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ORIGINAL ARTICLE

Evidence for non-random co-occurrences in a white shark aggregation

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Abstract

Groups or aggregations of animals can result from individuals being attracted to a common resource or because of synchronised patterns of daily or seasonal activity. Although mostly solitary throughout its distribution, white sharks (*Carcharodon carcharias*) seasonally aggregate at a number of sites worldwide to feed on calorie-rich pinnipeds. At the Neptune Islands, South Australia, large numbers of white sharks can be sighted throughout the year, including during periods of low seal abundance. We use a combination of photo-identification and network analysis based on co-occurrence of individuals visiting the site on the same day to elucidate the population structure and aggregatory behaviour of Australia's largest aggregation of sub-adult and adult white sharks. We photo-identified 282 sharks (183 males, 97 females, 2 unknown) over a 4.5-year period (June 2010–November 2014) and found that white sharks did not randomly co-occur with their conspecifics, but formed four distinct communities. Tendency to co-occur varied across months with males co-occurring with more individuals than females. Sex-dependent patterns of visitation at the Neptune Islands and resulting intraspecific competition likely drive the observed community structure and temporal variability in co-occurrences. This study provides new insights into the aggregatory behaviour of white sharks at a seal colony and shows for the first time that white shark co-occurrence can be non-random.

Significance statement

White sharks are top marine predators that are typically solitary but can also form aggregations around seal colonies to feed. Using a combination of photo-identification and network analysis, we investigated the co-occurrence patterns of white sharks. We showed, for the first time, that white sharks form non-random associations with conspecifics. We hypothesise that the observed sex-dependant variations in co-occurrence are linked to intraspecific competition for resources, providing new insights into the aggregatory behaviour of white sharks at a seal colony. Our study adds to the growing literature of animals showing non-random interaction or co-occurrence patterns, providing important comparative knowledge for other researchers as it broadens our knowledge to marine top predators.

Keywords Social network analysis · Gregariousness · Social behaviour · Aggregation · Photo-ID · *Carcharodon carcharias*

Introduction

The formation of groups or aggregations has been documented in a wide range of terrestrial, freshwater, and marine taxa (Krause and Ruxton 2002). However, spatio-temporal co-occurrence of individuals does not necessarily result in social interactions. While individuals may actively prefer to associate with conspecifics (Couzin et al. 2005; Guttal and Couzin 2010) and form groups, animal aggregations form as a result of different individuals being attracted to a common resource such as food or critical habitat (Johnson et al. 2002), or because of synchronised patterns of daily or seasonal activity (Guttal and Couzin 2010). An important distinction must therefore be made between aggregations that do not involve

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social attraction (referred to as 'aggregation') and those that do (referred to as 'social groups'). In the case of aggregations, the spatio-temporal variation in the availability and distribution of resources (e.g. refuge or nest availability, prey availability, reproduction) strongly influences where and when individuals aggregate (Komdeur 1992).

Aggregation behaviour has been investigated in a range of marine species, including euphausiids (Northern krill, *Meganyctiphanes norvegica*) (Lavoie et al. 2000), copepods (calanoida nauplii, *Neocalanus plumchrus*) (Mackas and Louttit 1988), teleosts (pacific herring, *Clupea pallasi*) (Hay and McKinnell 2002), and in elasmobranchs (blacktip reef shark, *Carcharhinus melanopterus*; lemon shark, *Negaprion brevirostris*) (Guttridge et al. 2011; Jacoby et al. 2012; Mourier et al. 2012). The white shark (*Carcharodon carcharias*), although mostly solitary throughout its coastal temperate and subtropical distribution (Klimley and Ainley 1996; Domeier 2012), has also been reported to aggregate at a number of sites worldwide. These include Seal Island, Gansbaai, and Mossel Bay in South Africa (Kock et al. 2013), Guadalupe Island off Mexico (Domeier and Nasby-Lucas 2007), the Chatham Islands off New Zealand (Duffy et al. 2012), Cape Cod in Massachusetts, USA (Skomal et al. 2012), and the Neptune Islands in Australia (Robbins 2007). Most aggregation sites have been suggested to provide important feeding grounds for white sharks (Semmens et al. 2013) and aggregations have been shown to be driven by seasonal availability and abundance of prey species (Goldman and Anderson 1999; Robbins 2007; Weng et al. 2007). However, at the Neptune Islands, the timing of white shark aggregations is more complex. Up to 20 white sharks can be observed at the Neptune Islands in a day, but the number of white shark using this aggregation site and sex ratio is highly variable over time (Nazimi et al. 2018). While the abundance of white sharks at this site peaks in early winter, presumably to take advantage of inexperienced and more vulnerable weaned seal pups, white sharks can also be sighted throughout the year, including during periods of low seal abundance (Bruce and Bradford 2015; Nazimi et al. 2018). This suggests that factors other than the seasonal abundance of seal pups may affect the timing of white shark aggregations at the Neptune Islands. Aside from environmental factors such as food availability, benefits of co-occurrence could also contribute to visitation and residency pattern of white sharks at the Neptune Islands. In this study, we aim to understand the structure of this aggregation of white sharks and investigate whether sharks co-occur with certain other individuals more frequently than expected by chance. Understanding whether visitation is synchronised among individuals (i.e. whether they co-occur together at the Neptune Islands more frequently than expected if visitation was independent of each other) will shed light onto the drivers of this shark aggregation and provide deeper insight into the population dynamics beyond our current understanding of variations in sex-dependent abundance over time (Bruce and Bradford 2015).

Understanding the co-occurrences between aggregating individuals can often be a complex and difficult task (Croft et al. 2008), particularly for large and highly mobile species, such as white sharks (Marshall et al. 2011). The regular use of aggregation sites has, typically, been documented and studied for years and sometimes decades using photo-ID or acoustic telemetry (Nasby-Lucas and Domeier 2012; Kock et al. 2013). Most studies using these methods focused on shark residency, frequency of visits, and timing of occurrence, but did not provide a quantitative assessment of whether non-random co-occurrences or communities are formed by individuals (but see Mourier et al. 2012; Jacoby and Freeman 2016; Jacoby et al. 2016). Network analysis techniques provide a powerful tool to explore intraspecific co-occurrences, and the drivers of aggregation behaviour, due to its ability to up-scale individual behaviour to population structure (Krause et al. 2007). Network analysis has been widely used to quantify the underlying mechanisms influencing aggregation and social behaviour in groups of many taxa, including insects (Fewell 2003), lizards (Leu et al. 2016), ungulates (Cross et al. 2004), primates (Bezanson et al. 2008), teleosts (Croft et al. 2011), cetaceans (Lusseau et al. 2006), and sharks (Mourier et al. 2012; Wilson et al. 2015; Jacoby et al. 2016). To date, the only study which used network analysis on white sharks was undertaken in Mossel Bay, South Africa, where cage-diving and chumming occur and found no evidence for non-random co-occurrences among individuals (Findlay et al. 2016).

In the present study, we use network analysis to investigate whether the spatio-temporal dynamic of the white shark population visiting the Neptune Islands shows a non-random structure. Specifically, we (1) characterise the network of white sharks aggregating at the Neptune Islands and assess whether it differs from random, (2) identify frequent co-occurrence of individuals, (3) identify communities of individuals more likely to spatio-temporally co-occur, and (4) identify whether individuals aggregate with individuals of the same sex more often than suggested by chance. Improving our understanding of the aggregation behaviour in sharks and the dynamic nature of their co-occurrences may help elucidate the drivers underpinning co-occurrences between individuals and the trade-off influencing the establishment of an aggregation.

Methods

Study site

This study was conducted within the Neptune Island Group (Ron and Valerie Taylor) Marine Park, South Australia (35° 17.5′ S; 136° 05.4′ E). The Neptune Islands are a series of granite formations about 25–30 km from the South

Australian mainland (Fig. 1). This island group consists of two pairs of islets, North Neptune and South Neptune Islands, separated by about 12 km. The study site is a well-recognised year-round aggregation site for white sharks, with shark cage-diving operators (SCDO) frequently taking tourists to the Neptune Islands since the late 1970s (Bruce and Bradford 2013; Huveneers et al. 2013; Huveneers et al. 2017). As part of standard cage-diving operations, sharks were attracted to the boat using a near-constant odour corridor of berley (or chum), minced southern bluefin tuna (*Thunnus maccoyii*), and a tethered bait. The increased residency resulting from this industry (Bruce and Bradford 2013) might be facilitated or enhanced co-occurrences. The potential effects of the study being undertaken at a cage-diving site are described in the 'Discussion'. Shark identification was not undertaken by the person taking photographs to avoid potential biases and ensure that a blinded method was used.

Data collection

Photographs were taken during standard cage-diving operations by a single person with 20 years of expertise in cage-diving and white shark photography. Photographs were taken on 316 days between June 2010–December 2011 and July 2013–November 2014. Although the cage-diving industry operates all year round, the number of trips per month varies depending on weather and shark abundance, resulting in the number of days during which photographs were taken ranging 1–18 days month^{-1} (mean ± standard error 9.6 ± 0.79; Fig. S1). Photographs between January 2012 and June 2013 were not deemed reliable due to staff absences affecting the amount of effort spent taking photographs, hence reducing the likelihood that all sharks sighted were photographed. On each day of operation, photographs of white sharks were taken, with the aim to catalogue all sharks sighted on the day with the number of photographs taken per day ranging from < 10 to > 2000. A total of 272,583 photographs were obtained and processed (mean = 863 day^{-1}) (for more information about photographs collected, see Nazimi et al. (2018)).

Individual white sharks were identified using five areas: caudal fin, pelvic fins, first dorsal fin (hereafter dorsal fin), gills, and pectoral fins. Established white shark identification methods were used (Domeier and Nasby-Lucas 2007; Anderson et al. 2011), where a combination of pigmentation patterns (countershading, rosettes, islets, freckles, spots), notches or scoops, amputations, scoliosis, and scarring are used to identify individuals based on their unique variation in these physical characteristics. Photo-identification was undertaken by two of the study's authors using cross-validation to ensure accuracy. While some natural pigmentation pattern may change in a small number of individuals (Domeier and Nasby-Lucas 2007; Robbins and Fox 2013), the ability to use multiple areas to identify and resight individuals reduces the likelihood of misidentification. Photo-identification of white sharks using the same method as this study has been extensively used (Domeier and Nasby-Lucas 2007; Gubili et al. 2009; Towner et al. 2013), and the suitability of this method for long-term identification has been demonstrated in white sharks for a period of up to 22 years (Anderson et al. 2011). Side by side comparison of fin silhouettes (dorsal, caudal, or pectoral), ventral pigmentation patterns on the tip of pectoral fins, and image series or videos of sharks turning and showing both sides were used to link left- and right-hand sides to individual sharks. Sex was determined based on clasper presence. The size of sharks was not recorded by the cage-diving operators or photographer and could not be reliably estimated from photographs due to image distortion from wide-angle lenses. Previous studies show that total length of white sharks frequenting the Neptune Islands is mostly ~ 3–4.5 m, representing sub-adults and adults (Bruce and Bradford 2015).

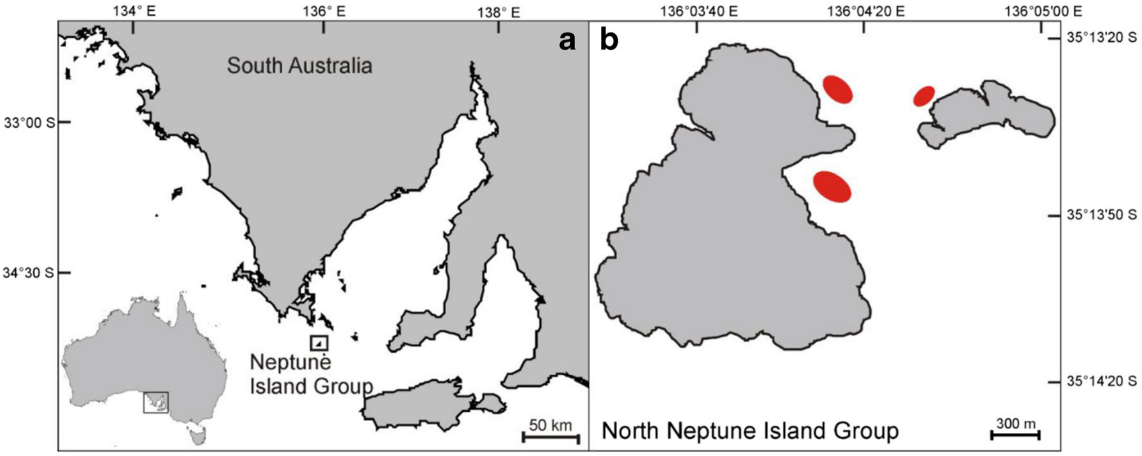

Fig. 1 Approximate location of the Neptune Islands Group Marine Park and areas where cage-diving operators typically anchor at the North Neptune Islands Group (red ellipses) as a function of prevailing wind and swell directions. Size of the ellipses varies between locations because of differences in the level of exposure and habitat suitable for anchors across these locations

Data analysis

Co-occurrence definition and network construction

In the context of this study, we defined co-occurrences as spatio-temporal co-occurrence of individuals and recognise that it does not represent social interactions. This was due to time of sighting not being recorded by cage-diving operators or the photographer, hindering the ability to determine when sharks were in proximity of each other or sighted simultaneously. We defined all sharks sighted at the same diving location on the same day (typically from ~ 9.00 a.m. to ~ 5.00 p.m.) as co-occurring (Franks et al. 2010). White sharks are not permanent residents at the Neptune Islands. Some individuals showed extended residency (temporary residents), while others are only sighted on a small number of occasions (transients) (Nazimi et al. 2018). Rarely sighted individuals within a network have a poor likelihood of having their true behaviour accurately characterised, and further have the potential to obscure the real co-occurrence structure (Farine and Whitehead 2015). In addition, they can also represent transient individuals (Nazimi et al. 2018) that are not representative of the potential co-occurrence structure. As a result, individuals sighted on less than five occasions across the entire study period were removed from the dataset and excluded from the analysis, following Mourier et al. (2012). We accounted for short-term residency by randomising our co-occurrence data within a 1-week sampling period, as it is the mean residency of white sharks at the Neptune Islands based on acoustic telemetry data (Rogers and Huveneers 2016; Huveneers and Lloyd 2017). If two individuals (also referred to as nodes) were seen on the same day, at least once during a sampling week, we connected them with an edge, representing the relationship between nodes (i.e. co-occurrence).

We summarised these weekly binary co-occurrence networks into a weighted network reflecting co-occurrence strength between individuals across the entire study period (June 2010–December 2011 and July 2013–November 2014). We used the half-weight co-occurrence index (HWI) to estimate co-occurrence strength among pairs of individuals, referred to as dyads. The HWI ($\mathrm{HWI}_{\mathrm{ab}} = \frac{x}{\{0.5\ (n_a+n_b)\}}$) is a measure of the proportion of time two individuals spent together in relation to the time spend apart (Cairns and Schwager 1987), where x represents the number of sampling periods when sharks a and b were co-occurring, n_a is the total number of sampling periods that shark a was observed, and n_b is the total number of sampling periods shark b was observed. A HWI can range in value from 0 to 1 (Bejder et al. 1998), where a dyad is never sighted together (0), or always sighted together (1). This index was selected because it reduces biases associated with observation heterogeneity among individuals (Cairns and Schwager 1987; Whitehead 2008). HWI was calculated with the package *asnipe* (Farine 2013) in the R environment (R Core Team 2017).

Randomisation procedures

An important part of quantifying a population's co-occurrence structure is to establish whether this structure differs from random, that is differs from the structure if individuals co-occur with each other randomly. To do so, we compared our empirical network to networks derived from a randomisation process. Comparing our empirical networks with these randomised networks allowed us to identify dyads that showed frequent co-occurrence across our weekly sampling periods. This method uses a data stream permutation procedure and, based on the stack of individual by individual matrix for each sampling week, swaps individuals between associations within sampling weeks, and then recalculates the weighted summary network after each swap (Farine 2017). Randomisations were undertaken within each weekly period and test statistics calculated between sampling periods to test for long-term associations. This permutation procedure controls for the number of observations and group size. Permutations were increased incrementally using steps of 5000, until the p values stabilised, which was at 10,000 permutations. This randomisation method allows to identify the presence of preferred relationships, which occurs if the standard deviation of association strengths is higher in the observed network than in a network where individuals associate with others at random (and thus more equally). The observed mean (or SD) was considered significantly higher than expected if it fell outside of the 95% range of the random mean (or SD) distribution (Farine and Whitehead 2015).

Community structure

We used an eigenvector-based modularity method (i.e. the *leading.eigenvector.community* function implemented in R package *igraph*; Csárdi and Nepusz 2006) to determine if the population was divided into different communities (clusters) (Newman 2006), and whether we could identify groups of individuals that were more densely connected in the network by calculating the leading non-negative eigenvector of the modularity matrix of the graph. We calculated modularity using the difference between the proportion of total co-occurrences within clusters and their expected proportion given the sum of co-occurrences of inter-cluster individuals. Modularity (Q) values exceeding ~ 0.3 have been suggested as a useful threshold to identify different communities (Newman 2004).

Network statistics

We investigated the co-occurrence patterns in white sharks over time, and the difference between sexes using a generalised linear model (GLM) with post hoc analysis. Because network data cannot be analysed through classical statistics due to the non-independence of the data (Farine and Whitehead 2015), we used

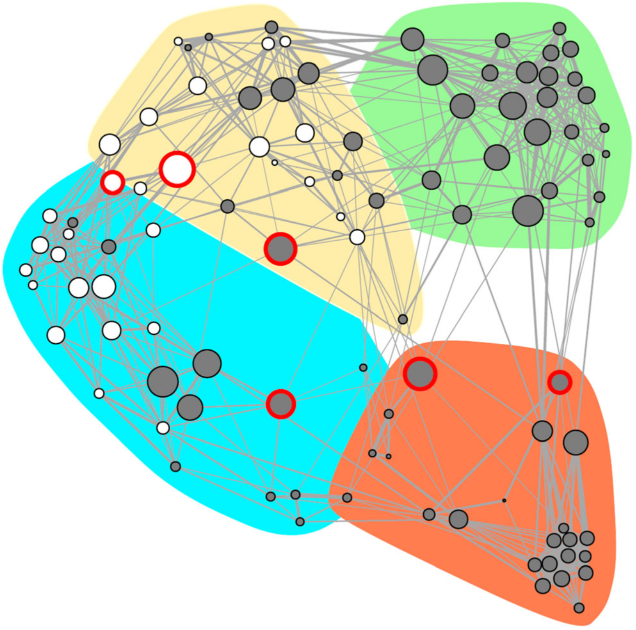

Fig. 2 Sociogram depicting the network of all co-occurring white sharks (*Carcharodon carcharias*). Nodes are individual sharks, grey circles represent males, white circles represent females, size of circles represents the number of times individuals were sighted. The relative position of individuals indicates their associative proximity. Colours encompassing multiple nodes represent communities: community 1 in yellow, community 2 in orange, community 3 in green, and community 4 in blue. Six sharks that repeatedly use the Neptune Islands at different times of the year and across periods are highlighted by a red circle. Note that only edges with a half-weight co-occurrence index over 0.1 are represented to improve clarity. The Force Atlas 2 algorithm with *igraph* R package was used to draw the network

randomisation procedures in our analysis. Due to cage-diving operations varying over time (Huveneers and Lloyd 2017), some months include data from 4 years (July–November), while others had data from 2 years. The randomisation process accounted for the discrepancy in sampling effort. Similar to above, we generated a weighted co-occurrence network, separately for each month. We then calculated for each individual and each month the centrality statistics binary degree (degree) and weighted degree (strength). The binary *degree* is the number of edges connected to the node, i.e. the number of individuals that the focal individual co-occurred with. The *strength* is the weighted equivalent of binary degree and is the sum of all edge weights (i.e. co-occurrence indices) connected to the node. Strength reflects the relative interaction frequency with other individuals (scaled to the observation frequency). We constructed a GLM with sex and month as fixed factor to investigate the influence of sex on *degree* and *strength* across months. The residuals of binary degree analysis using the empirical data conformed to a normal distribution but is a discrete variable, so we used a Poisson distribution for modelling. However, a Gaussian distribution was fitted for strength as the residuals were normally distributed. We then extracted the coefficient of the slope from the data of these observed networks. Observed networks were then randomised to generate 10,000 random networks by using the 'pre-network data permutation' procedure (Farine 2017) as described above. Then, *degree* and *strength* were re-calculated for each random network. The coefficients of the same models were extracted from the 10,000 random networks and their distribution was compared with the coefficient value of the observed networks to identify whether any difference was significant. The necessary number of randomisations was based on stabilisation of the coefficient values. Results were significant if the empirical coefficient fell outside the 95% interval of the distribution of coefficients of the randomised networks.

Finally, we calculated assortativity coefficients to test for preferred co-occurrences within or between sexes (males, females, male-females) (Farine 2014). Assortment in a network describes the tendency of individuals to be connected to any other individuals that share some characteristics. The assortativity coefficient range from − 1 to 1 and is positive if nodes of similar phenotypes are more often connected than expected, whereas negative assortment suggests avoidance of alike nodes. Finally, we calculated the significance of sex-based assortativity using 25,000 network randomisations of the observed network. Assortativity was calculated using R package *assortnet* (Farine 2014). The number of randomisations performed was determined by stabilisation of the p_{rand} value.

Results

A total of 282 sharks (183 males, 97 females, 2 unknown) were identified across the two periods. Of those, 181 were sighted less than five times and removed from the analysis, resulting in 101 individuals (70 males, 31 females) included in the network analysis (median sightings = 7; range = 5–24; mean ± standard error = 9.5 ± 0.5 days). Mean (0.028) and standard deviation (0.079) of the co-occurrence indices (HWI) were higher than expected by chance (random networks 0.025 ± 0.0004, $p < 0.001$ for both), suggesting some long-term preferred co-occurrences between individual white sharks. Twelve individuals (11.9% of the 101 sharks included in the analysis) formed six dyads that co-occurred more than expected by chance, all of which were between same-sex individuals (4 male dyads; 2 female dyads). Our analysis of network modularity showed that the network was divided into four main communities including two mixed-sex communities and two male-only communities, and that none of the sharks included in the analysis were isolated in the network (Qmax = 0.54; Fig. 2).

The population demographic structure changed over time, with more females than males present between April and July, and more males than females present between August and March (Fig. 3). Females were present in low number from October to November and mostly absent from December to

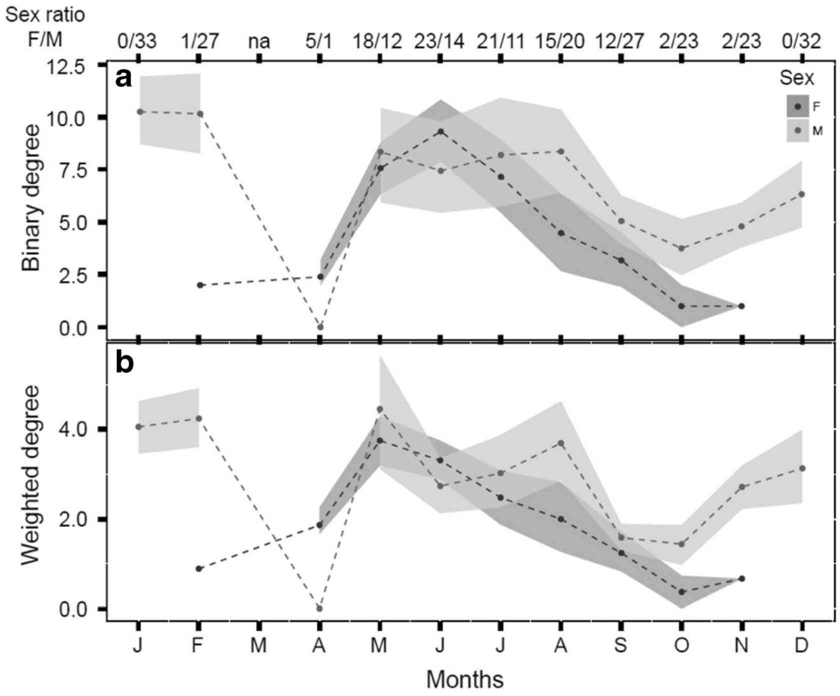

Fig. 3 Seasonal differences in **a** degree and **b** strength between the sexes. Number of occurrences for females and males (F:M) is indicated for each month on top. The mean value and 95% confidence intervals are represented, with females in dark grey and males in light grey. Note that no data was recorded in March. NA indicates that no data was collected that month, which was due to the cage-diving operator undertaking survey and maintenance

March (Fig. 3, S1). Overall strength and degree were 2.8 ± 0.12 and 17.8 ± 0.8 respectively. In June and September, degree differed from the baseline month (May) more strongly than when co-occurrences were random (Table 1). Post hoc analyses showed that female degree and strength in June is higher than the other months, while male strength was variable between May and September (Table 2). Degree and strength were also significantly different between males and females in August (Table 2). We did not test for sex differences in degree and strength during October–April because females were either absent or present in very low numbers during these months.

Overall, assortment was significant for females ($r = 0.155$; random networks 0.147 ± 0.004; $p = 0.016$) but not for males, despite positive assortment ($r = 0.657$; random networks 0.657 ± 0.004; $p = 0.947$) or for the opposite sex combination ($r = 0.093$; random networks 0.098 ± 0.003; $p = 0.446$).

Table 1 Estimated generalised linear model (GLM) coefficients for the observed network and mean coefficient and standard deviation (SD) of the 10,000 random networks. p_{rand} value represents the probability of the observed network being different than the random network. p_{rand} values for each effect were calculated by comparing the coefficient from the model based on the observed data to the distribution of coefficients from the same model based on the randomised data. We considered effects to be significant if the coefficient values fell outside the 95% range of the random coefficient distribution. Bold values show significant results (p_{rand} value < 0.05). Baseline levels are female and May

	Binary degree (degree)				Weighted degree (strength)			
	Observed	Random	SD	p_{rand} value	Observed	Random	SD	p_{rand} value
(Intercept)	2.02	2.38	0.06	1.00	3.76	4.15	0.21	0.98
Male	0.10	0.03	0.10	0.37	0.70	0.09	0.47	0.16
June	0.21	− 0.02	0.07	**< 0.01**	− 0.44	− 1.02	0.03	1.00
July	− 0.06	− 0.10	0.07	0.76	− 1.27	− 1.33	0.29	0.63
August	− 0.53	− 0.52	0.11	0.50	− 1.76	− 1.97	0.37	0.74
September	− 0.87	− 1.09	0.11	**< 0.05**	− 2.52	− 2.84	0.25	0.89
Male × June	− 0.32	− 0.17	0.13	0.92	− 1.27	− 0.34	0.53	**0.04**
Male × July	0.04	− 0.08	0.12	0.18	− 0.15	− 0.24	0.53	0.55
Male × August	0.53	0.22	0.18	**0.04**	1.00	0.40	0.69	0.23
Male × September	0.37	0.37	0.16	0.58	− 0.36	0.15	0.50	0.14

The two alternative GLM formulas were degree~sex × period and strength~sex × period, for degree and strength respectively

Table 2 Post hoc results from the generalised linear model (GLM). p_{rand} value represents the probability of the observed network being different than the random network. p_{rand} values were calculated by comparing the coefficient from the model based on the observed data to the distribution of coefficients from the same model based on the randomised data. We considered effects to be significant if the coefficient values fell outside the 95% range of the random coefficient distribution. Bold values show significant results (p_{rand} value < 0.05)

Contrast	Binary degree (degree)	Weighted degree (strength)
F, May − M, May	0.357	0.168
F, May − F, Jun	**0.001**	0.995
F, May − M, Jun	0.995	0.846
F, May − F, Jul	0.659	0.564
F, May − M, Jul	0.747	0.968
F, May − F, Aug	0.223	0.555
F, May − M, Aug	0.996	1.000
F, May − F, Sep	1.000	0.933
F, May − M, Sep	1.000	0.987
M, May − F, Jun	0.270	0.479
M, May − M, Jun	0.828	0.184
M, May − F, Jul	0.292	**0.037**
M, May − M, Jul	0.986	0.595
M, May − F, Aug	0.104	**0.045**
M, May − M, Aug	1.000	0.992
M, May − F, Sep	0.890	0.220
M, May − M, Sep	0.997	0.269
F, Jun − M, Jun	0.135	0.089
F, Jun − F, Jul	**0.003**	**0.001**
F, Jun − M, Jul	0.378	0.585
F, Jun − F, Aug	**0.006**	**0.035**
F, Jun − M, Aug	1.000	0.577
F, Jun − F, Sep	0.365	**0.045**
F, Jun − M, Sep	0.853	**0.034**
M, Jun − F, Jul	0.764	0.317
M, Jun − M, Jul	0.356	0.401
M, Jun − F, Aug	0.059	0.267
M, Jun − M, Aug	0.496	**0.004**
M, Jun − F, Sep	0.697	0.595
M, Jun − M, Sep	0.963	0.735
F, Jul − M, Jul	0.164	0.083
F, Jul − F, Aug	0.134	0.483
F, Jul − M, Aug	0.787	**< 0.001**
F, Jul − F, Sep	0.967	0.940
F, Jul − M, Sep	0.998	0.989
M, Jul − F, Aug	**0.013**	**0.037**
M, Jul − M, Aug	0.963	**0.030**
M, Jul − F, Sep	0.434	0.080
M, Jul − M, Sep	0.862	0.089
F, Aug − M, Aug	**< 0.001**	**0.001**
F, Aug − F, Sep	0.985	0.794
F, Aug − M, Sep	0.871	0.878
M, Aug − F, Sep	**0.039**	**0.005**
M, Aug − M, Sep	0.102	**0.001**
F, Sep − M, Sep	0.205	0.297

Discussion

Our study uses network analysis to go beyond presence/absence information generally collected through photo-ID or acoustic telemetry. Importantly, with this approach we are able to compare the empirically measured co-occurrence of shark individuals to expected co-occurrence patterns if visitation of the Neptune Islands was not synchronised, i.e. random, providing insight into possible mechanisms driving co-occurrence. First, we reveal that some individuals preferably co-occur and form co-occurrence communities, showing that some white sharks are more likely to use the site simultaneously than expected by chance. This contrasts the only previous study investigating white shark co-occurrences using network analysis in Mossel Bay, South Africa, which reported random associations among individuals (Findlay et al. 2016). The discrepancy between the two studies might be related to shark size or sex differences between the two aggregations. In Mossel Bay, 74% of the sharks included in the analysis were juvenile females (1.75–3 m total length), while white sharks frequenting the Neptune Islands are mostly ~ 3–4.5 m, representing sub-adults and adults (Bruce and Bradford 2015). Differences in the definition of co-occurrence (sighted on the same day in the present study vs. sighted within 2 h in the Mossel Bay study) might have also contributed to the divergence of results.

Direct interactions between white sharks have previously been described near whale or seal carcasses (Compagno 2001; Klimley et al. 2001), in the presence of feeding baits (Sperone et al. 2010), and during their movements around islands (Goldman and Anderson 1999; Klimley et al. 2001). These interactions were related to agonistic display (Martin 2007) or social interactions (Sperone et al. 2010) and often linked to interactions occurring when competing for food (Sperone et al. 2012). In most of these studies, social structure could not be established because interacting individuals were not identified, or consistency of behaviour was not investigated. In contrast, while our study cannot describe direct interactions, we show that there might be some repeated co-occurrences between individuals, which is a pre-requisite for the emergence of social behaviour.

Beyond the non-random population structure, we identified four co-occurrence communities which differed in their sex composition. The four communities correspond to sharks co-occurring at the Neptune Islands during different seasons and periods. The mixed-sex communities (communities 1 and 4) are composed of females and males mostly seen during the Austral autumn–winter (April–September) of either 2010/2011 or 2013/2014, with some individuals of each community sighted during both periods. These individuals did not have obvious common traits or attributes that would differentiate them from sharks observed in one period only (e.g. large adults, small juveniles, underweight, pregnant). The other two communities are composed of males, mostly observed during one period only, community 2 was observed during spring–summer 2010–2011 (October–February), and community 3 during spring–summer 2013–2014 (November–February). The inability to reliably collect photographs from January 2012 to June 2013 hindered the likelihood of having individuals within communities sighted across multiple years. Four individuals were, however, sighted in all 4 years (2010, 2011, 2013, and 2014), with another 11 white sharks sighted in at least 2010 and 2014 showing repeated use of the Neptune Islands, similarly to other white shark aggregations (Anderson et al. 2011; Nasby-Lucas and Domeier 2012; Hewitt et al. 2018). What is unique about this network study is that it provides insight into the connectedness of an open population across time that allows emigration and immigration into the study area.

Six individuals that repeatedly use the Neptune Islands, and do so at different times of a year when the demographic composition of the population differs (highlighted in Fig. 2), establish the important links between the identified communities. These individuals were typically sighted more frequently (mean number of days sighted 16.5 vs. 4.71) and had higher degree values (mean 30.8 vs. 17.8) than other sharks. These sharks link the communities to a connected population network, contributing to the non-random structure of the white shark population visiting the Neptune Islands. Individuals that connect communities play an important role in population processes such as transmission. Transmission processes can be both beneficial such as information transmission, but also costly, for instance the transmission of pathogens and diseases (Godfrey et al. 2009; Leu and Godfrey 2018). The effectiveness of transmission processes can be largely dependent on network structure (Sah et al. 2017), where a few centrally placed individuals have the potential to widely disseminate information or other processes throughout a population. In a Great Tit (*Parus major*) population, the introduction of a novel foraging technique to two individuals resulted in its transmission to 75% of the population, including across successive generations (Aplin et al. 2015). White sharks are known to employ different predation behaviours, e.g. breaching (Martin et al. 2005), sun-tracking predation strategy (Huveneers et al. 2015), which might be transmitted between individuals through co-occurrences. The central positioning of six individuals in our network, including their recurrent sightings, highlight the ease with which transmission processes could occur within the sharks visiting the Neptune Islands.

Co-occurrence strength and degree varied throughout the year and was highest in June and progressively decreased through to September. Observed population size was generally very low in April, which could explain the relatively low measures of network connectedness (degree, strength). Then, from April to July, females were more abundant than males. Following female arrival in May and June, female network connectedness (degree and strength) steadily declined over time, whereas, male connectedness appears to be more variable over time. Interestingly, male and female connectedness (strength) differed in the month that follows the arrival (June, prand=0.089) and departure of females (August, prand=0.001), illustrated by the female:male sex ratio. Following the arrival of females at the Neptune Islands, males show lower connectedness than females. Conversely, when females start decreasing in number in August, male connectedness was higher than female connectedness. However, care should be taken when interpreting these findings because of the small number of males or females during some months hindering the ability to assess changes of connectedness throughout the whole year. One possible explanation for the observed connectedness patterns could be that the female arrival disrupts co-occurrence behaviour of males resulting in reduced connectedness. This might also explain why females were generally more likely to co-occur with other females than with males. In contrast, while males appeared to show preferences to co-occur with males as shown by a high assortment coefficient, this was not higher than under random structure of the populations. At the Neptune Islands, female peak abundance coincides with weaned long-nosed fur seals starting to venture further away from the safety of shallow rock pools (Baylis et al. 2005; Goldsworthy 2006; Bruce and Bradford 2015), indicating that females time their visit to the Neptune Islands when abundance of vulnerable pinnipeds is highest in autumn–winter. At this time, females might outcompete males that are usually smaller (4–5 vs. 3–4 m total length; CH unpublished data). Similarly, grey reef sharks (*Carcharhinus amblyrhynchos*) disperse more widely as a result of interference competition (Papastamatiou et al. 2018), which would also reduce the likelihood of co-occurrence. When female abundance is low in October–November, competition from females is diminished and males reduce their ranging areas, resulting in increased male co-occurrence frequencies, whereas co-occurrences of females continued to decrease. Consequently, we found a significant difference in network connectedness between sexes in August, the time females start leaving the area. This possible explanation of how male and female space use around the Neptune Islands affects co-occurrence patterns is speculative at this point and could be an area for further research. The effect of female arrival and departure could be heightened by dominance effects, as females are larger than males and have been suggested to be dominant in mixed-sex aggregations. However, one study has shown that dominance hierarchies in sharks are not necessarily linked to size (Brena et al. 2018), and future studies should aim to investigate the effect of dominance or size on network connectedness or individual centrality. While further studies are needed to investigate this in depth, our findings are supported by sex-dependent seasonal changes in white shark abundance at the Neptune Islands that found females mostly occur in late autumn and winter while males occur in most months of the year but peak in summer (Bruce and Bradford 2015; Nazimi et al. 2018). Such patterns of abundance are rare as other aggregation sites around seal colonies are often seasonal, e.g. Seal Island, False Bay in South Africa, Guadalupe Islands in Mexico, and Stewart Island in New Zealand. Although white sharks can be seen at these locations at other times of the year, sightings are generally near the coast rather than at the aggregation site (Kock et al. 2013). For example, male and female white sharks are mostly seen around the seal colony in False Bay in autumn and winter. In summer, females frequent inshore areas instead while males are seldom detected. This is typical of other aggregation sites (Ryklief et al. 2014). The switch of preferred habitat in False Bay is linked to shift in prey abundance and availability (Kock et al. 2013). The Neptune Islands must, however, also hold sufficient white shark prey throughout the year to support males being present throughout most of the year.

The observed co-occurrences might also be driven by other factors not measured in this study, e.g. personalities, familiarity, genetic relatedness. For example, studies have found evidence for personalities in sharks (see Finger et al. 2017 for a review) that may also influence shark behaviours in a social (e.g. Jacoby et al. 2014) and baited context (Brena et al. 2018). While co-occurrence with familiars has been documented across many vertebrate classes, it has only recently been experimentally shown in chondrichthyans (Keller et al. 2017). Similarly, the occurrence of kinship-based affiliations is commonly recorded in group-living and fission-fusion species (e.g. delphinids; Möller et al. 2006); other species with less frequent interactions may also prefer to co-occur with kin. In the case of white sharks, similar personalities, familiars, or closely related individuals might be more likely to visit the Neptune Islands at concurrent periods and form dyads or communities. Behavioural assays and a genetic study of the individuals forming the dyads and communities identified in the present study would enable to test whether personality or kinship influences white shark non-random co-occurrence.

We acknowledge that our study has some limitations related to the way in which data was collected (during regular white shark cage-diving tours): (1) photos were unavailable in 2012 and half of 2013, which led to a period with no data and reduced our ability to detect sharks across multiple years; (2) the presence of sharks was only recorded on a daily basis instead of a finer temporal scale (e.g. every hour), and were, therefore, not necessarily sighted simultaneously; and (3) the behaviour of some white sharks might have been affected by repeated cage-diving events. For example, the response to the scent and bait used by cage-diving vessels might decrease through time due to habituation (Laroche et al. 2007), resulting in the probability of recording some individuals to vary through time. The use of bait can also affect the co-occurrence of sharks around the bait due to mechanisms of tolerance and dominance hierarchy (Brena et al. 2018). However, we argue that these limitations did not affect our findings. This is further supported by the following notions: 25 individuals were sighted across multiple years and non-random structure was detected regardless of the data gap; although edges between sharks were defined as co-occurrence on the same day, in practice, this time window is often smaller, as multiple sharks are often sighted around the bait at the same time (CH, unpublished data). Nevertheless, due to the time window of 1 day, we refer to white sharks co-occuring rather than socially interacting; and temporal variability of ‘capture probability’ is a limitation of many photo-ID studies (Marshall and Pierce 2012) and could be avoided using other means of recording the presence of individuals, such as acoustic telemetry (e.g. Bruce and Bradford 2013). However, photo-ID allows for a greater sample size than acoustic telemetry due to the costs of transmitters and the effort needed to tag individuals. For example, the number of white sharks included in this study was 101 compared to 23 spotted wobbegongs (*Orectolobus maculatus*) using acoustic telemetry (Armansin et al. 2016). As variability of capture probability varies across individuals (Laroche et al. 2007), a large sample size using photo-ID mitigates this effect to some extent.

Our network analysis provided new insights into the aggregatory behaviour of white sharks at a seal colony and showed that some individuals co-occur more frequently than expected by chance. We suggest that sex-dependent patterns of visitation at the Neptune Islands drive the observed community structure, with females only co-occurring with some males in autumn–winter, while males co-occur with other males in summer. Further studies should attempt to unravel the mechanism driving the observed co-occurrence patterns. Associating with kin can result in numerous fitness benefits such as reduced time to locate resources, decreased aggression, enhanced social learning and social cohesion, increased growth, health condition, longevity and reproductive success, and potentially develop reciprocal altruism (Milinski 1987; Höjesjö et al. 1998; Croft et al. 2004; Atton et al. 2014). In the case of white sharks, closely related individuals might be more likely to visit the Neptune Islands at concurrent periods and form dyads or communities. A genetic relatedness study of the individuals forming the dyads and communities identified in the present study would enable to test whether kinship influences white shark non-random co-occurrence. Further network analysis using alternative datasets, e.g. acoustic tracking (Guttridge et al. 2010; Armansin et al. 2016), can complement this study and provide comparative data when operators are not present and when berleying does not take place.

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Data availability The datasets generated and analysed during the current study are available from the corresponding author on reasonable request.

Compliance with ethical standards

Ethical approval AF owns a cage-diving licence and business at the study sites which enabled the photographs to be collected. The study conformed with the Australian code for the care and use of animals for scientific purposes.

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

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