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Using an unbaited stationary video system to investigate the behaviour and interactions of bull sharks *Carcharhinus leucas* under an aquaculture farm

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Bull sharks *Carcharhinus leucas* are common along the coast of Reunion Island (South-West Indian Ocean) and were suspected to aggregate in the vicinity of an aquaculture farm in Saint-Paul Bay on the west coast. In order to understand the behaviour and interaction of bull sharks near aquaculture cages at Saint-Paul Bay, we deployed an experimental unbaited stationary video camera. From 175 hours of recording during daylight hours from March to April 2012, eight individual female bull sharks (seven adults and one immature) were identified based on their natural markings. These sharks were resighted between 3 and 45 times. Residency analysis revealed site attachment under the aquaculture cages for at least three individuals over the course of the study. Recorded behaviours included intraspecific social interactions such as synchronised swimming. Social interactions and relatively strong paired associations for two pairs of females suggest some level of sociality among bull sharks around Reunion Island. Overall, our results demonstrate the utility of unbaited video systems to monitor the behaviour of adult coastal sharks.

Keywords: intraspecific associations, site fidelity, social relationships, unbaited video camera

Online supplementary material: Supplementary video clips of two sharks in straight-line synchronised swim can be found online at http://dx.doi.org/10.2989/1814232X.2016.1156578.

Introduction

Understanding the behaviour of large predatory sharks is challenging, but critical to gaining a complete understanding of their roles in marine communities. Over the past decade, acoustic and satellite telemetry have greatly expanded our ability to quantify movement patterns and habitat selection of sharks of a variety of species and in various contexts (Eckert et al. 2002; Heupel and Simpfendorfer 2005; Daly et al. 2014). However, these methods generally conceal fine-scale interactions, both interspecific and intraspecific (Heupel and Simpfendorfer 2005).

Remote underwater video provides another means for observing aquatic species across varying spatial and temporal scales with minimal observer effect (Tessier et al. 2005; Watson et al. 2005; Stobart et al. 2007; Chabanet et al. 2012). Video has been used not only for assessment of community structure and dynamics (Cappo et al. 2004; Shortis et al. 2007), but also to study fish behaviour, including predator–prey interactions and diel patterns of fish diversity (Harvey et al. 2002). Moreover, the individual identification of fishes, such as elasmobranchs, using photo-identification enables us to improve our understanding of fine-scale movements, site fidelity (Clua et al. 2010; Marshall and Pierce 2012) and sociality (Whitney et al. 2004; Mourier et al. 2012).

The bull shark *Carcharhinus leucas* is a large predatory species that is able to exploit a diversity of marine, brackish and freshwater habitats (Heupel and Simpfendorfer 2008). Most studies of bull sharks have been conducted on juveniles in nursery habitats (Simpfendorfer et al. 2005; Heupel and Simpfendorfer 2008; Matich and Heithaus 2014). However, very little is known about the behaviour of adult bull sharks (but see Brunnschweiler et al. 2010; Carlson et al. 2010; Brunnschweiler and Baensch 2011; Brunnschweiler and Barnett 2013; Daly et al. 2014), including their social interactions and grouping patterns. In 2011, multiple occurrences of shark bites on swimmers and surfers were recorded in the coastal waters of Reunion Island (South-West Indian Ocean), leading to the establishment of a research programme on the ecology of large coastal sharks. For several of the interactions involving bull sharks (the species probably associated with most of the bites), multiple sharks were observed, raising the possibility of group movements by adult individuals.

Fish farms have been documented to attract wild predatory fishes, including bull sharks (Boyra et al. 2004; Uglem et al. 2009; Papastamatiou et al. 2010). In order to understand better the behaviour and interaction of bull sharks with the aquaculture farm of Saint-Paul Bay, on the north-west coast of Reunion Island, we deployed an experimental unbaited stationary video camera beneath a floating aquaculture cage. We aimed to investigate short-term site attachment, abundance, behaviour and grouping patterns of bull sharks during daylight hours.

Material and methods

Study site

Reunion Island is a tropical volcanic island located in the south-west Indian Ocean (21°07′ S, 55°32′ E), about 800 km east of Madagascar and 220 km west of Mauritius (Figure 1). Saint-Paul Bay is a sandy embayment located off the north-west coast of the island (Figure 1). It is characterised by relatively high turbidity due to freshwater inputs from a small lake (Tessier et al. 2005). An aquaculture farm was established in the bay in 1999 to breed red drum *Sciaenops ocellatus* and goldlined seabream *Rhabdosargus sarba*. The structure includes four cages, spaced 50 m apart in 30 m of water. The cages, which are 12 m deep, have an interior net that contains the farmed fish and an outer anti-predator net.

Data collection

We used a high-definition video camera (Sony HDCAM 750) equipped with a Canon 90° lens and contained in a Subspace high-definition housing. The shooting angle of the camera was maintained at 90°. The camera was mounted on a 3 m-high stainless-steel tripod (Figure 2). The tripod was set to allow shooting to be adjusted by 180° from top to bottom and by 360° from right to left in order to define the best shooting angle once the video camera had been set up. Together, the tripod and the video camera weighed 300 kg, but 400 kg of additional weights were added to stabilise the structure. The camera was linked by cables to a surface housing (150 cm × 70 cm) mounted on the flotation buoys of the aquaculture cages. The housing contained a solar-rechargeable battery (12V-75A) that supplied power to the camera and a player/recorder (Atomos Samurai Blade) that stored video clips (Figure 2). Data were transmitted to the surface through an HDMI video cable and clips were recorded on several 0.5–1.0 TB hard drives. Recordings were made continuously during daylight hours between 9:00 and 18:00 (variable with access opportunities to the fish farm) from 6 March to 6 April 2012. The system was checked and data were downloaded twice a day.

Videos were transcribed by two researchers viewing at 8× speed until sharks were detected. One sighting was defined as the presence of a shark in the frame (two or more observations of an individual within 15 minutes were considered as one sighting). A resighting was defined as a second observation of an identified individual within 15 minutes. For each sighting, we quantified the duration of presence, foraging activities and identity of individuals based on their natural markings, including fin shape, pigmented spots and scars (e.g. Brunnschweiler and Baensch 2011; Marshall and Pierce 2012). Sharks were considered to be associated when two or more individuals were seen simultaneously and within a sample duration of <15 minutes. We recorded the nature of interactions when two or more sharks were seen together, including following (straight-line synchronised swim), parallelling or milling (Mourier et al. 2012). Straight-line synchronised swim was characterised by a shark following another one. Parallelling was characterised by two or more sharks observed within one body length of each other moving in the same direction at the same speed. Milling was when two or more sharks were within one body length but did not exhibit any coordinated directional changes (Guttridge et al. 2011; Mourier et al. 2012). The gender of sharks was determined by recording the presence (male) or absence (female) of claspers. In order to estimate the size of sharks, a diver of known body size was filmed at 1-m incremental distances from the video camera. The distance of a shark from the camera was gauged according to features on the substratum. These pictures were then compared to images of sharks at similar distances and each shark was categorised into a size class with 50-cm increments: 100–150, 150–200, 200–250, and 250–300 cm. According to size categories, we also defined the sexual maturity of identified sharks (Cliff and Dudley 1991; Cruz-Martínez et al. 2005; Neer et al. 2005).

Data analysis

Using identification data, we obtained the number of sightings for each identified individual and assessed the occurrence per day for each shark. To investigate associations among sharks we used the half-weight index (HWI) (Cairns and Schwager 1987), to calculate coefficients of association (CoAs), following the equation:

$$\mathrm{CoA} = X/[X + 0.5(Y_a + Y_b)]$$

where X is the number of times both individual *a* and *b* were seen together, Y_a is the number of times individual *a* was seen without individual *b*, and Y_b is the number of times individual *b* was seen without individual *a*. CoAs ranged from 0, for two sharks never seen together in a group, to 1, for two individuals that were always observed together. To determine whether the patterns of association between individuals were non-random, an association matrix from calculated CoAs between sharks was built using SOCPROG 2.4 (Whitehead 2009) with a daily sampling period. The permutation test (Bejder et al. 1998) was used to determine whether sharks associated preferentially with other individuals and/or avoided one another (Whitehead 2008). In order to test the null hypothesis of no preferred companions between sharks we randomly permuted associations 9 000 times until the p-value stabilised within the same 15-minute period. The p-value indicated whether the permutation test was significant and thus facilitated comparison of the real dataset with the random dataset.

Results

Survey effort and shark sightings

A total of 175 hours of recording were obtained, with an average of 5.5 hours (representing the duration of access opportunities to the fish farm) of recording each day from

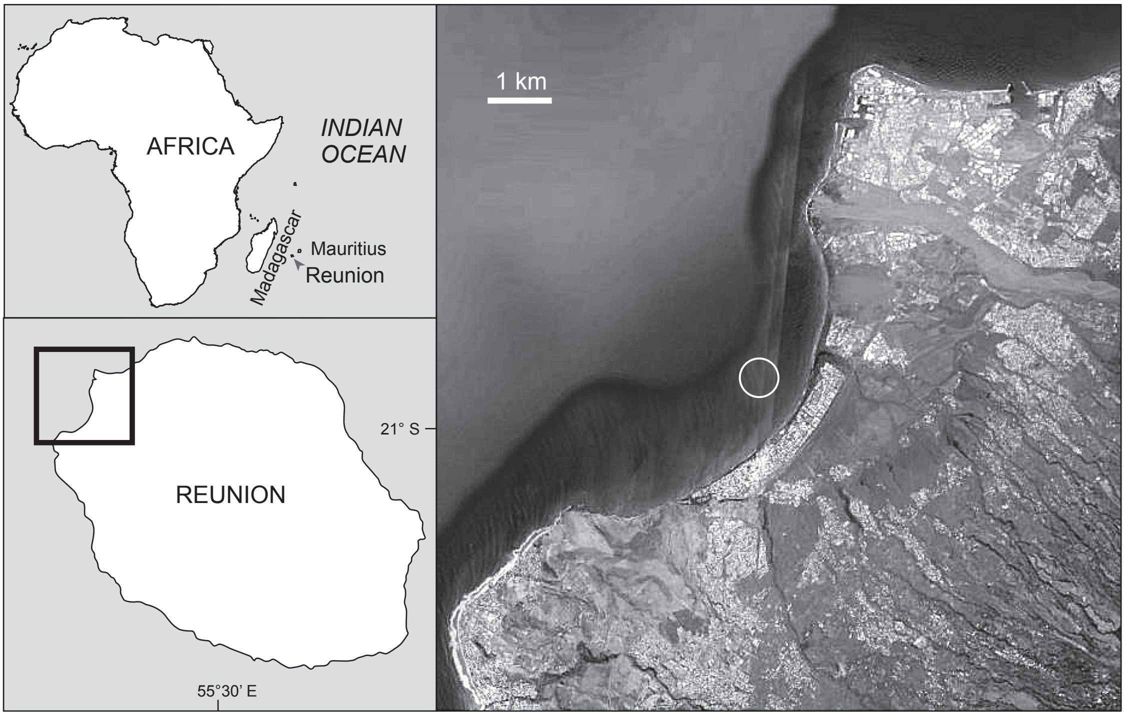

Figure 1: Map of Reunion Island showing the location of the study area in Saint-Paul Bay. The study site at the aquaculture farm is depicted as a white circle (image source: Google Earth)

6 March to 6 April 2012. Over the study period, 218 shark observations were recorded, including 217 of bull sharks (Table 1) and one of a tawny nurse shark *Nebrius ferrugineus*. These 217 observations represented 190 shark sightings. Sharks were detected on 22 days (73%), with a peak number of observations between 14 and 16 March (maximum of 36 sightings in one day) (Figure 3). No sharks were detected from 21 to 24 March (Figure 3). From the 190 bull shark sightings, it was possible to identify eight individuals in 161 sightings (numbered from 1 to 8, Table 1). In 29 sightings, individuals could not be identified and sex could not be determined due to poor visibility. The bull sharks were estimated to be between 150 and 300 cm total length (TL) (Table 1). Sharks were mostly observed in the afternoon (Figure 4).

Residency and association patterns

Identified sharks were resighted from 3 to 45 times (mean = 20 [SD 13.6] resightings per individual) (Table 1). The number of resightings reached 45 (23% of sightings) for shark #1 (immature individual) with a mean time-interval between resightings of 15 hours (SD 37) (Table 1). The other two individuals most frequently seen were shark #2 (33 resightings, 17.3%) and shark #3 (20 resightings, 10.5%). A total of 50 associations of two or more sharks were recorded. Mean CoAs ranged from 0.03 to 0.32 and maximum CoAs ranged from 0.11 to 0.55 (Table 2). All sharks were associated with an average CoA of 0.18 (SD 0.19) (Table 3). The mean associations in the real dataset were equal to the random dataset (0.18; Table 3), whereas the SDs and CVs were higher in the real dataset (0.19 and 1.06, respectively) than in the random one (0.18 and 1.01,

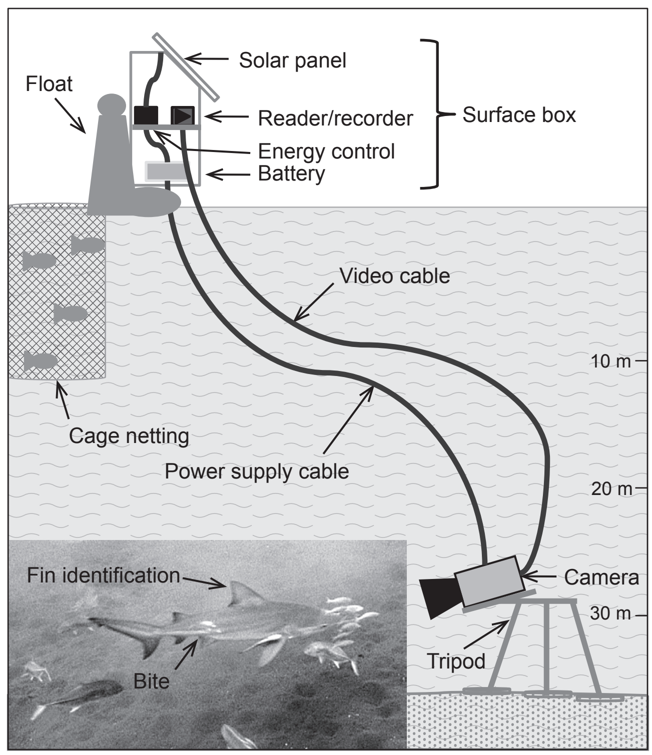

Figure 2: Schematic representation of the moored video camera system used for the study

Table 1: Characteristics of each identified individual shark recorded at the fish farm in Saint-Paul Bay: size (total length), sex, maturity (life-history stage), sightings (number), days (number of days on which each individual was detected), time (h:min) (mean time elapsed between sightings). $D_f - D_l$ denotes the number of days between the first and the last observations

Identification number	Size (cm)	Sex	Maturity	Sightings	Days	Time (SD)	$D_f - D_l$
1	150–200	F	Immature	45	13	14:58 (37:16)	31
2	200–250	F	Adult	33	9	17:47 (43:41)	24
3	250–300	F	Adult	20	11	29:48 (43:42)	24
4	200–250	F	Adult	21	7	22:49 (47:30)	17
5	250–300	F	Adult	20	9	14:31 (14:47)	10
6	250–300	F	Adult	11	6	32:05 (65:42)	14
7	250–300	F	Adult	8	6	92:18 (106:41)	26
8	250–300	F	Adult	3	3	179:05 (58:07)	15

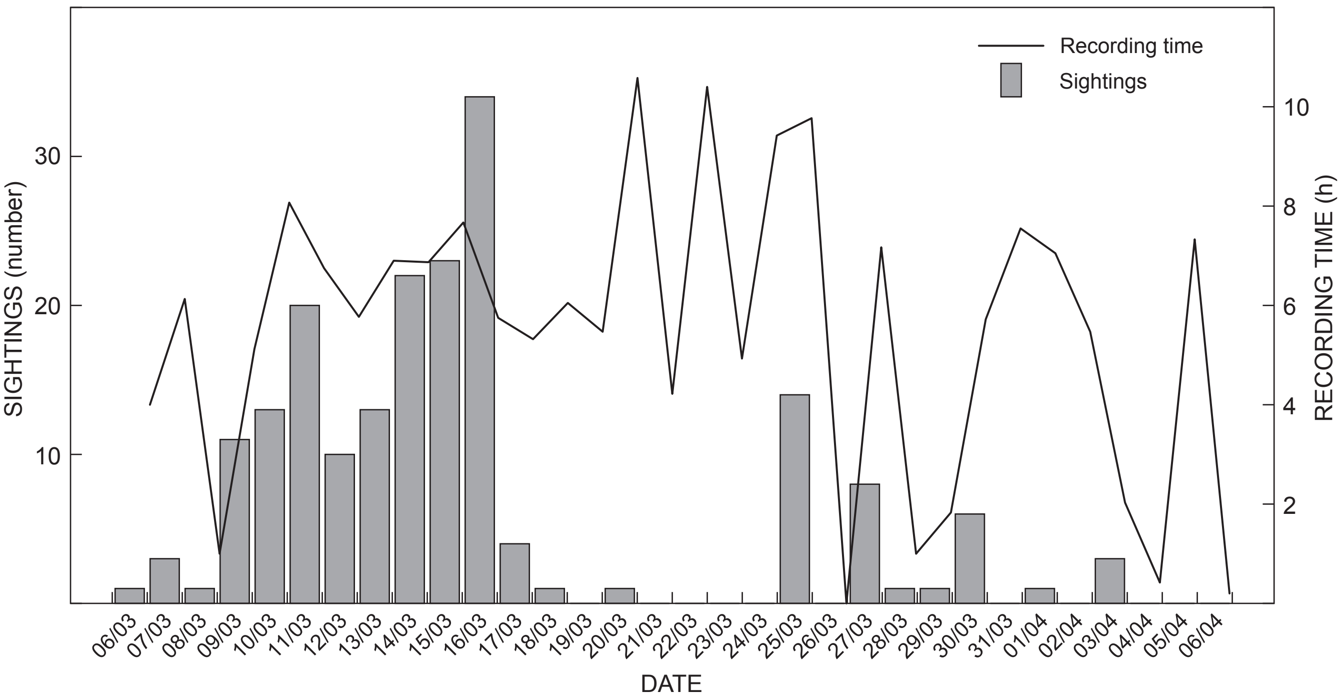

Figure 3: Daily recording time and number of shark sightings at the study site, 6 March–6 April, 2012

respectively; Table 3). The *p*-values for SD and CV were high (0.916 and 0.933, respectively), indicating that some associations were preferred (Table 3). The cluster analysis revealed a strong association between shark #1 and shark #2 (CoA = 0.55), and between shark #4 and shark #6 (CoA = 0.46; Figure 5). To examine whether some sharks avoided others, we analysed the proportion of non-zero association indices in both datasets (real and random). Our results suggest that some sharks avoided others, because the proportion of non-zero association indices was lower in the real dataset (proportion = 0.57) than in the random one (proportion = 0.63, $p = 0.047$, Table 3).

In the 217 observations, sharks were mostly observed swimming alone (179 times, 82%) or in pairs (35 times, 16%). Groups of three, four and five individuals were observed on one occasion. On 13 occasions, pairs of individuals were seen in straight-line synchronised swim (see video clips S1 and S2 in supplementary material, available online). Larger individuals were not systematically in lead position. During the 25 other interactions, sharks were milling and did not exhibit coordinated directional changes. Benthic foraging was observed on two occasions but prey was not identifiable.

Discussion

Despite the short sampling period and some unusable observations due to poor visibility, we could identify 85% of individuals detected through use of their natural markings. Their gender could be also determined, and their maturity estimated. Our study shows short-term patterns of site attachment of bull sharks to the aquaculture farm for several identified individuals (particularly sharks #1, #2 and #3). Interestingly, a bull shark tagged with an acoustic transmitter has shown a similar pattern of residency around the farm (Blaison et al. 2015). Active fish farms have

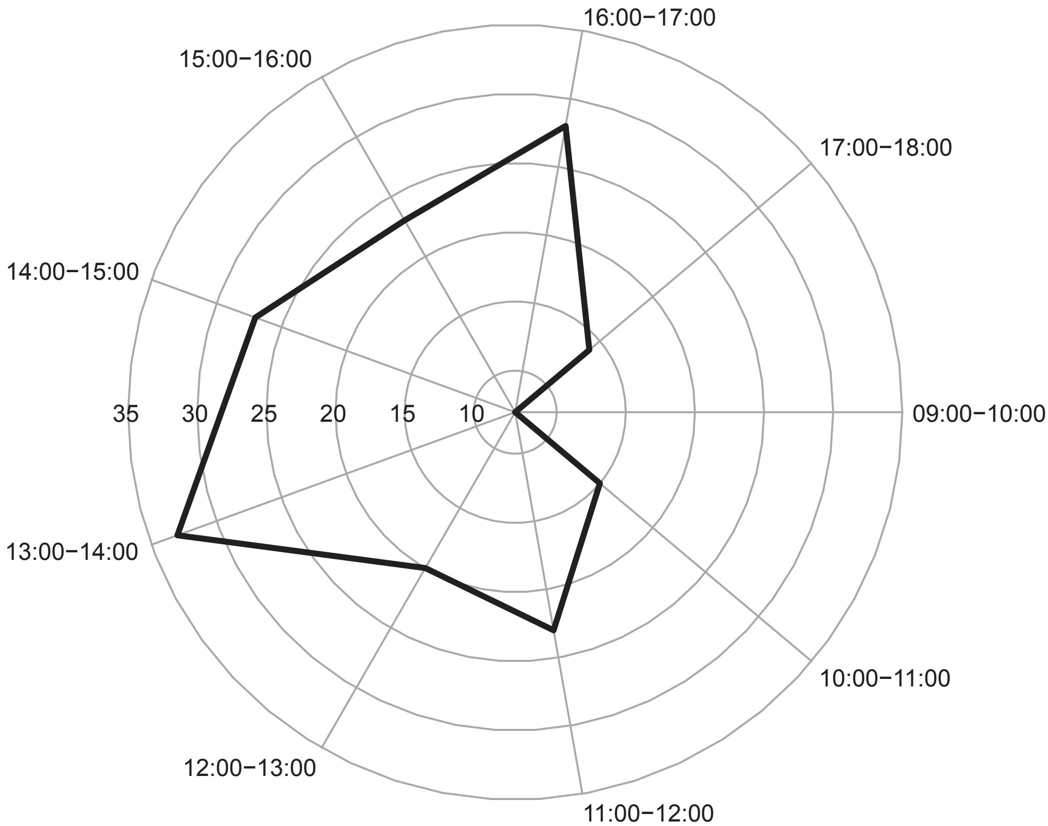

Figure 4: Number of sightings as a function of time of day

Table 2: Mean and maximum half-weight indices (HWI) between identified bull sharks

Identification number	Mean HWI	Maximum HWI
1	0.32	0.55
2	0.28	0.55
3	0.17	0.38
4	0.21	0.50
5	0.17	0.33
6	0.21	0.53
7	0.03	0.11
8	0.04	0.29

Table 3: Statistics of preferred and avoided (non-zero) associations

Statistic	Real	Random	*p*-value
Mean CoA	0.17973	0.18035	0.389
Median CoA	0.10819	0.12823	0.024
SD CoA	0.19140	0.18284	0.916
CV CoA	1.06495	1.01382	0.933
Proportion non-zero element	0.57143	0.63618	0.047
Mean non-zero element	0.31453	0.28423	0.961
SD non-zero element	0.14572	0.15071	0.312
CV non-zero element	0.46328	0.53221	0.081

been documented to attract wild predatory fishes such as sharks that can show strong site fidelity around aquaculture cages (Boyra et al. 2004; Uglem et al. 2009). For instance, fish farms in Hawaii appear to attract a number of large predators, such as tiger sharks *Galeocerdo cuvier* and sandbar sharks *Carcharhinus plumbeus* (Papastamatiou et al. 2010). Based on this study, we could not determine unequivocally whether fish farms of Reunion Island attract bull sharks, because there is no baseline information on the occurrence of bull sharks in Saint-Paul Bay prior to the deployment of the cages. We did not find any evidence of bull sharks attempting to attack the cage under which the camera was deployed, even when fish were fed. However, it is possible that fish farms may serve as 'landmarks' for bull sharks moving along the west coast of Reunion Island (Papastamatiou et al. 2010).

The individual identification of sharks using natural markings has drawbacks (see review of Marshall and Pierce 2012). Moreover, visibility and distance of sharks from the video system can potentially affect the detection of known individuals. Nevertheless, our dataset enabled an examination of the association patterns among individuals. Although CoA values found in our study are lower than those found for other shark species, such as blacktip reef sharks *Carcharhinus melanopterus* off Moorea, French Polynesia (mean CoA >0.56; Mourier et al. 2012), the combination of association patterns and observed social behaviour suggests that some bull sharks are more gregarious than others. Grouping is widespread in both

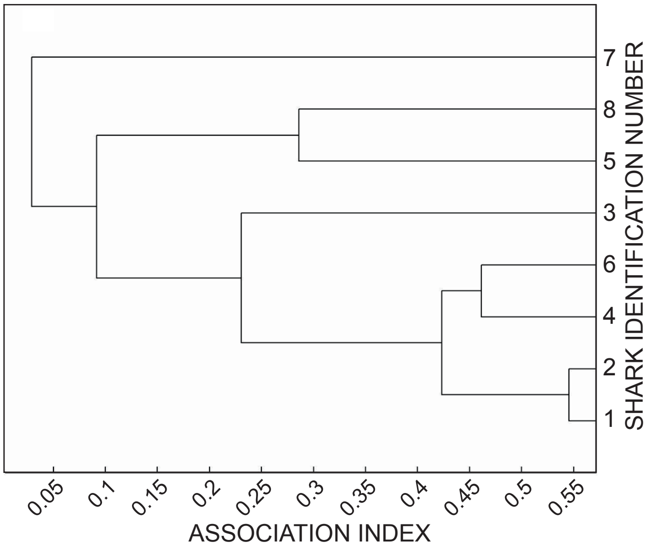

Figure 5: Cluster analysis of associations between identified sharks (1–8)

adult and juvenile sharks of various species, but individual association patterns have received relatively little attention (Jacoby et al. 2012). For example, juvenile lemon sharks *Negaprion brevirostris* are known to have preferred companions in some locations, with individuals spending time with similar-sized individuals (Guttridge et al. 2009). Predator avoidance is likely to be a major driver of grouping and social interactions among juvenile sharks (Guttridge et al. 2013). Because of the large body sizes of bull sharks in our study, antipredator benefits are very unlikely to be a driver of preferred associations observed in some individuals. Other drivers that could explain the associations include improved foraging efficiency and reproduction (Economakis and Lobel 1998; Heupel and Simpfendorfer 2005). Our recordings include footage of two bull sharks foraging in association on the benthic substratum, which could support the foraging-efficiency hypothesis. However, our dataset is too limited to be conclusive. Male reproductive strategy promotes frequent mating with multiple receptive partners and could negatively impact female fitness due to the aggressive nature and energetic expense of mating (Pratt and Carrier 2001). Female associations might constitute a strategy to improve detection and deterrence of males, or might be a consequence of habitat segregation of female and male bull sharks.

The most noticeable advantage of video sampling is to observe the behaviour and swimming patterns of sharks, alone or in association with conspecifics. There are descriptions and observations of close-following behaviours in a number of shark species, including blacktip reef sharks, whitetip reef sharks *Triaenodon obesus*, nurse sharks *Ginglymostoma cirratum* and basking sharks *Cetorhinus maximus*, both in the wild (Carrier et al. 1994; Sims et al. 2000) and in captivity (Myrberg and Gruber 1974; Klimley 1980; Mourier et al. 2012). Straight-line synchronised swim might reflect hierarchy among individuals (Myrberg and Gruber 1974). Guttridge et al. (2009) hypothesised that smaller sharks follow larger (older) individuals because the latter have accumulated more information about the habitat, predators and prey. Observation of lemon sharks (Guttridge et al. 2009) and bonnethead sharks *Sphyrna tiburo* (Myrberg and Gruber 1974), confirmed this hypothesis. Larger individuals tend to occupy a lead position in follow formations. In our study, larger individuals were not systematically in lead position, which suggests that leadership during swimming may not be related to body size and age.

This preliminary study shows the utility of unbaited video to study shark behaviour. Development of low-energy-consuming systems, as well as miniaturisation and cost reduction of video technology, facilitates the use of such monitoring methods, especially in areas with relatively high shark abundance. Future studies that incorporate unbaited video technology, paired with a record of environmental variables, will greatly enhance our current understanding of shark behaviour and of the nature and dynamics of social interactions within their community.

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