


How solitary are white sharks: social interactions or just spatial proximity?

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Abstract

White sharks (*Carcharodon carcharias*) are circumglobally distributed large apex predators. While ecologically important, there is very limited study of their social behaviour. Although evident in other large, apex marine predators (e.g. toothed whales) and smaller elasmobranchs (e.g. blacktip reef sharks), the ability of any large pelagic elasmobranch to demonstrate social preferences, tolerance or grouping behaviour is largely unknown. Here, we test whether white sharks in a near-coastal environment form non-random associations with other conspecifics or simply share the same space at the same time. We photo-identified 323 individuals—74 % juvenile females (175–300 cm)—during chumming events at six different sites in Mossel Bay, South Africa, over a 6-year period (2008–2013), and tested for grouping behaviour. We found evidence for random associations among individuals, though spatio-temporal co-occurrence of white sharks in close proximity was weakly structured according to sex and, potentially, body size. Such biological traits may play a minor part in structuring co-occurrence of individuals at fine spatio-temporal scales, which could reflect ontogenetic preferences in diet and site fidelity, or differing tolerance levels for conspecifics of different sexes and sizes. Our study strengthens

the evidence that large pelagic shark species are generally solitary and display limited social behaviour.

Significance statement

Large pelagic shark species are important top predators, but we know little about their social behaviour. We tested the ability of white sharks (*C. carcharias*) to form groups and display social preferences for other individuals when they congregate at scavenging events in a coastal environment, where social interactions may be more likely. We found that white sharks co-occur at random, displaying no preferred or avoided associations for other individuals. Nevertheless, there was a minor influence of biological traits, with individuals aggregating according to gender and, possibly, body size. While we hypothesise these effects could represent preferences in diet and site fidelity, or more tolerance for similar-sized individuals of the same sex, our study strengthens the evidence that white sharks are mostly solitary foragers.

Keywords *Carcharodon carcharias* · Association · Social network · Group · Aggregation · Tolerance

Introduction

White sharks (*Carcharodon carcharias*) are large apex predators with a circumglobal distribution in temperate and tropical waters (Compagno, 2002). While generally solitary, they are known to have seasonal sites of high individual densities, often located near pinniped colonies (e.g. Bruce 1992; Anderson et al. 2011). However, very little is known about white shark social behaviour, despite the evidence for sociality in smaller coastal elasmobranchs (e.g. Mourier et al. 2012) and particularly in other large pelagic marine predators (e.g. Ford et al. 2000; Whitehead 2003). Elasmobranchs have a large brain-to-body mass ratio relative to teleost fish, which

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is comparable to social mammals and birds (see Northcutt 1977; Guttridge et al. 2009; but see Yopak et al. 2007; Mull et al. 2011). Moreover, recent and growing evidence shows some shark species organized into structured social networks (Guttridge et al. 2009; Jacoby et al. 2010; Mourier et al. 2012) in which they engage in social behaviour.

Benthic species such as Port Jackson sharks (*Heterodontus portusjacksoni*) and small-spotted catsharks (*Scyliorhinus canicula*) rest in groups, during which social interactions can occur (Sims et al. 2001, 2005; Powter and Gladstone 2009). Individuals of lemon, nurse and catsharks can display preferred associations (Guttridge et al. 2009; Jacoby et al. 2010; Guttridge et al. 2011), while blacktip reef sharks can maintain long-term dyadic associations (Mourier et al. 2012). What unites these findings is that they are for small coastal, reef and benthic sharks. Large pelagic species have received far less attention, possibly due to the inherent logistical challenges involved in studying wide-ranging and potentially dangerous animals in the open ocean (e.g. Lessa et al. 1999; Domeier and Nasby-Lucas 2013).

Pelagic sharks are generally regarded as largely solitary; but social behaviour may be unravelled as data are accumulated from long-term studies. For instance, scalloped hammerhead sharks (*Sphyrna lewini*), while generally solitary feeders, can display diel periods of non-random interactions (Sims 2003) with regular, polarized schooling of individuals around seamounts (Klimley and Nelson 1984). Evidence for social behaviour in white sharks is even more limited, and derived from descriptive and observational studies rather than specific hypothesis testing for sociality. For instance, during scavenging (e.g. chumming events; around whale carcasses), dominance hierarchies (dependent on body size but not sex) may emerge, limiting intra-specific aggression (e.g. Dudley et al. 2000; Curtis et al. 2006; Dicken 2008; Sperone et al. 2010; Fallows et al. 2013). However, non-random associations, in which two or more individuals are consistently found together (Whitehead 1999, 2008a), have not been tested in white sharks, only in a few other shark and large pelagic fish species (Mourier et al. 2012 for blacktip reef sharks, *Carcharhinus melanopterus*, and Stehfest et al. 2013 for yellowfin tuna, *Thunnus albacares*). Non-random associations suggest preference and/or avoidance for particular conspecific individuals (Whitehead 2008a), together with the ability of individuals to identify one another and engage in a larger social network (Croft et al. 2008). In general, these associations are a necessary prerequisite for social interactions, relationships and structure (Hinde 1976), and the lack thereof can indicate that individuals aggregate for other reasons, such as food resource availability or for mating purposes.

Here, we test whether white sharks simply share the same space and time in a near-coastal environment, or whether they demonstrate social preference for specific individuals. We evaluate the weight of evidence for non-random associations

in white sharks in Mossel Bay, South Africa, where they concentrate due to a Cape fur seal colony (Johnson et al. 2009; Delaney et al. 2012; Rykklief et al. 2014). The majority of white sharks in Mossel Bay are juvenile females. Thus, a large number of individuals with similar trophic ecology congregate together at this location, providing a better opportunity to observe potential social interactions than during solitary oceanic movements. Sharks were attracted to the surface for photo identification with chumming and baiting, which is loosely comparable to scavenging events, during which multiple sharks already present in the general area congregate. We tested whether white sharks are found in close spatio-temporal proximity at random or with specific other individuals, and further examined whether body size and sex could structure their co-occurrence in the area.

Methods

Study area and data collection

We sampled six independent sites (Table 1) in Mossel Bay, South Africa (Fig. 1). Mossel Bay is known for year-round white shark aggregations, and for the Cape fur seal (*Arctocephalus pusillus pusillus*) colony of approximately 4500–5000 adults at Seal Island (Kirkman et al. 2007). Sampling took place twice a day (morning and afternoon) when weather permitted, usually from Mondays to Fridays between 10 February 2008 and 18 August 2013. During the austral summer, sampling focused on the two furthest sites (Blue Houses and Groot Brak) because of research permit restrictions. During the winter, the focal site was Seal Island due to increased movements of Cape fur seals to and from Seal Island—particularly the first foraging days by pups—which induce white sharks to increase use of this area (Rykklief et al. 2014).

Upon arrival at the sampling site, geographical position and time were recorded. White sharks were attracted using chum (sardine *Sardinops sagax*) and bait (mostly, heads of yellowfin tuna *Thunnus albacares*). The bait served as a visual attractant to bring sharks to the surface to make a photographic record of their dorsal fin for the purpose of later individual identification. The sharks were not intentionally fed this bait; although they were occasionally able to consume it, such sporadic events have little influence on conditioning (Johnson and Kock 2006; Laroche et al. 2007). For each individual shark, we recorded arrival and departure time, sex and body length. The time of arrival and departure (specifically 15 min after a shark was last seen) was recorded with precision of 1 min. This 15-min “buffer” limited the potential bias of individuals being under and around the boat (and hence not directly visible), rather than having departed. The visibility in Mossel Bay can be poor (0.5–4 m), and this buffer enables greater certainty that

Table 1 Number of sightings, body length and sex for individuals identified with high-quality photographs (4 or 5 on a 5-point scale) at each site in Mossel Bay

Location	Average length (cm)	Standard deviation	Number of male sightings	Number of female sightings	Number of unknown sex sightings
Blue Houses	250.6	35.4	2 (1 %)	144 (86 %)	22 (13 %)
Groot Brak	256.2	36.1	1(1 %)	129 (90 %)	13 (9 %)
Hartenbos	265.3	52.2	1 (1 %)	107 (91 %)	9 (8 %)
Klein Brak	257.8	36.9	0 (0 %)	57 (95 %)	3 (5 %)
Railway	268.5	36.3	0 (0 %)	12 (86 %)	2 (14 %)
Seal Island	256.5	40.6	7 (1 %)	385 (81 %)	83(18 %)
Overall	256.75	40.57	11 (1 %)	834 (85 %)	132 (14 %)

individuals have actually departed when we record them as doing so. Whenever possible, we inferred the sex of individuals by the presence of claspers, or with underwater video from a remote camera mounted on a pole. Finally, we estimated body length (relative to the 7-m vessel) and later categorized it into bins of 50 cm. We used the average length of each individual over the entire time period by averaging the midpoints of each observation's length bin. Chumming events varied in duration, from a minimum of 15 min to maximum 4 h; thus, we split the data into fixed time windows of 10 min (shorter than the minimum duration) to minimize the chance of missing overlaps between individuals (see Psorakis et al. 2015). The final data consisted of 5472 10-min observation events.

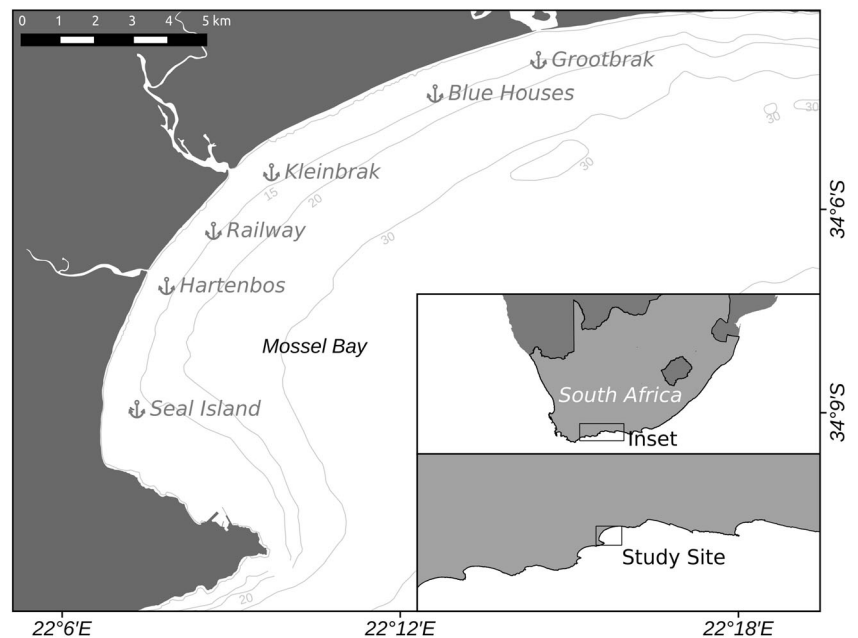
The primary data (associations among photo-identified individuals) were recorded blindly due to two inherent characteristics of our sampling protocol. First, it was very difficult to identify individuals with the naked eye in the field, and we photographed every animal close to the research vessel with no preference for any (either more or less distinctive)

individuals. Second, the photographs were sorted and the individuals identified several months later by researchers who did not participate in the data collection.

Photo identification of individual sharks

To identify individual sharks, photographs were taken of both sides of their dorsal fin and catalogued by chumming event (Ryklief et al. 2014). Marks such as large black or white pigmentations ("rosies"), notches in the trailing side of the dorsal fin, scars or deformities complemented the identification. Photographs were ranked in quality from unreliable (1) to excellent (5, i.e. entire dorsal fin above the water, on a perpendicular angle). Individuals were compared to a photo identification catalogue for this bay. Potential matches were superimposed for direct comparison of the notches and other marks (see Gubili et al. 2009). To ensure the data used were as accurate as possible, only recordings with photos ranked 4 and 5 were used.

Fig. 1 The study site, Mossel Bay, South Africa, and the six sites where white sharks were attracted to the surface with chumming to identify individuals with photographs



Definitions of co-occurrence and association among individuals

We defined an association between individuals as a co-occurrence in the same place at the same time, according to the “gambit of the group” hypothesis (Whitehead and Dufault 1999). Non-random proximity is a necessary prerequisite for most social behaviours; however, the reliability of proximity-based measures as a proxy for social behaviour is taxon-dependent (Castles et al. 2014; Farine 2015) and sharks in proximity may not necessarily be socially interacting. Therefore, given the lack of standardized terminology in the literature, here, we define three classes for clustering in white sharks (adapted from Whitehead 2008a): “aggregations”, “asocial groups” and “groups”. In “aggregations”, individuals would cluster spatio-temporally due to a third factor (e.g. a resource), would gain no benefit from each other and would often compete for the available resources. In “asocial groups”, individuals would cluster due to the advantages of proximity with conspecifics (e.g. protection, mating, hunting efficiency, travelling), but the particular individuals they cluster with are not relevant. Both in aggregations and in asocial groups, clustering may be structured by factors such as size or sex; and while individuals could engage in apparently coordinated movement, there are no preferred associations among them. Finally, in “groups”, individuals also cluster for the advantages of being among conspecifics, but they choose, prefer, or care who they associate with, so social bonds of varying strengths are present. Therefore, we would expect non-random dyadic associations to occur only within groups.

For the statistical analyses, we considered sets of spatio-temporally adjacent individuals observed within the same sampling period (a day) within a 15-min window of one another at a chumming event. We chose a 15-min interval period to account for the sampling protocol, since the departure time was recorded 15 min after the last sighting of an individual. To reduce subjectivity and ensure reliability of our findings, we performed a sensitivity analysis, by defining associations within interval periods of 7.5, 15, 30, 60 and 120 min and repeating the test (see below) of our main hypothesis of random association among individuals. We defined the maximum interval as 120 min because after this period individuals are very likely in different study sites: White sharks in Mossel Bay move at an average rate of 3.2 km/h (Johnson et al. 2009); thus, in 120 min, they would cover over 6 km, which is longer than the average distance between our study sites (Fig. 1).

We estimated the strength of the associations among pairs of individuals with the half-weight index (HWI) of similarity (Whitehead 2008a). The HWI measures the proportion of sightings of the pair together relative to the number of sightings apart: $HWI = \frac{x}{x + y_{AB} + \frac{1}{2}(y_A + y_B)}$, where x is the number of sampling periods (days) with individuals A and B observed together, y_A is the number of sampling periods with just A identified, y_B is the number of sampling periods with only B

identified and y_{AB} is the number of sampling periods with both A and B identified (see Whitehead 2008a). The HWI is the least biased index when the assumption that if one individual is identified, all individuals in the sampling period are also identified is violated (Cairns and Schwager 1987; Whitehead 2008a). This is likely to be true in our case due to the limitation of getting high-quality photographs for every individual shark and the fact that not all individuals present in the area may respond to chumming.

Testing association patterns

We tested the null hypothesis of random associations among pairs of individuals using permutations (Bejder et al. 1998; modified by Whitehead 1999, 2005) in SOCPROG 2.5 (Whitehead 2009). Specifically, we tested for preferred or avoided associations by examining if the standard deviation (SD) and coefficient of variation (CV) of the observed HWI between sampling periods (days) were significantly higher or lower (respectively) than permuted values. We permuted individuals in close spatio-temporal proximity (“associations within samples”, see Whitehead 2008a, 2009), keeping rows and column totals constant. We performed 20,000 iterations to stabilize the p values (Bejder et al. 1998), with 1000 flips at each time to prevent non-independence of the random matrices (see Whitehead 2008a). We set the sampling period to 1 day to ensure that associations within each sampling period would not be exaggerated as they would be with longer sampling periods (i.e. sharks can be co-associated 1 day but not the next).

We compared the SD and CV of the observed association indices to the benchmark distribution of SD and CV produced by the permutation procedure. Observed values larger than the 97.5 % confidence interval (CI) of the benchmark distribution indicate associations significantly higher than expected by chance that represent “social preference” among individuals within the population; likewise, observed values smaller than the 2.5 % CI indicate significantly lower associations, representing “social avoidance” (Whitehead 2008a). This test is robust to individual differences in gregariousness (i.e. tendency to form larger groups) and to individual movements in and out of the study area (Whitehead 1999, 2008a). To minimize the possibility of spurious associations, we removed from this analysis all individuals identified less than five times during the study, a commonly used observation threshold (see Croft et al. 2011; Whitehead 2008a). We therefore evaluated 5180 observations among 143 individuals.

Testing the influence of sex and body length

To test the null hypothesis that sex and body size do not influence co-occurrence of individual white sharks, we performed Mantel tests (Pearson’s correlation, 999 permutations)

using the full data set, with all individuals identified in high-quality photographs (without the minimum observation threshold). We tested whether the association indices (HWI) between individuals within sex body length classes were higher than associations between classes (e.g. whether males associate more frequently with males; juveniles with juveniles). There was one comparison for sexes (males vs. females) as individuals of unknown sex were excluded from this analysis. For the size classes, we used three categories (based on Bruce and Bradford 2012): young of the year (YOY ≤ 175 cm), juveniles ($175 < 300$ cm) and sub-adults (> 300 cm); three adults were observed (males > 350 cm and females > 460 cm). We created three comparisons: YOY vs. juveniles, YOY vs. sub-adults and juveniles vs. sub-adults. Since there were only 23 YOY individuals, we also tested a single-size class separation (< 300 vs. > 300 cm) to examine the robustness of the results. This size division reflects previous research indicating a dietary shift in individuals of around 3 m from primarily fish-based to primarily marine mammals (Estrada et al. 2014). In a further test of robustness, we also conducted these analyses in the absence of sharks that have changed size sufficiently to move from one size class to another during the study ($n = 40$).

We illustrated these results with a network representation of the full association matrix, plotted using a force-directed drawing algorithm. In the network, nodes representing individuals were connected by links whose thicknesses were proportional to the HWI values. The topology of the giant component of the network was described with three global properties (e.g. Croft et al. 2008); density (proportional of realized links, i.e. associations observed); average degree (average number of links per node, i.e. mean number of association per individual shark) and average path length (average number of links separating all pairs of nodes; i.e. how close individuals are in the network). We further explored the tendency for individuals of same sex or similar body lengths to associate by performing a network assortment analysis and by calculating average node strength (i.e. sum of all weighted links) per sex and body length classes. We used two indices that range from 1 (fully assorted) to -1 (fully disassorted): the weighted assortativity index for the two sex categories and the continuous weighted assortativity index to relate strength of association with actual average body length (Farine 2014). We did not include in these analyses individuals of unknown sex and who were observed less than five times.

Caveats

Here, we acknowledge the three potential limitations of our methods and describe how we minimized them. Firstly, manual individual identification using photography can be subjective (Araabi et al. 2000). We avoid false-positive or false-negative matches by having two researchers independently perform the

identification using only high-quality photos (rated 4–5). Secondly, using chumming to attract sharks could restrict the generality of our results due to conditioning affecting residence behaviour (Orams 2002; Johnson and Kock 2006; Laroche et al. 2007; Clua et al. 2010). In the effort to prevent food conditioning, we carried out the chumming events seasonally (when tourism and beach activity were low), alternated them among the 6 study sites, used only 5–6 tuna heads per event and aborted the event if all baits were taken. Finally, the chumming may increase individual heterogeneity in sighting probability, since not all individuals may be equally attracted to the chum and sharks may lose interest in it over time (Johnson and Kock 2006). In Mossel Bay, the effectiveness of chumming in bringing sharks close enough to the surface for photo identification was evaluated; 54 % of the time, the same individuals detected via acoustic tags in the area were successfully detected visually from the chumming vessel (Johnson and Kock 2006; Delaney et al. 2012). In our association analyses, we minimized biases of the potential undersampling of some individuals by employing the half-weight index, which is the most robust to imperfect detection of individuals (Whitehead 2008a). Moreover, our relatively long data set (2008–2013) yielded a large number of individuals ($n = 143$) seen greater than five times ($H = 5.52$), which combined with the high social differentiation among the sampled individuals ($S = 2.08$) indicated that our permutation tests had sufficient statistical power to detect significant associations if they were present ($S^2 H = 23.8 > 5$), (Whitehead 2008b). Therefore, potential sampling biases would be unlikely to affect our ability to detect significant relationships between white shark individuals.

Results

The permutation tests failed to reject the null hypothesis of random associations among individuals within Mossel Bay, regardless of the length of the period used to define an association (from 7.5 to 120 min). Neither the standard deviation nor the coefficient of variation of the empirical association indices were different than the null expectation (Empirical HWI SD = 0.042, random SD = 0.042, $p = 0.48$; Empirical HWI CV = 7.24, random CV = 7.28, $p = 0.62$; shown here only for our main association period of 15 min). Therefore, we found no evidence for non-random associations (between daily sampling periods) among the individual white sharks sighted within Mossel Bay during the 5-and-a-half-year period of observation. This pattern was robust to variation in the length of the association period: in all the other four tested periods, from 7.5 to 120 min, the SD and CV of empirical association indices were not different from random (all p values > 0.34). The networks depicting the associations (HWI) between individuals displayed no clear large-scale topological structure (Fig. 2), further suggesting random associations.

We found a low, yet significant, correlation between association strength and sex classes (Mantel test, 999 iterations, $r = 0.072$, $p = 0.018$), as well as a moderately low weighted assortativity index for sexes ($r_d^w = 0.151 \pm 0.065$ SD). These findings suggested that there was a tendency for individuals to co-occur with others of the same sex more often than with individuals from different sexes. Likewise, there was small but significant difference in the strength of association between young of the year (YOY) vs. juveniles ($r = 0.094$, $p = 0.001$) and between YOY vs. sub-adults ($r = 0.190$, $p < 0.001$). On the other hand, there was no difference between YOY and juveniles combined vs. sub-adults ($r = 0.035$, $p = 0.078$) nor between juveniles and sub-adults ($r = 0.039$, $p = 0.077$). Conducting the same tests while removing individuals that switched class during the study period did not change the significance of the strength of association by sex ($r = 0.03$, $p = 0.042$), but the association strengths for the size class relationships became non-significant (YOY vs. juveniles; $r = 0.025$, $p = 0.096$; YOY vs. sub-adults; $r = 0.11$, $p = 0.26$; juveniles vs. sub-adults; $r = 0.0040$, $p = 0.44$). Coupled with the low weighted continuous assortativity index ($r_c^w = 0.050 \pm 0.018$ SD), the variable significance of the correlations indicated the overall small effect size of body

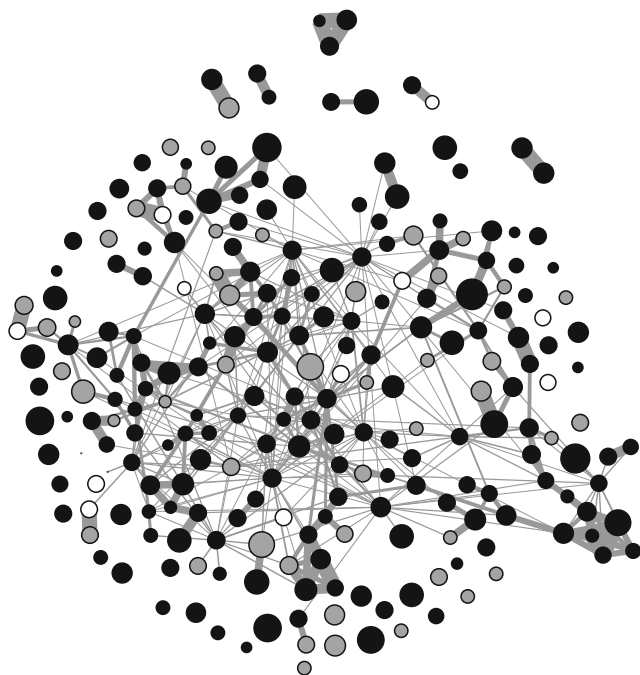


Fig. 2 Network representation of all white sharks observed during chumming events in Mossel Bay, South Africa. Nodes representing photo-identified individuals are connected by links representing their co-occurrence during chumming events. Node sizes are proportional to individual body size and colour code depicts sex (female = *black*, male = *white*, unknown = *grey*). The thicknesses of the links are proportional to the time that individuals were seen together, estimated by half-weight indices. The network is sparse and unstructured, illustrating the few and random individual associations among white sharks, but with a low degree of assortativity by body size and sex

length on associations. The effect of sex on associations, however, appears to be more robust.

These results should be interpreted in the context of the random association findings above; that is, individuals may tend to co-occur more frequently within the same sex and size class, but within those classes they associate randomly rather than with particular individuals. It is important to note that the effect size of these significant correlations is small, because the overall strength of association was low (mean HWI = 0.15 ± 0.26 SD) and our data set was skewed towards small females (Table 1, Fig. 2). However, although the number of males was low ($n = 11$), as was the number of adults ($n = 3$ individuals >4 m), we were still able to detect some degree of intra-class (sex and body size) aggregation.

The network topology further illustrates the combined results of the permutation, Mantel tests and assortment analysis (Fig. 2). The number of disconnected nodes suggests that many individuals are usually seen alone. Among the individuals that co-occurred in the chumming events (i.e. are directly or indirectly connected in the giant component of the network), there seemed to be some assortativity among females of similar body sizes. The average strength within sex classes was higher than between (females = 0.156 ± 0.254 SD; males = 0.333 ± 0.577 SD; male-female = 0.072 ± 0.195 SD), and the average strength within individuals <300 cm (YOYs and juveniles = 0.151 ± 0.248 SD) was higher than within individuals >300 cm (sub-adults and adults = 0.117 ± 0.283 SD) and between these two classes (0.129 ± 0.262 SD). Combined, the large-scale topological metrics indicated a sparse and unstructured network, in which individuals engaged in few associations (Fig. 2). The density of the giant component was very low ($D = 0.03$; i.e. 3 % of the potential associations), and so was the average degree ($k = 5.2$; i.e. on average individuals interacted with 5 others); consequently, the average path length was relatively high ($l = 3.2$; individuals are separated by at least three other individuals).

Discussion

While the focus of studies of shark social patterns has been on small coastal species (e.g. Guttridge et al. 2009; Mourier et al. 2012), here we broaden the search for social behaviour in large pelagic species (but see Sperone et al. 2010; Fallows et al. 2013) by exploring the possibility of preferred associations among white sharks in a near-coastal environment. Apart from seasonal aggregations, white sharks and other large pelagic shark species are believed to be generally solitary. Our findings support that within these seasonal aggregations where several white sharks can be observed near to the coast, there are no preferred nor avoided associations among individuals, which are general pre-requisites for social grouping. The random association pattern among individuals using Mossel Bay suggests that white sharks form asocial aggregations, meaning the co-

occurrence at a fine spatial scale may be due to the influence of an external factor (such as prey availability; Heithaus et al. 2008) or the advantages of associating with conspecifics (e.g. mating), rather than individuals actively seeking to associate with one another. We found, however, that ontogenetic factors may stratify spatio-temporal proximity, as shown by a positive (but weak) tendency for white sharks to co-occur with similarly sized individuals of the same sex. We herein hypothesise that the effect of these biological traits on the fine-scale co-occurrence of individuals could potentially reflect preferences in habitat and/or diet, or differences in tolerance levels towards conspecifics.

Our main findings on the random association pattern among white shark individuals ultimately reinforce that apex predators may not be under strong selective pressures to develop multiple and/or lasting social relationships (Krause and Ruxton 2002). This is perhaps because white sharks are efficient solitary foragers and lack the need to cooperate for defence against predators. While white sharks have anatomical specializations—such as a large brain and acute sensorial apparatus—that provide the potential for social complexity (Northcutt 1977; Dunbar and Shultz 2007; Jacoby et al. 2012), it may be that such specializations are better related to enhanced foraging efficiency on agile prey living in a dynamic and multidimensional environment (Yopak et al. 2007), and reproductive investment (Mull et al. 2011). Moreover, although white sharks congregate repeatedly in preferred feeding grounds, they are known to commonly travel great distances including transoceanic migrations (Bonfil et al. 2005, 2009; Weng et al. 2007; Jorgensen et al. 2010; Block et al. 2011; Hamady 2014). This fact, coupled with low estimated population sizes (Cliff et al. 1996; Burgess et al. 2014; Towner et al. 2013) could mean that white sharks generally experience low probabilities of encountering conspecifics. Therefore we would expect a tendency to be relatively solitary for long periods in the open ocean environment compared to coastal ecosystems.

When we scale up from dyadic associations to patterns of co-occurrence, we found that white sharks of same sex, and possibly those of similar size, tended to co-occur more frequently during the scavenging events. Assortment by size has been observed in a few smaller benthic and reef shark species (Guttridge et al. 2009; Clua et al. 2010; Jacoby et al. 2012; Mourier et al. 2012). Unlike these studies on species that are more easily observed, we cannot definitively identify the underlying cause of the weak stratification by sex and potentially body size observed here. We also note that the majority of individuals in our study were juvenile females, and we acknowledge that this age and sex structure may produce an unavoidably imbalanced sample. However, we note that we still did detect evidence for stratification. Here, we outline two non-exclusive hypotheses for this clustering.

Firstly, clustering of similar individuals could reflect ontogenetic preferences in habitat choice and diet. While reproductive

females and neonates are usually associated with shallow coastal areas (Simpfendorfer and Milward 1993), the overall abundance of white sharks in other habitats fluctuates with seasonally predictable prey availability (e.g. Heithaus et al. 2008; Goldman and Anderson 1999; Domeier and Nasby-Lucas 2008; Anderson et al. 2011). For instance in South Africa, more individuals are found during the austral winter and spring at sites with pinniped colonies (i.e. higher sightings per unit effort, SPUE) when there are more inexperienced pups learning to forage away from the island (e.g. False Bay and Mossel Bay; Kock et al. 2013; Hewitt 2014; Rykklief et al. 2014). Conversely, SPUE are higher during the austral summers in inshore waters around reefs where fish are abundant. Since small white sharks (<300 cm) feed primarily on teleost fish and small elasmobranchs, and larger ones (>300 cm) tend to prioritize marine mammals (Estrada et al. 2014), these dietary differences may increase the probability of co-occurrence with individuals of similar body size. The mean length of our sampled population was 257 cm, considered by Bruce and Bradford (2012) to be juveniles, with three sharks around 400 cm and the largest sharks between 450 and 475 cm, suggesting that there were indeed few white shark adults at Mossel Bay. It is possible that our sampling method has influenced the observed body size distribution. However, there appeared to be some evidence for weak size structuring with this potentially compressed size and age spectrum, though additional study would be needed to ensure that this is a robust result. A potential route to exploring this in future studies could be coupling acoustic or satellite telemetry with observational data to reduce any heterogeneity in detection probability among individuals, as well as to provide more refined data on the movement of the individuals, both within the study area and in more offshore waters (e.g. Jorgensen et al. 2010).

Secondly, the co-occurrence of similarly-sized individuals of the same sex could represent differing tolerance levels for other conspecifics. Avoiding larger sharks may reduce the probability of being preyed upon through “safety in numbers” and simply minimizing spatial co-occurrence with adult sharks. This aligns with the evidence (although limited) for co-preferred occurrence among the young of the year when compared to juveniles and sub-adults. However, the effects on competition for similar food may partially counteract this effect if resources are limited. Sexual segregation has been recorded for elasmobranchs since Ford’s (1921) observations from fish trawling grounds. White sharks seem to sexually segregate during the summer when females occupy inshore, and males are rarely seen (Kock et al. 2013). This may represent a variation in reproductive metabolic needs by the sexes (Wearmouth and Sims 2008) and differential water temperature effects on mating success (Sims 2003; Sims et al. 2005). Females may prefer warmer temperatures to grow themselves and embryos faster and thus search for suitable areas for gestation (Hight and Lowe 2007). Males may prefer cooler temperatures where sperm

productivity and viability is increased but, as a consequence, may spend more time searching for mates (Kime and Hews 1982; Hight and Lowe 2007).

Ultimately, the key finding of our study is the evidence for a random association pattern among white sharks at scavenging events. This suggests that, at least in near-coastal environments, white sharks do not form social groups and lack strong social interactions, such as preferred dyadic associations. Rather, our findings indicate that white sharks form either aggregations due to a third factor such as food availability, or asocial groups that cluster due to the benefits of proximity with conspecifics. Such clustering of individuals in close proximity may be sex- and, potentially, body size-structured. We hypothesise that the influence of such biological traits may reflect ontogenetic preferences or differing tolerance behaviour for other classes of conspecifics. To better distinguish these possibilities and expand the scope of our findings, we recommend future studies coupling association, behavioural and movement data over larger areas and multiple habitats including the open ocean, using additional tools such as satellite and acoustic telemetry (e.g. Jorgensen et al. 2010; Stehfest et al. 2013, Lee et al. 2014).

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Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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