Imperial College London

Can migratory behaviour be predicted from individuals' localised movements, within a commercial fishery area?

Katherine Bickerton

Submitted: August 2019

A thesis submitted in partial fulfilment of the requirements for the degree of Master of Research at Imperial College London

Formatted in the journal style of the Marine Ecology Progress Series

Submitted for the MRes in Computational Methods in Ecology and Evolution

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.

Abstract

Introduction

Why do we need to understand movements?

Shark movements - what we know about shark movements so far

The use of acoustic arrays in shark monitoring - link to network analysis

What we know about sandbar and dusky sharks

This study will... Hypotheses

Methods & Materials

Data Collection

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

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

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

During the eight years of monitoring, 130 of the 207 sharks tagged were detected (Table 1), 68 *C. obscurus* and 62 *C. plumbeus*, across 183 of the 437 receivers, with a total of 196,507 detections. The majority of these detections, 191,448, occurred with the residential range of both populations, the Ningaloo reef. Within the Ningaloo reef, 118 sharks were detected across 57 receivers. For each

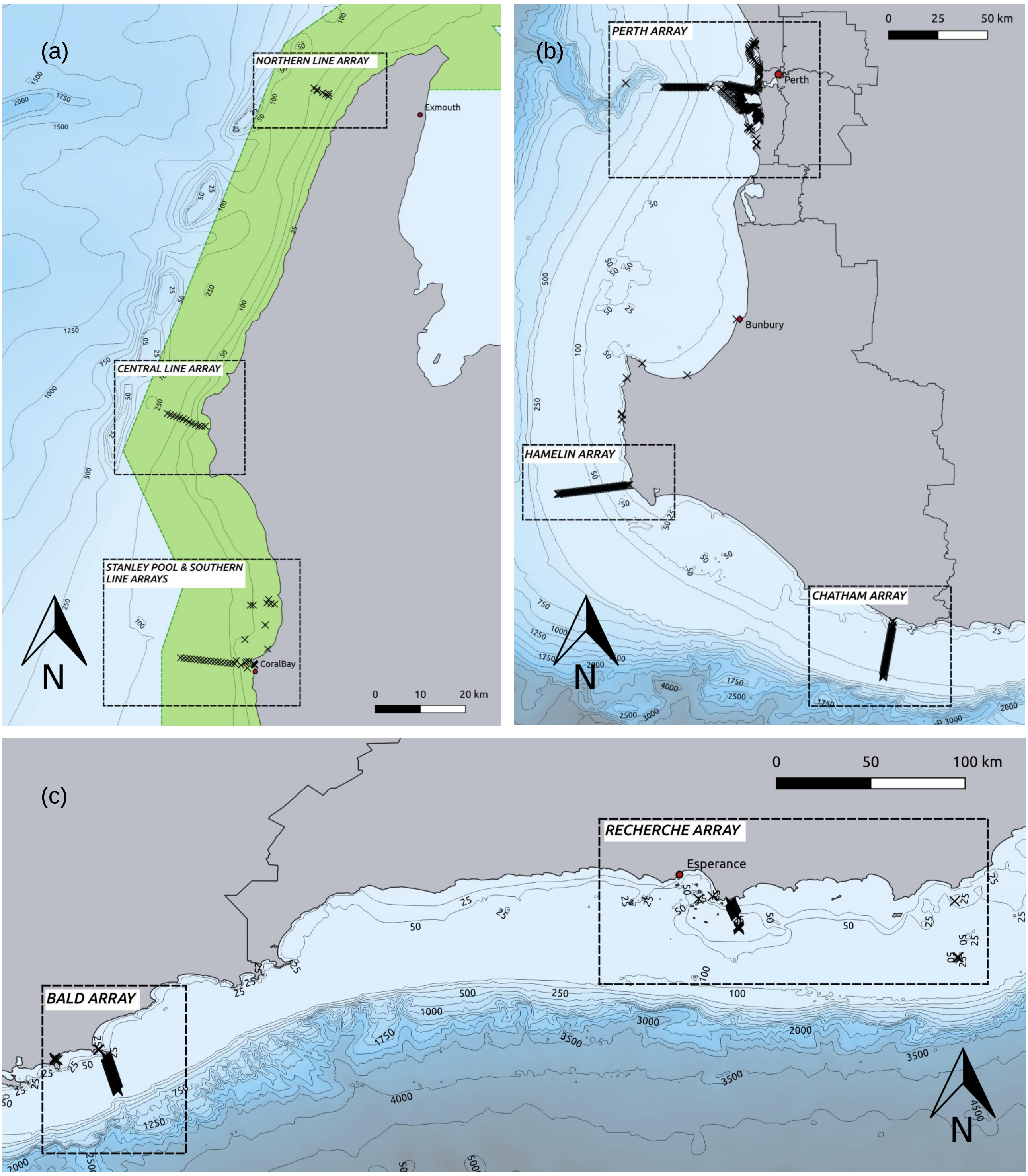

Figure 1: Distribution of acoustic receivers in Western Australia, each cross representing an individual receiver. (a) Northern receivers within the Ningaloo reef, total = 57, Northern Line array = 7, Central Line array = 13 and Stanley Pool and Southern Line arrays = 37. Green shading represents the 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).

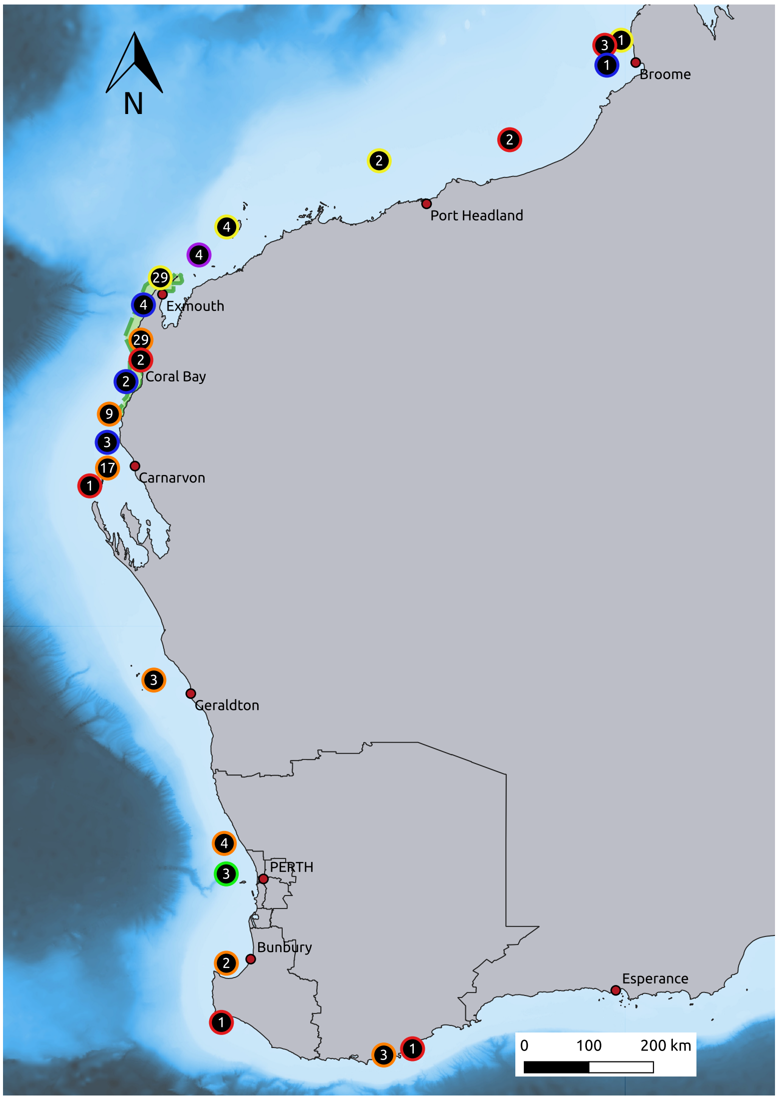

Figure 2: Locations of shark tagging of sharks detected between 2011 and 2018 (n = 130). The number within each circle gives the number of sharks tagged at that location and the coloured border gives the year of tagging (yellow = 2011, orange = 2012, red = 2013, purple = 2014, blue = 2015, green = 2017, no tagging occured 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).

detection, the location, time, date, depth and tag code were recorded. This dataset, along with the size and sex data for each individual, and the location and depth of each receiver, was used in the 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	Time Monitored
	M	F	U	Total	(m)	(days)
Carcharhinus obscurus	24	43	1	68	1.5 - 2.98	7 - 1987
Carcharhinus plumbeus	19	43	-	62	1.22 - 1.58	8 - 1976
Total	43	86	1	130	-	-

Data Analysis

All data manipulation, analysis and model building was carried out using R version 3.6.1 (R Core Team, 2019). The tidyverse package (Wickham, 2017) was used for all data manipulation and plots and the lubridate package (Grolemund & Wickham, 2011) for formatting temporal data. Analyses used detections from the Ningaloo reef arrays exclusively (defined as any detection north of 24S), as both species are show high residency to the reef (Braccini et al. 2017 (rensing, langois paper)). The analysis was split into four sections: spatial network analysis, home range estimation using centres of activity, residency patterns using a residency index, and detection patterns examining detections per day. A combination of analyses methods were used as although spatial networks can be used to explain a movement dynamics, more traditional approaches can also provide valuable insight (Baeyaert et al. 2018).

In each section of the analyses, linear mixed models were used to examine the relationship between the response variable (network density, kernel utilisation distribution, residency index and depth index respectively) and a range of fixed explanatory variables, using the lme4 R package (Bates et al. 2015). Linear mixed models were chosen so non-independent individual variation could be included as a random variable, and as data was linear but not normally distributed in all cases. Between and within species variation were both modelled. Model distribution was chosen by comparing the fit of quantile-quantile plots again normal, log normal, Poisson, negative binomial and gamma probability distributions, using the car (Fox & Weisberg, 2019) and MASS (Venables & Ripley, 2002) packages in

R. Test files were then generated, and each model tested, then outputs compared against the original data to check model fit, using the merTools package (Knowles & Frederick, 2019).

Fixed explanatory variables used were species, sex, season, time of day and migratory status. For 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, de Lestang & McAuley, 2017). 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, de Lestang & McAuley, 2017, 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 & Schielzeth, 2013). Each model was then checked using a traditional likelihood ratio test (anova) comparing each model with a null model.

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 & 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.

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.

Home Range

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

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

Residency Patterns

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

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

Detection Patterns

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

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

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 & Shielzeth, 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 & 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.

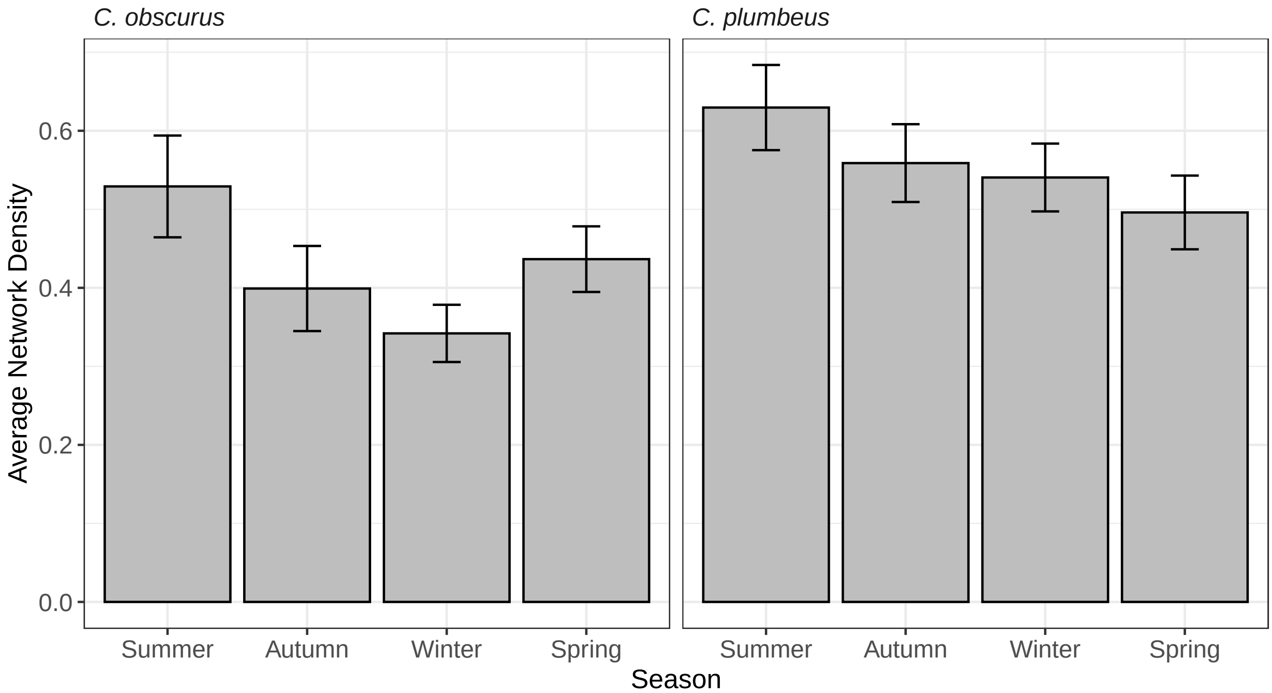

Figure 3: Seasonal variation in network density of *Carcharhinus obscurus* (n = 53) and *Carcharhinus plumbeus* (n = 58). Bars give mean average network density and error bars give standard error. Seasons are defined as standard Austral seasons.

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 & 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: χ^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.

RI varied more significantly by season within the *C. obscurus* subset, explaining 22.2% of deviance, and having the lowest AIC of -461.8. RI was lowest in the summer, then increased through autumn and winter, then decreased again in spring (Figure 4). Time of day also had a low value of AIC within it's subset (-740.5), with a slight increase in RI at night but only this accounted for 5% of deviance. Sex explained 18.2% of deviance in RI, with higher RI in females, but a high AIC value. RI did not vary with migratory status.

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

Detection Patterns

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

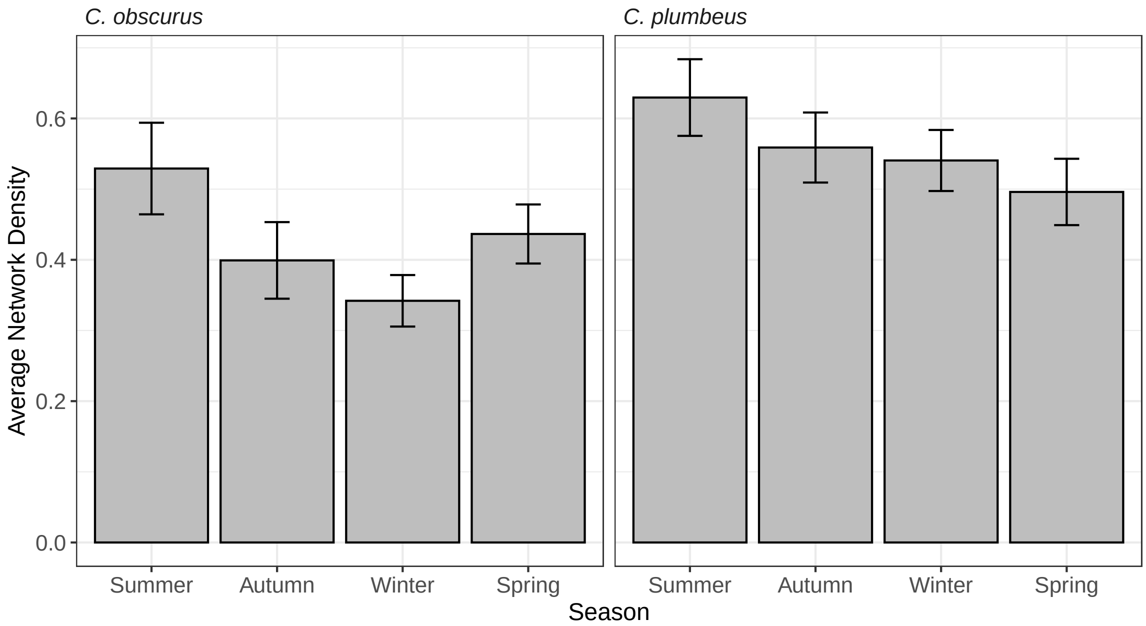

Figure 4: Seasonal variation in residency index of *Carcharhinus obscurus* (n = 51) and *Carcharhinus plumbeus* (n = 59). Bars give mean average residency index and error bars give standard error. Seasons are defined as standard Austral seasons.

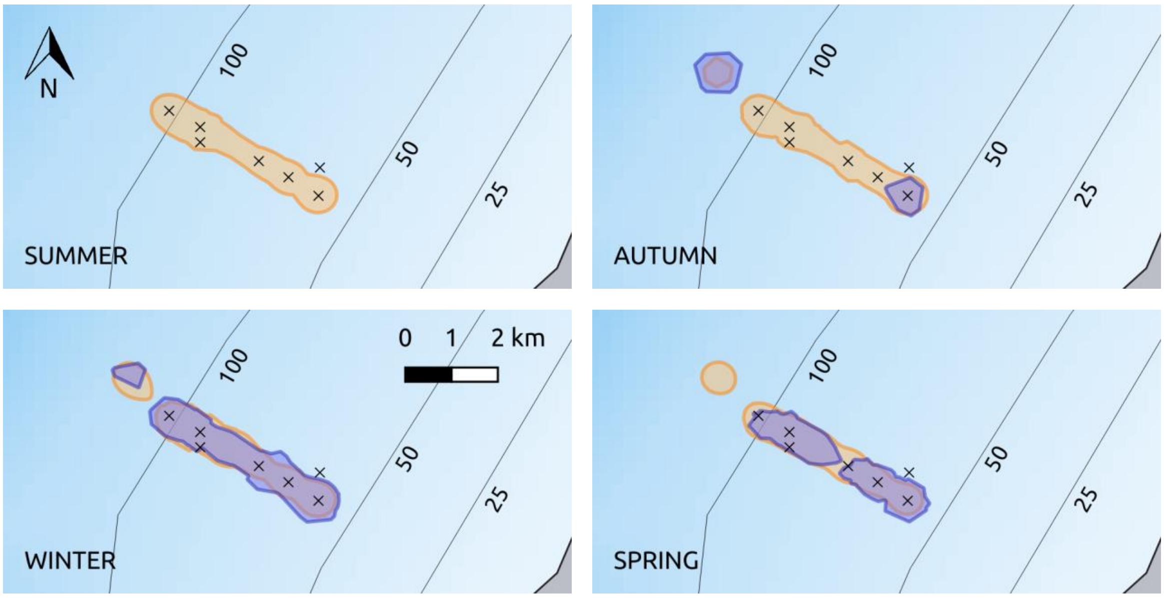

Figure 5: Seasonal variation in core kernel utilisation areas of *Carcharhinus obscurus* (purple) and *Carcharhinus plumbeus* (orange), within the northern line array, Ningaloo reef, WA. Black crosses show acoustic receiver locations and water depth is given parallel to each bathymetry contour This map 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).

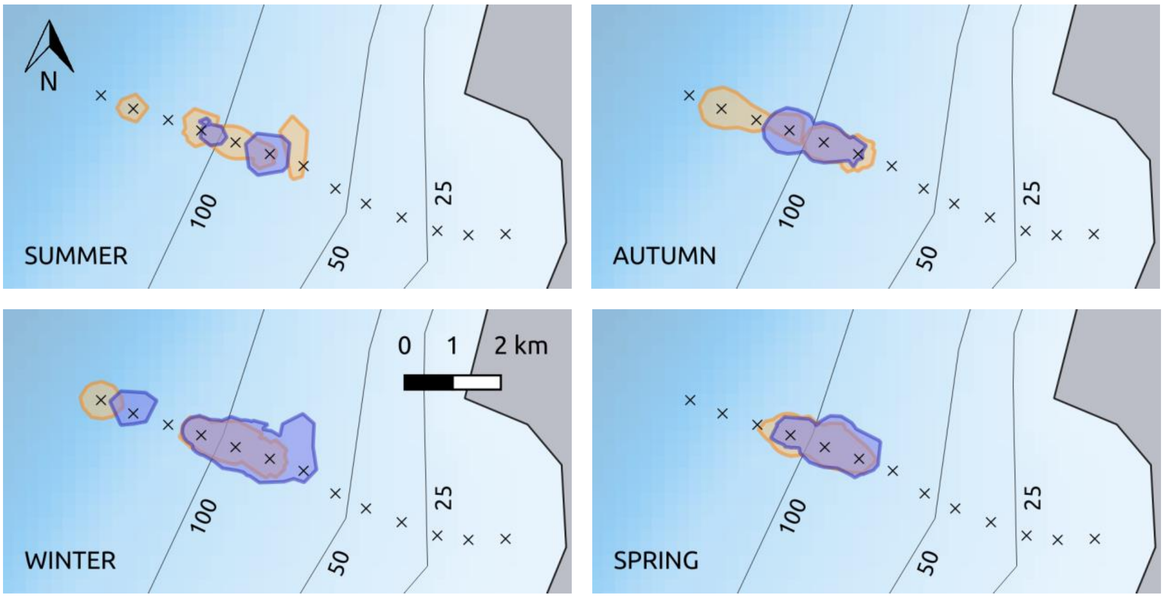

Figure 6: Seasonal variation in core kernel utilisation areas of *Carcharhinus obscurus* (purple) and *Carcharhinus plumbeus* (orange), within the central line array, Ningaloo reef, WA. Black crosses show acoustic receiver locations and water depth is given parallel to each bathymetry contour This map 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).

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

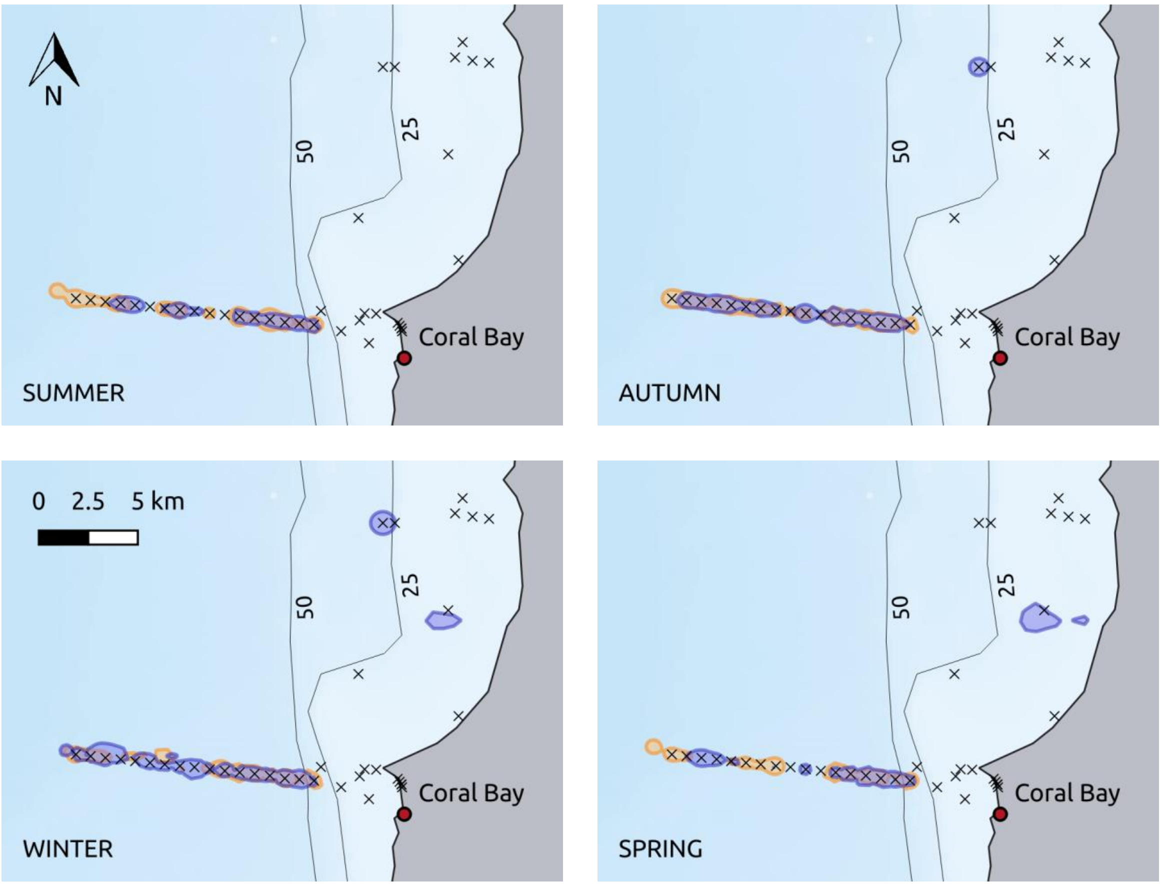

Figure 7: Seasonal variation in core kernel utilisation areas of *Carcharhinus obscurus* (purple) and *Carcharhinus plumbeus* (orange), within the Stanley Pool and southern line arrays, Ningaloo reef, WA. Black crosses show acoustic receiver locations and water depth is given parallel to each bathymetry 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

Restate hypotheses

Individual Variation

Network Use and Acoustic Arrays

Area and Depth Use

Seasonal variation Lack of sexual variation Link to ecology

Migration & Residency

Residency indices Seasonal variation Combine knowledge about dusky sharks with results

Predictions What can we tell about one species from knowledge of the other

Drawbacks of Acoustic Telemetry

Huge effects of individuals

Future directions for research

Conclusions

Acknowledgements

Data & Code Availability

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

References

Appendices

Model Outputs

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 χ^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, χ^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^2_m	R^2_c	χ^2	*df*	*p*
All						
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
Network Density $\sim$ Season	**65.09**	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
Carcharhinus obscurus						
Network Density $\sim$ 1	59.45	-	0.779	-	2	-
Network Density $\sim$ Sex	59.95	0.130	0.785	3.436	4	0.064
Network Density $\sim$ Season	**48.39**	**0.159**	0.850	20.28	6	$<$**0.001**
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
Carcharhinus plumbeus						
Network Density $\sim$ 1	7.460	-	0.709	-	3	-
Network Density $\sim$ Sex	9.420	0.012	0.712	0.334	4	0.563
Network Density $\sim$ Season	**5.115**	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 χ^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, χ^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}	χ^2	*df*	*p*
All					
KUD $\sim$1	345.0	288.3	-	3	-
KUD $\sim$Species	**334.9**	**285.8**	12.13	4	$<$**0.001**
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
Carcharhinus obscurus					
KUD $\sim$1	**178.2**	163.1	-	3	-
KUD $\sim$Sex	**178.2**	**162.2**	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
Carcharhinus plumbeus					
KUD $\sim$1	**153.4**	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
KUD $\sim$Time of Day	-	**123.6**	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 χ^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, χ^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^2_m	R^2_c	χ^2	*df*	*p*
All							
RI $\sim$ 1	-646.3	-1076.0	-	0.992	-	3	-
RI $\sim$ Species	-345.8	-1075.7	0.038	0.992	1.422	4	0.233
RI $\sim$ Sex	-644.9	-1074.4	0.018	0.992	0.605	4	0.437
RI $\sim$ Season	**-730.7**	-	0.037	0.994	90.38	6	$<$**0.001**
RI $\sim$ Time of Day	-	**-1217.6**	0.006	0.999	143.6	4	$<$**0.001**
Carcharhinus obscurus							
RI $\sim$ 1	-404.8	-610.0	-	0.996	-	3	-
RI $\sim$ Sex	-406.0	-608.3	**0.182**	0.996	2.155	4	0.142
RI $\sim$ Season	**-461.8**	-	**0.222**	0.998	63.00	6	$<$**0.001**
RI $\sim$ Time of Day	-	**-740.5**	0.050	0.999	132.5	4	$<$**0.001**
RI $\sim$ Migratory Status	-403.7	-734.9	0.060	0.996	0.921	4	0.337
Carcharhinus plumbeus							
RI $\sim$ 1	-299.1	-509.8	-	0.989	-	3	-
RI $\sim$ Sex	-297.4	-507.9	0.015	0.989	0.288	4	0.592
RI $\sim$ Season	**-349.0**	-	0.033	0.991	55.92	6	$<$**0.001**
RI $\sim$ Time of Day	-	**-589.1**	0.004	0.999	81.29	4	$<$**0.001**

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 χ^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, χ^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^2_m	R^2_c	χ^2	*df*	*p*
All							
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
Det $\sim$Season	**101232**	-	<0.001	0.234	260.4	7	<0.001
Det $\sim$Time of Day	-	124915	<0.001	0.155	34.72	4	<**0.001**
Det $\sim$Depth Band	101477	124549	<0.001	0.233	463.4	8	<**0.001**
Carcharhinus obscurus							
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
Det $\sim$Depth Band	**7354.9**	7846.9	0.0012	0.136	59.35	7	<**0.001**
Carcharhinus plumbeus							
Det $\sim$1	93174	116707	-	0.231	-	3	-
Det $\sim$Sex	93174	116707	<0.001	0.224	1.365	4	0.243
Det $\sim$Season	**92927**	-	<0.001	0.244	252.6	6	<**0.001**
Det $\sim$Time of Day	-	116678	<0.001	0.177	31.26	4	<**0.001**
Det $\sim$Depth Band	92733	**116303**	<0.001	0.235	450.8	8	<**0.001**