, and individual scale behaviours examined. The  
54 aims of the study are to (1) compare variation in acoustic network use within and between species,  
55 (2) compare variation in area and depth use between and within species and (3) compare resi-  
56 dency patterns between and within species, all within their residential range with respect to individual,  
57 sex, season and time of day. This will then be linked as to what drives movements within the species  
58 home ranges and whether these movements can be extrapolated to give information regarding large  
59 scale movements.

## 60 **Methods & Materials**

### 61 **Data Collection**

62 In this study, acoustic telemetry was used to track the movements adult and sub-adult dusky sharks,  
63 *Carcharhinus obscurus*, and sandbar sharks, *Carcharhinus plumbeus*, over an array of 437 acoustic  
64 receivers located along the coast of Western Australia (Figure 1). Detection data was used from  
65 2011 to 2018, with the first detection on the 2nd July 2011 and the last on the 5th September 2018.  
66 All shark tagging and deployment and retrieval of receivers was carried out by the Government of  
67 Western Australias Department of Fisheries (DoF), and raw dataset compiled by Dr Matias Braccini  
68 of the DoF.

69  
70 A total of 207 adult or sub-adult sharks, 103 *C. obscurus* and 104 *C. plumbeus*, were tagged be-  
71 tween April and September 2011-2015 and 2017 by experienced taggers during surveys by the DoF.  
72 All sharks tagged were measured and sexed, and date and location of release recorded. Tagging  
73 was carried out along the coast between Broome and Esperance, WA, mainly within the Ningaloo  
74 reef (Figure 2). For more details on the tagging procedure please refer to Braccini et al. 2017a.

75  
76 The receivers were split into northern (Figure 1a) and southern arrays (Figure 1b & c). In the north,  
77 57 receivers were deployed in three lines arrays between the Tantabiddi Creek and Coral Bay, 21.5S  
78 - 23.5S, 113.5E - 114E, with a depth range of 2 - 161 meters. Although shark tagging occurred further  
79 to the north, cyclone exposure and the width of the continental shelf prevented more receivers from  
80 being deployed. The 380 southern receivers were split into five line arrays, two on the west coast and  
81 three on the south coast between Perth and the Recherche Archipelago, 31S - 35.5S, 114E - 124E,  
82 with a depth range of 9 - 198 meters. The receivers were initially set up to mitigate against white and  
83 tiger shark attacks in the south (McAuley et al., 2016), and to monitor coral reef fish spawning (Bab-  
84 cock et al., 2017) therefore are in line arrays as opposed to the grids that are used in most network  
85 analysis experiments. For full details of the model of receivers used and data recovery, see Braccini  
86 et al. 2017a,c.

87  
88 During the eight years of monitoring, 130 of the 207 sharks tagged were detected (Table 1), 68  
89 *C. obscurus* and 62 *C. plumbeus*, across 183 of the 437 receivers, with a total of 196,507 detections.  
90 The majority of these detections, 191,448, occurred with the residential range of both populations,  
91 the Ningaloo reef. Within the Ningaloo reef, 118 sharks were detected across 57 receivers. For each  
92 detection, the location, time, date, depth and tag code were recorded. This dataset, along with the  
93 size and sex data for each individual, and the location and depth of each receiver, was used in the  
94 analysis.

Table 1: Summary of detected shark demographics, where M, F and U stand for male, female and unknown respectively. Size range represents fork length, measured at time of tagging in meters. Time monitored is the number of days between tagging and the most recent detection.

Species	Sex				Size Range (m)	Time Monitored (days)
	M	F	U	Total		
<i>Carcharhinus obscurus</i>	24	43	1	68	1.5 - 2.98	7 - 1987
<i>Carcharhinus plumbeus</i>	19	43	-	62	1.22 - 1.58	8 - 1976
Total	43	86	1	130	-	-

## 96 Data Analysis

97 All data manipulation, analysis and model building was carried out using R version 3.6.1 (R Core  
98 Team, 2015). The tidyverse package (Wickham, 2017) was used for all data manipulation and plots  
99 and the lubridate package (Grolemund and Wickham, 2011) for formatting temporal data. Analyses  
100 used detections from the Ningaloo reef arrays exclusively (defined as any detection north of 24S), as  
101 both species are show high residency to the reef (Braccini et al., 2017b). The analysis was split into  
102 four sections: spatial network analysis, home range estimation using centres of activity, residency  
103 patterns using a residency index, and detection patterns examining detections per day. A combina-  
104 tion of analyses methods were used as although spatial networks can be used to explain a movement  
105 dynamics, more traditional approaches can also provide valuable insight (Baeyaert et al., 2018).

106

107 In each section of the analyses, linear mixed models were used to examine the relationship between  
108 the response variable (network density, kernel utilisation distribution, residency index and depth in-  
109 dex respectively) and a range of fixed explanatory variables, using the lme4 R package (Bates et al.,  
110 2015). Linear mixed models were chosen so non-independent individual variation could be included  
111 as a random variable, and as data was linear but not normally distributed in all cases. Between and  
112 within species variation were both modelled. Model distribution was chosen by comparing the fit of  
113 quantile-quantile plots against normal, log normal, Poisson, negative binomial and gamma probability  
114 distributions, using the car (Fox and Weisberg, 2019) and MASS (Venables and Ripley, 2002) pack-  
115 ages in R. Test files were then generated, and each model tested, then outputs compared against  
116 the original data to check model fit, using the merTools package (Knowles and Frederick, 2019).

117

118 Fixed explanatory variables used were species, sex, season, time of day and migratory status. For

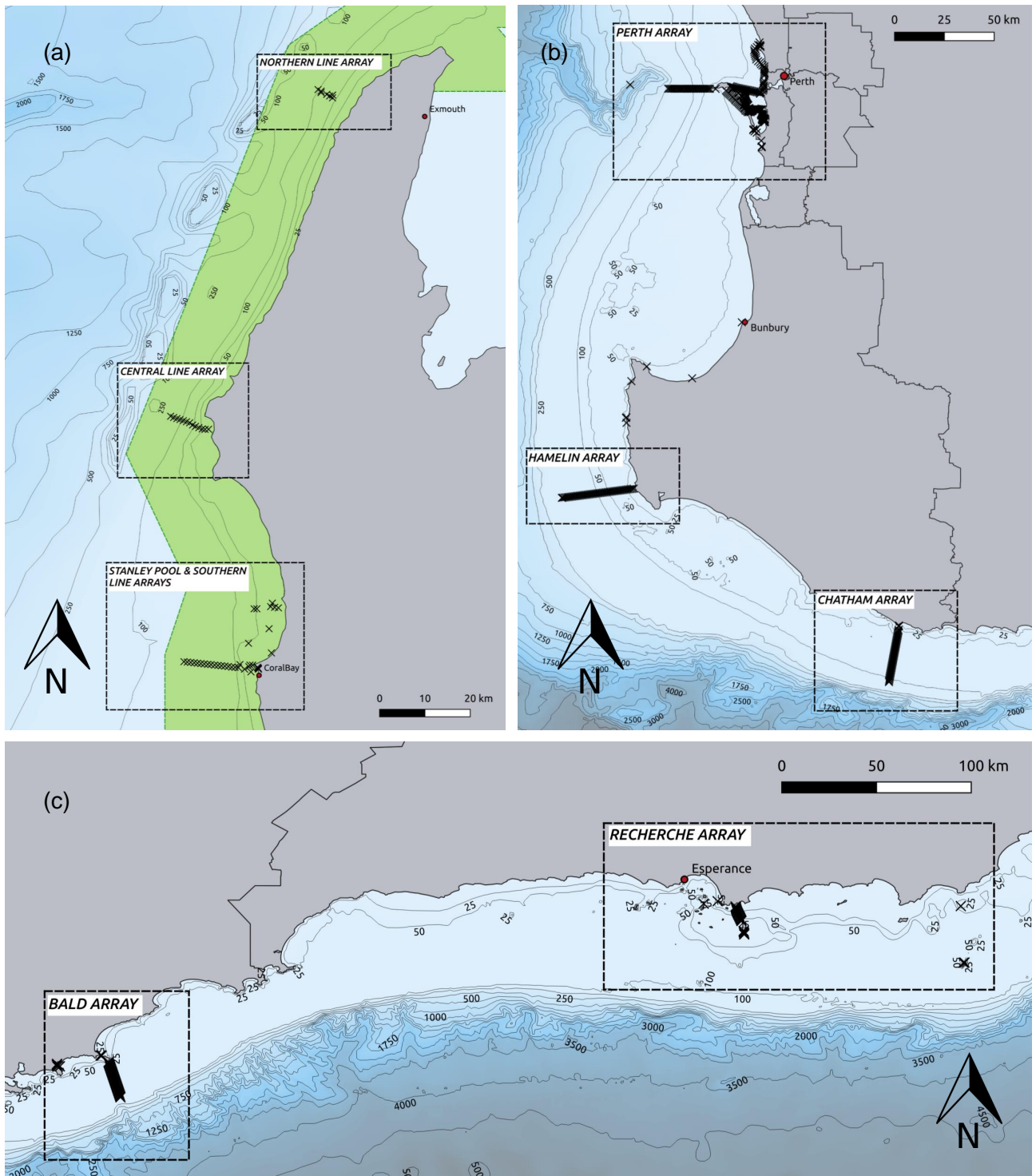


Figure 1: Distribution of acoustic receivers in Western Australia, each cross representing an individual receiver. (a) Northern receivers within the Ningaloo reef, total = 57, Northern Line array = 7, Central Line array = 13 and Stanley Pool and Southern Line arrays = 37. Green shading represents the Ningaloo marine World Heritage Site (Flanders Marine Institute, 2013). (b) Perth and South Western receivers, total = 324, Perth array = 232, Hamelin array = 48 and Chatham array = 44. (c) Southern receivers, total = 56, Bald array = 33 and Recherche array = 23. This map was generated using QGIS (QGIS Development Team, 2019), with a base map shapefile (Australian Bureau of Statistics, 2011), bathymetric contour shapefile (GEBCO Compilation Group, 2019) and bathymetry raster (Whiteway, 2009).



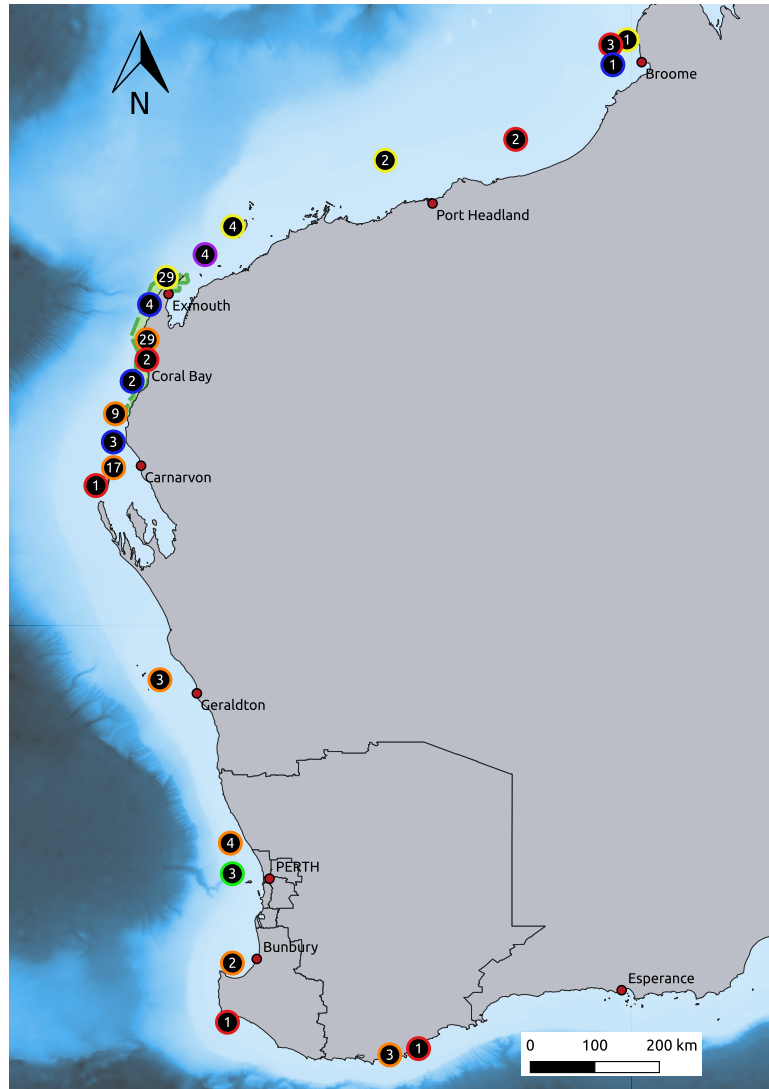


Figure 2: Locations of shark tagging of sharks detected between 2011 and 2018 ( $n = 130$ ). The number within each circle gives the number of sharks tagged at that location and the coloured border gives the year of tagging (yellow = 2011, orange = 2012, red = 2013, purple = 2014, blue = 2015, green = 2017, no tagging occurred in 2016 & 2018.) This map was generated using QGIS (QGIS Development Team, 2019), with a base map shapefile (Australian Bureau of Statistics, 2011) and bathymetry raster (Whiteway, 2009).

sex, one individual of unknown sex was excluded. Season and time of day (day or night) were assigned based upon Austral seasons (Summer: December February, Autumn: March May, Winter: June August, Spring: September November) and average sunrise and sunset times per month across the years of monitoring (Geoscience Australia, 2015). Data was not stratified by year due to small sample sizes in several years. In models examining *C. obscurus*, migratory status was used as an explanatory variable as the species are known to be resident in Ningaloo and make periodic migrations south (Braccini et al., 2017c). Migratory individuals were those that made at least one return journey between the Ningaloo receiver arrays and the southern arrays and were detected at least four times. Five *C. obscurus* were only detected in the southern arrays and are shown to be younger individuals, most likely moving north from their nursery grounds, by Braccini et al. 2017c, so were also excluded from this study. Model selection was carried out using the Akaike Information Criterion (AIC), for each subset with best fit denoted by the lowest AIC value and highest marginal  $R^2$  value, calculating using the MuMIn package for R (Barton, 2019), defined as individual variance explained (Nakagawa and Schielzeth, 2013). Each model was then checked using a traditional likelihood ratio test (anova) comparing each model with a null model.

134

## 135 **Spatial Networks**

Network analysis examines the relationship between nodes and the connections between them, known as edges (West, 2001). In this system, the receivers are used as the nodes and individual shark movements as edges. Spatial networks were built for each species, sex and individual, then individual networks were subset by time of day and season. To generate each network, movements between receivers were calculated. The R package igraph (Csardi and Nepusz, 2006) was used to calculate adjacency matrices and edge lists for each movement between receivers. Network density was calculated and is the number of edges in each network divided by the total number of possible edges (Mourier et al., 2018), representing the proportion of the total residential area (within the Ningaloo arrays) used by each individual. Network visualisations were generated using the rgdal package for R (Bivand et al., 2019) to aid analysis.

146

Network density was used as the response variable in each linear mixed model with a log normal probability distribution, and species, sex, season, time of day and migratory status (*C. obscurus* only) as fixed explanatory variables. Any individuals with no movements detected were excluded.

150

## 151 Home Range

152 To investigate home range, centres of activity were calculated for each individual, and subset for each  
153 season and time of day. The centre of activity (COA) of each shark was calculated using the VTrack  
154 package (Campbell et al., 2012), which calculates a weighted mean position based upon detection  
155 locations. This method was evaluated and found to be reasonably accurate within an array when  
156 compared to actively tracked individuals (Simpfendorfer et al., 2002). The COAs were used to cal-  
157 culate minimum convex polygons (MCPs), which define the minimum area containing all detections  
158 of an individual, centred on the COA. To calculate these, a minimum of four detections at different  
159 receivers within the Ningaloo arrays were required, individuals that did not meet this criterion were  
160 excluded. MCPs give an estimate of the extent of range within the Ningaloo reef however a better  
161 estimate for home range is a kernel utilisation distribution (KUD). This method uses location and den-  
162 sity of detections in a probability density function to estimate the probability of the individual being  
163 found within a certain area (Jacoby and Freeman, 2016). Core or home range was then calculated  
164 as the area within the KUD where the most activity occurred, with a size of 50% of the total KUD.  
165 MCPs and KUDs were calculated using the adehabitatHR package (Calenge, 2006), packages sp  
166 (Pebesma and Bivand, 2005, Bivand et al., 2013) and rgdal (Bivand et al., 2019) were used to trans-  
167 form between coordinate systems and export shapefiles of KUD areas respectively.

168  
169 KUD area was used as the response variable for linear mixed models examining home range. The  
170 models used a gamma distribution, and species, sex, season, time of day and migratory status (*C.*  
171 *obscurus* only) as fixed explanatory variables. Individuals with <5 movements in a subset were ex-  
172 cluded, consistent with the overall COA calculations.

## 174 Residency Patterns

175 To study residency patterns within Ningaloo reef, a residency index was calculated for each individ-  
176 ual over the monitoring period, and subsets taken and calculated for season, time of day and season  
177 stratified by time of day. The residency index was defined as the number of days detected within the  
178 Ningaloo arrays as a proportion of the number of days monitored, between release and last detec-  
179 tion (Espinoza et al., 2016). Values near 1 indicate a high residency to the reef and 0 a low residency.

180  
181 Residency index was used as the response variable in the linear mixed models, with a log proba-  
182 bility distribution (as the data was proportional). Fixed explanatory variables used were species, sex,  
183 season, time of day and migratory status (*C. obscurus* only). Individuals detected on <5 unique days  
184 were excluded as sample size was too small to give an accurate measure of residency.

## 186 **Detection Patterns**

187 Number of detections per day per individual were calculated then split by depth to allow investigation  
188 of depth use. Depth of detections were split into 25m bands, with receiver depths ranging between 1  
189 161 meters within Ningaloo reef.

190

191 Mixed models were built using number of detections per day as response variable, with a log normal  
192 distribution. Fixed explanatory variables used were sex, species, depth band, time of day, season  
193 and migratory status (*C. obscurus* only). To further examine depth patterns, fixed variables were  
194 tested as random variables with depth band as the only fixed variable, within further mixed models,  
195 again using a log normal distribution. Individuals with <5 unique days detected and depth bands with  
196 fewer than 5 detections were excluded in consistency with the rest of the study.

197

## Results

To examine movement behaviour of dusky, *Carchahinus obscurus*, and sandbar sharks, *Carcharhinus plumbeus*, generalised linear mixed effect models (GLMMs) were used with spatial network density, kernel utilisation distribution area, residency index and detections per day as response variables. Within and between species variation was accounted for by modelling both species together and separately. Individual shark ID was used as a random effect to account for individual variation and non-independence of related individuals and all models used a single fixed explanatory variable. The best model for each response variable was selected using the Akaike Information Criterion (AIC), where the lowest value indicates best fit (Bolker et al., 2009) and variance explained ( $R^2$ ), where possible (Nakagawa and Schielzeth, 2013). Traditional null model comparisons using likelihood ratio tests were also used as a third test of model fit however outputs from these were interpreted with caution as p-values are considered less relevant when using mixed effect models (Posada and Buckley, 2004). Models with multiple explanatory variables were tested and found, in all cases, to explain less of the variance and have a higher AIC value than models with single variables. Full model outputs can be found in the Appendices.

### Spatial Networks

Network density was used as the response variable for all spatial network models and gives the proportion of edges in the network used out of all possible edges (Mourier et al., 2018). Individual variation accounted for between 65.5 - 91.2% of deviance explained in each model, indicating high intra-species variation in network use. Detailed outputs of all models in this section are given in Appendix Table A1.

Species, as a fixed effect, had a relatively low AIC value (65.60) and accounted for 4.7% of deviance, with sandbar sharks using a higher proportion of the network than dusky sharks, on average (Figure 3). Sex had the highest AIC (67.52) and explained 4.9% of deviance across both species, with males using a slightly higher proportion of the network overall but not significantly so. Season gave the lowest value of AIC (65.09) and accounted for 3.2% of deviance. Highest network density occurred in Summer then decreased through Autumn into Winter, then increased again in Spring (Figure 3). Network density did not vary significantly with time of day, accounting for only 1% of deviance.

When subset for *C. obscurus*, sex accounted for 13% of deviance, with males having a higher network density than females. Seasonal variation gave the lowest AIC value (48.39) and accounted for 15.9% of deviance, with the same pattern as before, highest in summer, decreasing through autumn to winter then increasing again in spring (Figure 3). Time of day and migratory status accounted for

2.1% and 3.4% of deviance respectively and showed very little variation.

Network density in *C. plumbeus* again showed greatest variation and lowest AIC value (5.12) seasonally, which accounted for 3.3% of deviance. The highest value of network density occurred in summer and decreased through to winter as before, however continued to decrease in spring (Figure 3). Time of day and sex showed minimal variance and gave significantly higher AIC values of 8.46 and 9.42 respectively.

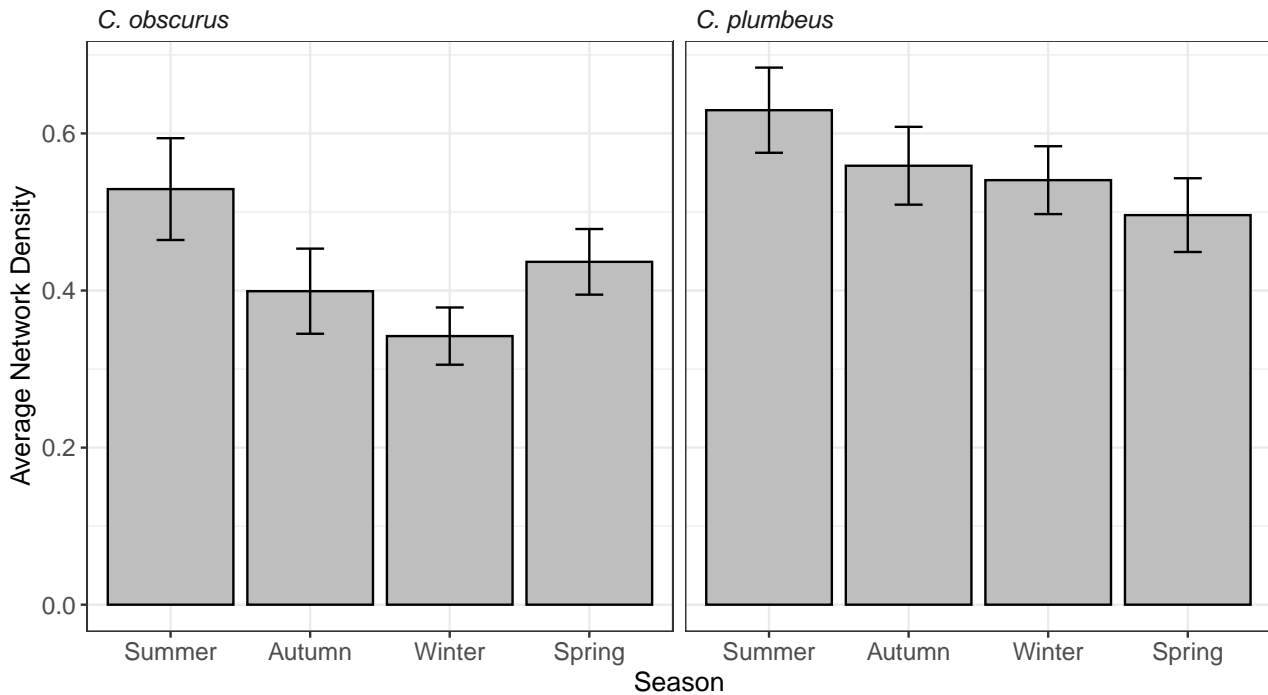


Figure 3: Seasonal variation in network density of *Carcharhinus obscurus* (n = 53) and *Carcharhinus plumbeus* (n = 58). Bars give mean average network density and error bars give standard error. Seasons are defined as standard Austral seasons.

## Home Range

Kernel utilisation area (KUD) was used as the response variable in each home range model, and gives the size of the core range of each individual, based upon detection number and location (Jacoby and Freeman, 2016). Model were selected using AIC and with reference to likelihood ratio tests as  $R^2$  lack accuracy for gamma distributed models. Individual variation had a significant effect in all models when tested against a null linear model.

The largest variation in KUD was between species, with the lowest AIC values for both season and time of day subsets (334.9 and 285.8), and a significant difference with the null GLMM (ANOVA:  $\chi^2_4 = 12.13$ ,  $p < 0.001$ ). *C. obscurus* had a larger average kernel area than *C. plumbeus*. Intraspecies

variation in area was also much lower in *C. plumbeus* than in *C. obscurus*. KUD showed little variation with sex, season, time of day or migratory status in all subsets. All model outputs are given in Appendix Table A2.

## Residency Patterns

Residency index (RI) was calculated as days detected within the Northern receiver arrays (Figure 1a), as a proportion of days monitored, and used as the response variable for all residency models. Individual variation was significant in all models, accounting for between 77.6 - 99.5% of deviance explained by each model. Full model outputs are available in Appendix Table A3.

There was little variation in RI with species and sex, and relatively high values of AIC (-345.8,-644.9), and low deviance explained (3.8% and 1.8%). RI varied with season, with the lowest AIC value of -710.7. RI decreased in summer and spring but was more consistent in autumn and winter, however this only explained 3.7% of the deviance. Seasonally, average sandbar RI was higher than dusky (Figure 4). Time of day also led to variance in RI, with residency being slightly higher at night, however only 0.6% deviance was explained by this model.

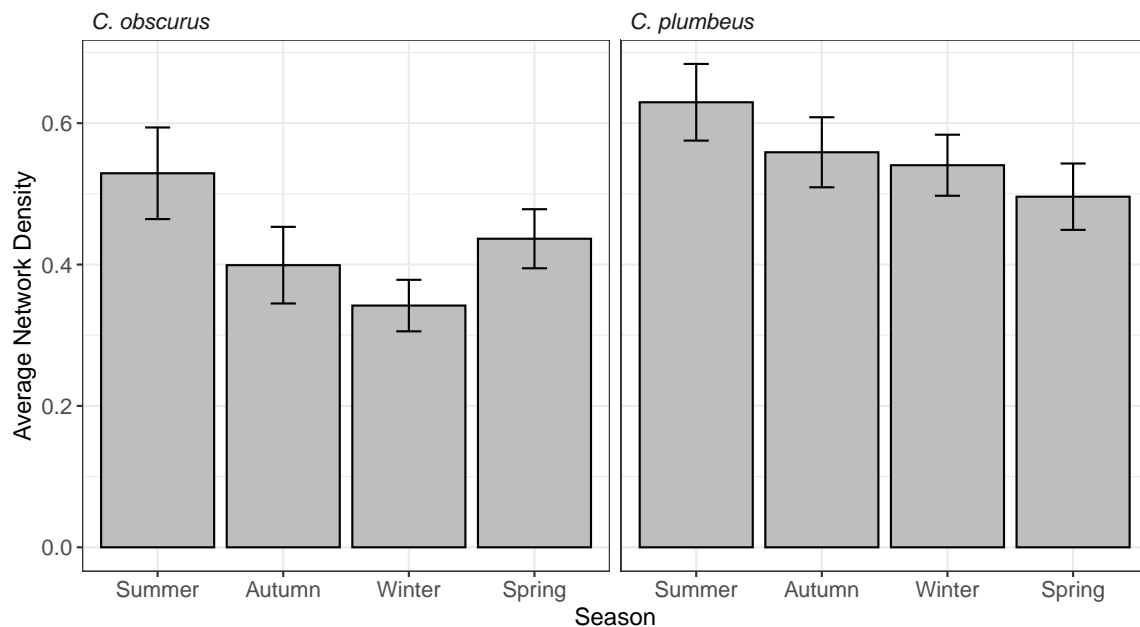


Figure 4: Seasonal variation in residency index of *Carcharhinus obscurus* (n = 51) and *Carcharhinus plumbeus* (n = 59). Bars give mean average residency index and error bars give standard error. Seasons are defined as standard Austral seasons.

RI varied more significantly by season within the *C. obscurus* subset, explaining 22.2% of deviance,

267 and having the lowest AIC of -461.8. RI was lowest in the summer, then increased through autumn  
268 and winter, then decreased again in spring (Figure 4). Time of day also had a low value of AIC within  
269 it's subset (-740.5), with a slight increase in RI at night but only this accounted for 5% of deviance.  
270 Sex explained 18.2% of deviance in RI, with higher RI in females, but a high AIC value. RI did not  
271 vary with migratory status.

272

273 Seasonal variation was also present in the *C. plumbeus* subset, with a AIC of -349, with values  
274 highest in summer, decreasing until Spring but only by a small proportion (Figure 4). Time of day and  
275 sex had very little effect on RI for sandbars, with a slightly higher average RI at night and in males.

## 276 **Detection Patterns**

277 Number of detections per day was used to examine detection patterns and calculated for each indi-  
278 vidual, per depth band (set at 25m intervals). AIC were all exceptionally high and  $R^2$  values very low  
279 for all models examined in comparison to all other response variables. Individual variation accounted  
280 for between 12.0 - 24.3% of deviance in each model and all fixed effects accounted for <0.1%. See  
281 Appendix Table A4 for all model outputs.

282

283 Depth of detections, although have a low  $R^2$  and high AIC value, did highlight seasonal trends. De-  
284 tections of *C. obscurus* between 0-25m and over 100m only occurred in winter and spring, whereas  
285 detections between 25-100m occurred in all seasons. None were detected above 125m. Detections  
286 of *C. plumbeus* between 0-125m occurred during all seasons, however the number of detections at  
287 depths below 25m were significantly lower. *C. plumbeus* were detected at depths >125m but only  
288 during winter and autumn. The northern lines array in Figure 5 shows the near constant distribution  
289 of sandbar sharks (orange) throughout the year and absence of dusky sharks (purple) in the summer.  
290 The central line array, Figure 6, shows the decrease in dusky sharks in summer and a more restricted  
291 depth range in the spring. The Stanley Pool and southern line arrays, Figure 7, show a decrease in  
292 dusky sharks through spring and summer, as well as more shallow water detections than in sandbars.  
293 Figures 5-7 all highlight the greater depths at which sandbars are found throughout the year.



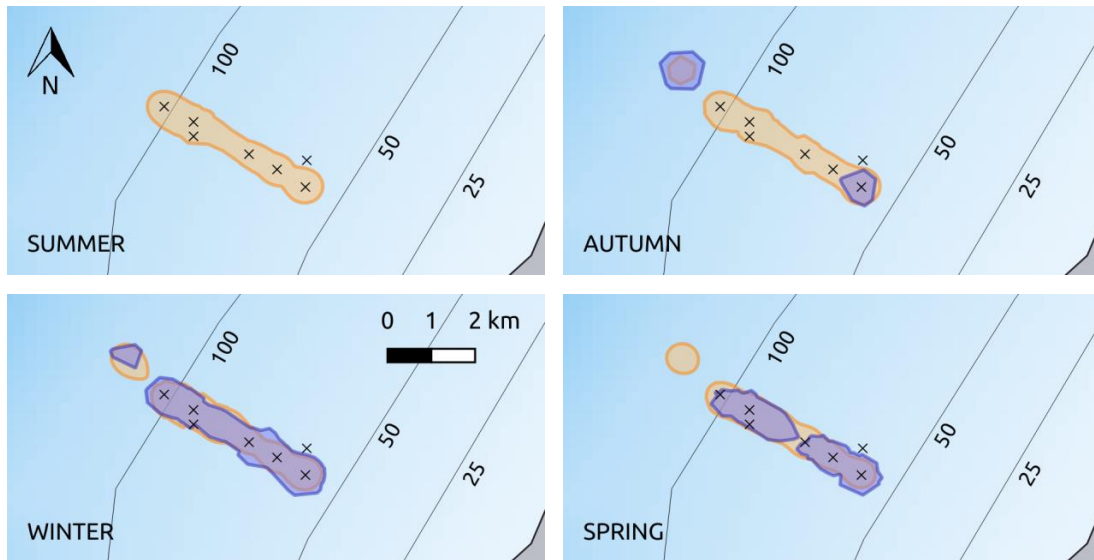


Figure 5: Seasonal variation in core kernel utilisation areas of *Carcharhinus obscurus* (purple) and *Carcharhinus plumbeus* (orange), within the northern line array, Ningaloo reef, WA. Black crosses show acoustic receiver locations and water depth is given parallel to each bathymetry contour. This map was generated using QGIS (QGIS Development Team, 2019), with a base map shapefile (Australian Bureau of Statistics, 2011), bathymetric contour shapefile (GEBCO Compilation Group, 2019) and bathymetry raster (Whiteway, 2009).

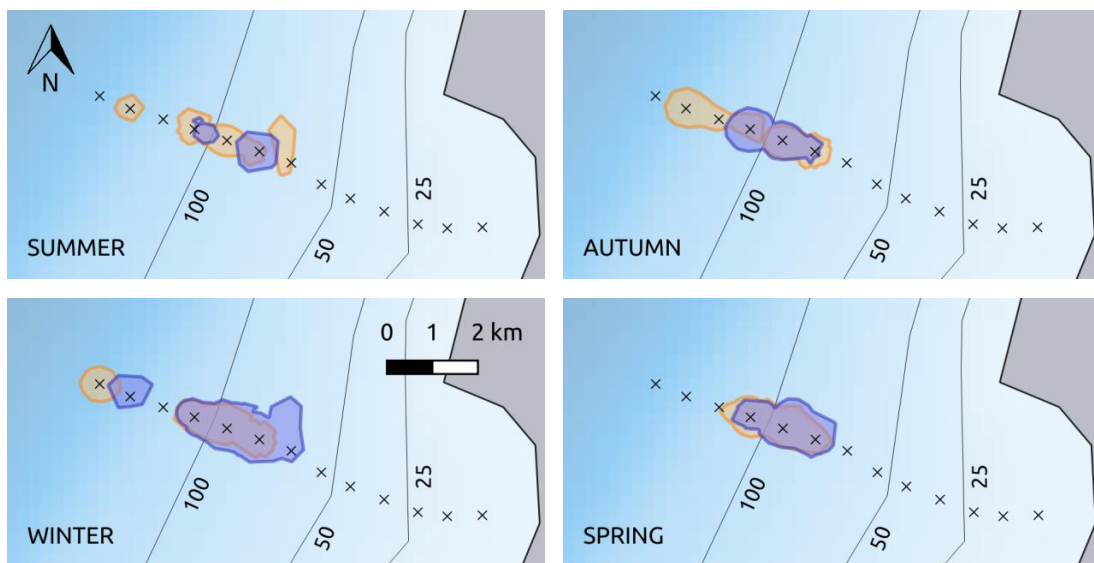


Figure 6: Seasonal variation in core kernel utilisation areas of *Carcharhinus obscurus* (purple) and *Carcharhinus plumbeus* (orange), within the central line array, Ningaloo reef, WA. Black crosses show acoustic receiver locations and water depth is given parallel to each bathymetry contour. This map was generated using QGIS (QGIS Development Team, 2019), with a base map shapefile (Australian Bureau of Statistics, 2011), bathymetric contour shapefile (GEBCO Compilation Group, 2019) and bathymetry raster (Whiteway, 2009).

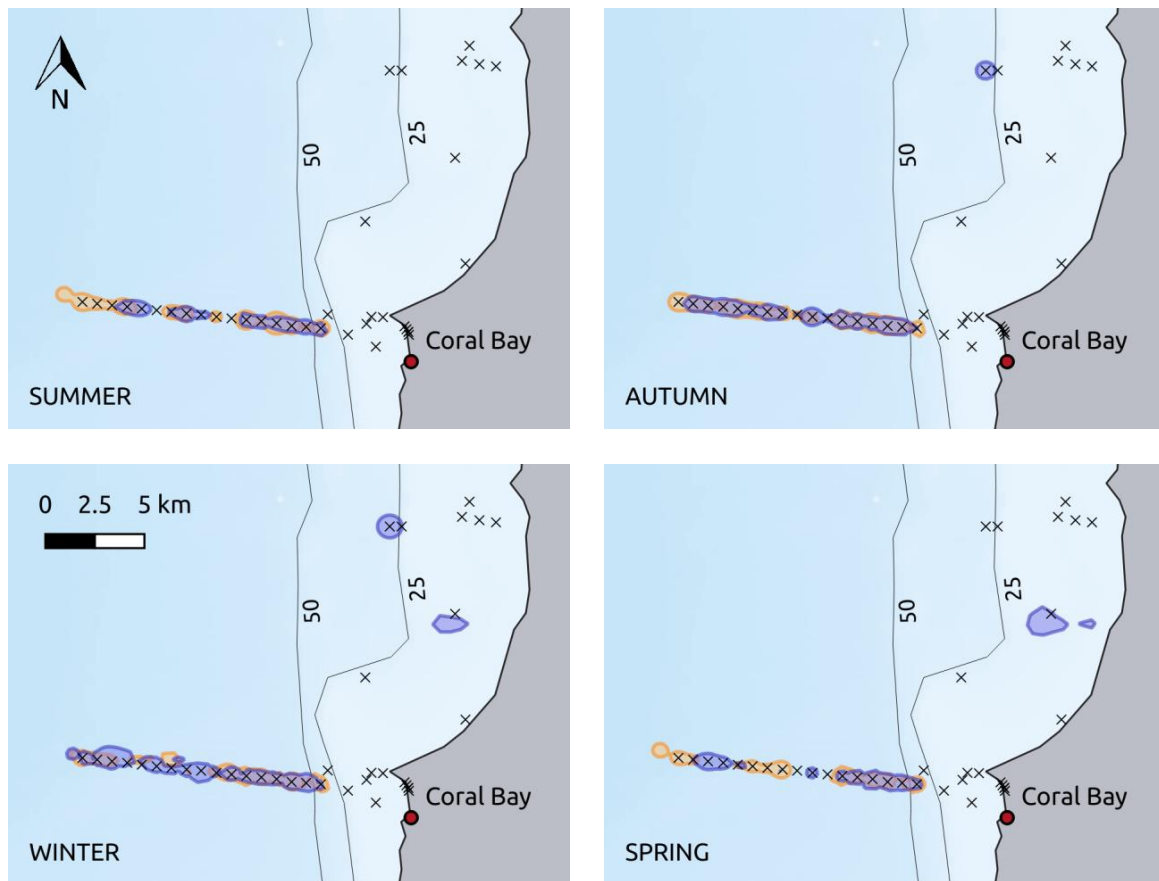


Figure 7: Seasonal variation in core kernel utilisation areas of *Carcharhinus obscurus* (purple) and *Carcharhinus plumbeus* (orange), within the Stanley Pool and southern line arrays, Ningaloo reef, WA. Black crosses show acoustic receiver locations and water depth is given parallel to each bathymetry contour. This map was generated using QGIS (QGIS Development Team, 2019), with a base map shapefile (Australian Bureau of Statistics, 2011), bathymetric contour shapefile (GEBCO Compilation Group, 2019) and bathymetry raster (Whiteway, 2009).

## Discussion

This study aimed to address the drivers of residential movements and whether they could be used to predict large scale movements by comparing variation in acoustic network use, area and depth use and residency between and within species. This was examined using acoustic telemetry data on two species of shark dusky, *Carcharhinus obscurus*, and sandbar, *Carcharhinus plumbeus*.

## Network Use

Spatial network analysis was used to assess use of the reef. Network density was chosen as the best network metric for this system as it contained line arrays as opposed to conventional grid arrays, and spanned a much larger area, rendering any network metric reliant on equal spacing of nodes meaningless. Network density is not as dependent on this, as it gives a proportion of the edges used

304 out of the total possible edges, as opposed to the length of each edge.

305

306 Network density showed very little variance between species, indicating both species use similar  
307 proportions of the reef. When split by season, dusky sharks showed a distinct pattern, with propor-  
308 tion used decreasing significantly in winter then increasing again in the summer.

309 Males = larger network than females in *C. amblyrhynchos* - grey reef shark - (Espinoza et al.,  
310 2015) no change in network size with sex in bull and silvertip - (Espinoza et al., 2015) Highlu variable  
311 between individuals = (Lea et al., 2016) increased activity at night in several adult shark species but  
312 no evidence in juveniles - sixgill, leopard, white tip reef, grey reef and lemon (Speed et al., 2010)

313 The close proximity of receivers within the same line array could have increased probability of  
314 detection however receivers in the same line were at different depths, removing a proportion of this  
315 bias, however outputs should still be interpreted with reference to other metrics; - justification of  
316 network density - results of network models and interpretations - ecologically - individual variation in  
317 networks

## 318 **Area & Depth Use**

319 - KUD results and implications main factor in grey reef and bull sharks = size (Speed et al., 2010)  
320 which is not application for this study due to small size range - individual variation in KUD

321 - Depth analysis through detection data and implications

322 - seasonal - During gestation female sand tiger sharks *C. taurus*, move north into warmer waters  
323 - link with moving to shallower water - could be gestation - and also carry out large scale migrations  
324 in S Africa and give birth in cooler southern waters (Dicken et al., 2007) juv sandbars = deeper  
325 dives in winter than summer - E coast of N america (Speed et al., 2010) juv lemon sharks - temp for  
326 optimal metabolic performance - movements over time with climate change/ drives depth changes  
327 over seasons (Speed et al., 2010) - time of day - links to movements of prey - in Caribbean reef shark  
328 more time spent at surface at night due to prey movements up (Speed et al., 2010)

329 - individual variation in depths

## 330 **Residency & Migration**

331 - results from RI models and ecological implications

332 resident in ningaloo due to high productivity of coral reefs (Espinoza et al., 2016) females more  
333 likely in bull shark more likely to leave residential area than males - for giving birth (Espinoza et al.,  
334 2016) - in contrast to dusky where the majority of males were migratory

335 - individual variation in RI

336 partial migration in bull sharks - ind variation - not all mature females migrate, some remain  
337 resident in E Aus (Espinoza et al., 2016) - could be why some dusgies remain partial also seen in

338 Port Jackson sharks, E Aus - (Bass et al., 2017) partial to most likely five birth in tiger sharks in Hawaii  
 339 but not all mature females and mainly females (Papastamatiou et al., 2013)  
 340 - lack of correlation with migration status in duskies - ecological applications  
 341 very little difference in sex distribution = fisheries captures in 1994-1999 in south gave very even  
 342 dis of both species of both sexes caught (Mcauley and Simpfendorfer, 2003)  
 343 - drivers of residential movements  
 344 cooler water temp in S Africa = upwellings along coast =  $\downarrow$  nutrients and increased teleosts so  
 345 more predators present incl sandbars (Wintner and Kerwath, 2018) very little effect of water temper-  
 346 ature on dusky movements in S Africa - could be more resilient hence detections further south than  
 347 sandbars in tiger sharks, movements between reefs are suggested to be due to foraging in Hawaii  
 348 and individual based (Papastamatiou et al., 2013)  
 349 - prediction of migration  
 350 very little effect of water temperature on dusky movements in S Africa - could be more resilient  
 351 hence detections further south than sandbars (Wintner and Kerwath, 2018) seasonal environ change,  
 352 reprod and foraging (Espinoza et al., 2015) give birth - e.g. move into temperate waters seen in C  
 353 taurus though warmer for gestation (Dicken et al., 2007) segregated by age - sandbar observed in  
 354 more temperature waters when young - in south at depths  $>80\text{m}$ , neonates from Geraldton to Broome  
 355 and caught in south below 26S (?) - extent of range potentially not as far south as perth receivers -  
 356 issue with layout of receivers but not being picked up on receivers in South - narrow continental shelf  
 357 along south coast in comparison with Ningaloo - may not be picked up - also adults tagged in south  
 358 sandbar catch much lower between 1994 and 1999 than dusky but were present in south (Mcauley  
 359 and Simpfendorfer, 2003) isolated reefs more likely to remain resident than well connected (Espinoza  
 360 et al., 2015) - Ningaloo not isolated so more likely to migrate sandbars physiologically in heat at same  
 361 time movement occurs within duskies (?)  
 362 - eval. of Acoustic Telemetry only gives presence or absence data but valuable long term (Bass  
 363 et al., 2017) relatively inexpensive (Speed et al., 2010) increased understanding of marine predators  
 364 (Espinoza et al., 2016) HUGE GAP in middle of arrays  
 365 - future directions for research  
 366 combination of catch data, such as that used in (Braccini, 2017) with acoustic data and more  
 367 receivers in central range or deeper southern range to accurately assess risk look further into depth  
 368 use - receivers at greater range of depths as space use may change with climate change - higher  
 369 temp = nearer shore, effects of climate change on this largely unquantified so far (Speed et al.,  
 370 2010) evidence of size being important - larger networks (Espinoza et al., 2015) and greater distances  
 371 moved (Papamatadiou 2013) - wider size range of sharks

## 372 **Conclusions**

373 As species that are slow to mature and have a low fecundity (Cortés, 2000), dusky and sandbar  
374 sharks are both slow to recover from overexploitation (Rogers et al., 2013).

375 management has been well implemented - easier than east coast due to single jurisdiction of WA.  
376 (Heupel et al., 2015)

377 - high individual variability challenging to explain (Espinoza et al., 2015) - seasonality - lack of  
378 sexual influence - overall drivers of residential movements - can we predict large scale movements

379 *Acknowledgements*

380

381 *Data & Code Availability*

382

383 All R code and raw data files are available in my GitHub repository as well as a bash script detailing  
384 the order to run each script file: <https://github.com/KBicks/CMEECourseWork/tree/master/Project>.

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Table A1: GLMM outputs for network density models, using a log normal distribution. All models used individual ID as a random effect and fixed effects are given in the first column. The null model is given by network density  $\sim 1$ , and was used as a comparison to calculate  $\chi^2$  and p-values for other models. Rows are divided into sections for both species (all,  $n = 111$ ), dusky sharks (*C. obscurus*,  $n = 52$ ) & sandbar sharks (*C. plumbeus*,  $n = 58$ ). Metrics of fit used are Akaike Information Criterion (AIC),  $R^2$  marginal giving the variance explained by fixed effects, and  $R^2$  conditional giving the variance explained by the whole model, the output of the likelihood ratio test,  $\chi^2$  and p-value, and the degrees of freedom (df). Bold text indicates the best fitting model and significant metrics. Models with multiple fixed variable were also tested however single variable models had better fit.

	AIC	$R_m^2$	$R_c^2$	$\chi^2$	df	p
<i>All</i>						
Network Density $\sim 1$	66.01	-	0.748	-	3	-
Network Density $\sim$ Species	65.60	0.047	0.752	2.514	4	0.113
Network Density $\sim$ Sex	67.52	0.049	0.755	2.692	4	0.101
<b>Network Density <math>\sim</math> Season</b>	<b>65.09</b>	0.032	0.763	12.47	6	0.006
Network Density $\sim$ Time of Day	67.05	0.010	0.908	7.862	4	0.005
<i>Carcharhinus obscurus</i>						
Network Density $\sim 1$	59.45	-	0.779	-	2	-
Network Density $\sim$ Sex	59.95	0.130	0.785	3.436	4	0.064
<b>Network Density <math>\sim</math> Season</b>	<b>48.39</b>	<b>0.159</b>	0.850	20.28	6	<b>&lt;0.001</b>
Network Density $\sim$ Time of Day	58.66	0.021	0.933	10.26	4	0.0013
Network Density $\sim$ Migratory Status	60.47	0.034	0.778	0.738	4	0.390
<i>Carcharhinus plumbeus</i>						
Network Density $\sim 1$	7.460	-	0.709	-	3	-
Network Density $\sim$ Sex	9.420	0.012	0.712	0.334	4	0.563
<b>Network Density <math>\sim</math> Season</b>	<b>5.115</b>	0.033	0.733	8.172	6	0.042
Network Density $\sim$ Time of Day	8.456	0.005	0.870	1.295	4	0.255

Table A2: GLMM outputs for kernel density utilisation models (KUD), using a gamma distribution. All models used individual ID as a random effect and fixed effects are given in the first column. The null model is given by  $KUD \sim 1$ , and was used as a comparison to calculate  $\chi^2$  and p-values for other models. Rows are divided into sections for both species (all,  $n = 77$ ), dusky sharks (*C. obscurus*,  $n = 39$ ) & sandbar sharks (*C. plumbeus*,  $n = 39$ ). Metrics of fit used are Akaike Information Criterion (AIC), the output of the likelihood ratio test,  $\chi^2$  and p-value, and the degrees of freedom (df). Two types of AIC are used as sample size was too small to subset both season and time of day, giving two subsets with non comparable AIC values (se = seasonal subset and dn = time of day subset). Bold text indicates the best fitting model and significant metrics. Models with multiple fixed variable were also tested however single variable models had better fit.

	$AIC_{se}$	$AIC_{dn}$	$\chi^2$	df	p
<i>All</i>					
KUD $\sim 1$	345.0	288.3	-	3	-
<b>KUD <math>\sim</math>Species</b>	<b>334.9</b>	<b>285.8</b>	12.13	4	<b>&lt;0.001</b>
KUD $\sim$ Sex	346.5	289.8	0.584	4	0.445
KUD $\sim$ Season	347.3	-	3.702	6	0.230
KUD $\sim$ Time of Day	-	289.8	0.476	4	0.491
<i>Carcharhinus obscurus</i>					
KUD $\sim 1$	<b>178.2</b>	163.1	-	3	-
<b>KUD <math>\sim</math>Sex</b>	<b>178.2</b>	<b>162.2</b>	2.032	4	0.154
KUD $\sim$ Season	181.8	-	2.485	6	0.478
KUD $\sim$ Time of Day	-	165.1	0.089	4	0.765
KUD $\sim$ Migratory Status	179.5	164.1	0.703	4	0.402
<i>Carcharhinus plumbeus</i>					
KUD $\sim 1$	<b>153.4</b>	124.1	-	3	-
KUD $\sim$ Sex	155.4	126.1	0.007	4	0.935
KUD $\sim$ Season	158.3	-	1.020	6	0.796
<b>KUD <math>\sim</math>Time of Day</b>	-	<b>123.6</b>	2.52	4	0.112

Table A3: GLMM outputs for residency index models (RI), using a log normal distribution. All models used individual ID as a random effect and fixed effects are given in the first column. The null model is given by  $RI \sim 1$ , and was used as a comparison to calculate  $\chi^2$  and p-values for other models. Rows are divided into sections for both species (all,  $n = 110$ ), dusky sharks (*C. obscurus*,  $n = 49$ ) & sandbar sharks (*C. plumbeus*,  $n = 59$ ). Metrics of fit used are Akaike Information Criterion (AIC),  $R^2$  marginal giving the variance explained by fixed effects, and  $R^2$  conditional giving the variance explained by the whole model, the output of the likelihood ratio test,  $\chi^2$  and p-value, and the degrees of freedom (df). Two types of AIC are used as sample size was too small to subset both season and time of day, giving two subsets with non comparable AIC values (se = seasonal subset and dn = time of day subset). Bold text indicates the best fitting model and significant metrics. Models with multiple fixed variable were also tested however single variable models had better fit.

	$AIC_{se}$	$AIC_{dn}$	$R_m^2$	$R_c^2$	$\chi^2$	df	p
<i>All</i>							
RI ~ 1	-646.3	-1076.0	-	0.992	-	3	-
RI ~ Species	-345.8	-1075.7	0.038	0.992	1.422	4	0.233
RI ~ Sex	-644.9	-1074.4	0.018	0.992	0.605	4	0.437
<b>RI ~ Season</b>	<b>-730.7</b>	-	0.037	0.994	90.38	6	<b>&lt;0.001</b>
<b>RI ~ Time of Day</b>	-	<b>-1217.6</b>	0.006	0.999	143.6	4	<b>&lt;0.001</b>
<i>Carcharhinus obscurus</i>							
RI ~ 1	-404.8	-610.0	-	0.996	-	3	-
RI ~ Sex	-406.0	-608.3	<b>0.182</b>	0.996	2.155	4	0.142
<b>RI ~ Season</b>	<b>-461.8</b>	-	<b>0.222</b>	0.998	63.00	6	<b>&lt;0.001</b>
RI ~ Time of Day	-	<b>-740.5</b>	0.050	0.999	132.5	4	<b>&lt;0.001</b>
RI ~ Migratory Status	-403.7	-734.9	0.060	0.996	0.921	4	0.337
<i>Carcharhinus plumbeus</i>							
RI ~ 1	-299.1	-509.8	-	0.989	-	3	-
RI ~ Sex	-297.4	-507.9	0.015	0.989	0.288	4	0.592
<b>RI ~ Season</b>	<b>-349.0</b>	-	0.033	0.991	55.92	6	<b>&lt;0.001</b>
RI ~ Time of Day	-	<b>-589.1</b>	0.004	0.999	81.29	4	<b>&lt;0.001</b>

Table A4: GLMM outputs for daily detection models (RI), using a log normal distribution. All models used individual ID as a random effect and fixed effects are given in the first column. The null model is given by number of detections  $\sim 1$ , and was used as a comparison to calculate  $\chi^2$  and p-values for other models. Rows are divided into sections for both species (all,  $n = 100$ ), dusky sharks (*C. obscurus*,  $n = 30$ ) & sandbar sharks (*C. plumbeus*,  $n = 40$ ). Metrics of fit used are Akaike Information Criterion (AIC),  $R^2$  marginal giving the variance explained by fixed effects, and  $R^2$  conditional giving the variance explained by the whole model, the output of the likelihood ratio test,  $\chi^2$  and p-value, and the degrees of freedom (df). Two types of AIC are used as sample size was too small to subset both season and time of day, giving two subsets with non comparable AIC values (se = seasonal subset and dn = time of day subset). Bold text indicates the best fitting model and significant metrics. Models with multiple fixed variable were also tested however single variable models had better fit.

	$AIC_{se}$	$AIC_{dn}$	$R_m^2$	$R_c^2$	$\chi^2$	df	p
<i>All</i>							
Det $\sim 1$	101930	124948	-	0.221	-	3	-
Det $\sim$ Species	101932	124949	<0.001	0.220	0.180	4	0.671
Det $\sim$ Sex	101930	124947	<0.001	0.216	2.083	4	0.149
<b>Det <math>\sim</math>Season</b>	<b>101232</b>	-	<0.001	0.234	260.4	7	<0.001
Det $\sim$ Time of Day	-	124915	<0.001	0.155	34.72	4	< <b>0.001</b>
Det $\sim$ Depth Band	101477	124549	<0.001	0.233	463.4	8	< <b>0.001</b>
<i>Carcharhinus obscurus</i>							
Det $\sim 1$	7406.3	7895.9	-	0.140	-	3	-
Det $\sim$ Sex	7407.5	7897.1	<0.001	0.137	0.813	4	0.367
Det $\sim$ Season	7399.0	-	<0.001	0.152	13.30	6	0.004
Det $\sim$ Time of Day	-	7890.1	<0.001	0.120	7.861	4	0.005
Det $\sim$ Migratory Status	7408.0	7897.4	<0.001	0.139	0.276	4	0.600
<b>Det <math>\sim</math>Depth Band</b>	<b>7354.9</b>	7846.9	0.0012	0.136	59.35	7	< <b>0.001</b>
<i>Carcharhinus plumbeus</i>							
Det $\sim 1$	93174	116707	-	0.231	-	3	-
Det $\sim$ Sex	93174	116707	<0.001	0.224	1.365	4	0.243
<b>Det <math>\sim</math>Season</b>	<b>92927</b>	-	<0.001	0.244	252.6	6	< <b>0.001</b>
Det $\sim$ Time of Day	-	116678	<0.001	0.177	31.26	4	< <b>0.001</b>
<b>Det <math>\sim</math>Depth Band</b>	92733	<b>116303</b>	<0.001	0.235	450.8	8	< <b>0.001</b>