

Marine Environment & Ecology



Effects of a cage-diving operation on the fine-scale movement of white sharks (*Carcharodon carcharias*)



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Final Report to the Department of Environment, Water and Natural Resources Wildlife
Conservation Fund and the Nature Foundation of South Australia



Government
of South Australia



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EXECUTIVE SUMMARY

This study investigated the fine-scale movement patterns of white sharks (*Carcharodon carcharias*) to assess the effects of the cage-diving industry at the Neptune Islands, South Australia. We compared the behaviour and swimming patterns of white sharks during berleying and non-berleying periods, and assessed the effects of the cage-diving operations on the swimming behaviour of white sharks.

A Vemco Radio-Acoustic Positioning (VRAP) system was deployed to monitor the fine-scale movement, and vertical and horizontal distribution of 21 acoustically tagged white sharks at the North Neptune Islands for three monitoring periods ranging from 96 to 187 days. A total of 22,329 locations were estimated, with individual sharks monitored for 1 to 17 days.

The size of the area in which white sharks spent 50% of their time was reduced by 28% when shark cage-diving operators (SCDO) were present. Sharks also swam at shallower depths during berleying periods. This suggests that the presence of SCDO changed the horizontal and vertical distribution of white sharks, and concentrated their three-dimensional spatial distribution into a small area around the berley source and at the surface in proximity to the teaser bait.

The amount of time white sharks spent within the monitored area increased when SCDO were present, with sharks also spending significantly more time in close proximity to the SCDO.

Location data indicated that white sharks did not always remain in close proximity to SCDO. On 34% of the days in which both operators and white sharks were present, sharks stayed more than 30 m from the SCDO, or left the study area before the operators arrived.

In situations when two SCDO were present simultaneously, all but one white shark were observed to partition their time between the two operators.

The white sharks monitored were not equally affected by the SCDO. This was observed in the proportion of detections obtained during berleying periods, the proportional amount of time spent in close proximity to the SCDO, swimming depth, rate of movement, and time partitioning between operators.

Since sharks present at the berleying site did not always directly interact with the SCDO, a combination of photo-identification and fine-scale positioning is necessary to define the nature and variability of direct interactions between white sharks and the SCDO.

Consideration should be given to recording additional parameters to account for the range of factors involved with SCDO that can impact white shark behaviour. The amount of berley used or the number of teaser baits consumed by white sharks may have a greater impact on the behaviour of white sharks than the number of days SCDO are present.

The disturbance caused by white shark cage-diving at the Neptune Islands is currently confined to one location. A better understanding of white shark population structure, and the fraction of the population visiting the Neptune Islands, would help to resolve the extent of possible impact by the cage-diving industry.

This study quantified for the first time how the fine-scale horizontal and vertical distribution of white sharks is modified by the SCDO. The impacts of these changes in terms of increased physiological costs (metabolic rate) and energetics are currently unknown and need to be investigated to better examine the potential impacts of the cage-diving industry.

1 INTRODUCTION

Growing motivation to experience natural environments has resulted in the development of a global wildlife tourism industry (Wearing and Neil, 2009). In recent decades, wildlife tourism has become increasingly popular and is one of the fastest growing sectors of the tourism industry (Scheyvens, 1999; Wearing and Neil, 2009). Despite its aim of bringing people closer to nature, wildlife tourism is often considered a threat to wildlife and ecosystems (Duffus and Dearden, 1990; Shackley, 1996), with the effects of such activity having been investigated for a range of taxa including avian, terrestrial, and marine organisms (Bejder *et al.*, 2006; Worlf and Croft, 2010; Steven *et al.*, 2011). Documented impacts vary from short-term changes in physiology (e.g. temperature, heart rate or stress hormone secretion) or behaviour (e.g. foraging, breeding, vigilance and evasion) of individual animals through to long-term effects, such as increased mortality or reduced breeding success (Green and Higginbottom, 2001; Orams, 2002; Green and Giese, 2004).

The feeding of wildlife has become a popular means to enhance wildlife tourism experiences and ensure close observation and interactions. The effects of provisioning wildlife have only begun to be empirically examined (Orams, 2002; Newsome and Rodgers, 2008). Regular provisioning of various predators has been shown to lead to increased population densities and competition (Asquith, 1989; Sullivan, 1990; Semeniuk and Rothley, 2008); increased frequency and duration of aggressive behaviours (Perrine, 1989; Orams *et al.*, 1996; Hodgson *et al.*, 2004; Hsu *et al.*, 2009; Clua *et al.*, 2010a); and physiological indications of impaired health through lower hematocrit and serum protein concentrations, and oxidative stress (Semeniuk and Rothley, 2009).

A review of shark-related wildlife tourism identified that some form of attractant is used at over 40% of the 267 reviewed sites to increase encounter rates and keep the focal species within viewing distance of clients (Carwardine and Watterson, 2002). The logistical difficulties associated with studying large marine predators have led to their responses to feeding remaining poorly understood. Nevertheless, research on the impacts of tourism and berleying on sharks has recently emerged, with studies investigating the physiological impacts of provisioning (Semeniuk *et al.*, 2007; Maljković and Côté, 2011); changes in seasonality, residency or abundance due to berleying or provisioning (Bruce *et al.*, 2005; Laroche *et al.*, 2007; Meyer *et al.*, 2009; Clua *et al.*, 2010a; Bruce and Bradford, 2011; Maljković and Côté, 2011); changes in vertical movements (Fitzpatrick *et al.*, 2011); and physical impacts of divers (Smith *et al.*, 2010; Barker *et al.*, 2011b; Barker *et al.*, 2011a). Studies of the impact of tourism and feeding activities can, however, be difficult. For

example, the lack of a control and the use of non-defined terms to characterise observed behaviours led to contentious findings on the impacts of feeding on sicklefin lemon sharks (*Negaprion acutidens*) at Moorea Island (see Brunnschweiler and McKenzie, 2010; Clua *et al.*, 2010a; Clua *et al.*, 2010b). The lack of a uniform effect across species and populations (see Meyer *et al.* (2009) and Maljković and Côté (2011) vs. Clua *et al.* (2010a) and Bruce and Bradford, (2011)) also suggests that findings cannot be generalised and may vary according to the frequency and types of activities as well as the targeted species.

The white shark (*Carcharodon carcharias*) occurs world-wide in coastal temperate and subtropical regions (Klimley and Ainley, 1996; Domeier, 2012). White sharks are long-lived, relatively slow growing, late in maturing, and low in reproductive potential (Cailliet *et al.*, 1985; Wintner and Cliff, 1999). This combination of life-history traits, and world-wide concerns regarding their population status, has prompted their protection across a number of jurisdictions. This includes listings under the International Union for the Conservation of Nature (IUCN – ‘Vulnerable’), the Convention on International Trade in Endangered Species (CITES – Appendix I + II), and the Convention on Migratory Species (CMS – Appendix I + II), all of which Australia is a signatory country. White sharks are listed as ‘Vulnerable’ under the Australian Commonwealth Government’s *Environment Protection and Biodiversity Conservation (EPBC) Act 1999* and are protected in all Australian and Commonwealth waters. However, as identified by the *National Recovery Plan for White Sharks*, the Australian white shark population is still threatened by interactions with commercial and recreational fishing, shark control activities, illegal trade in body parts, and the potential impacts of ecotourism and cage-diving operations (DEWHA, 2010).

Sites where white sharks aggregate are often targeted by wildlife tourism operators to run cage-diving tours. As a result, these sites are areas where white sharks can be exposed to frequent interactions and a high level of interference from human activities. For example, some sites in South Africa have up to seven different cage-diving operators working simultaneously, with some cage-diving operators hosting up to three expeditions per day.

The Neptune Islands are within a recently declared marine park located in the shelf waters of the eastern Great Australian Bight off South Australia. These islands support the largest aggregation of pinnipeds in Australia (Shaughnessy and McKeown, 2002; Goldsworthy and Page, 2007), and are presumed to be a feeding area for white sharks. This archipelago is currently the only area open to white shark cage-diving in Australia. Since 2000, two operators have possessed permits to take tourists on cage-diving trips, during which they commonly use berley (mixture of minced fish and blood) and teaser baits to attract sharks

close to the boat for viewing. In 2007, the cage-diving operators increased their activity from about 120 to 250 days per year (Bruce and Bradford, 2011), and additional expressions of interest and cage-diving license applications were received by the South Australian Government in 2009. Two additional licences were issued but those operators remained inactive until 2011, when one started operations without releasing berley. Consequent to the increased interest, a review of the white shark cage-diving tourism policy took place, and included a re-assessment and re-allocation of the licenses to undertake cage-diving activities. As a result of the review, a total of three licenses were allocated in May 2012 through a competitive expression of interest.

There is limited information on the extent of interactions of white sharks with cage-diving industries. In South Africa, sharks were found to swim closer to the surface during berleying (Laroche *et al.*, 2007). A trend of decreasing response to berley and teaser bait with time was also observed, suggesting that habituation was occurring (Laroche *et al.*, 2007). The majority of sharks, however, showed little interest in the food rewards being offered. In South Australia, a preliminary study examining the effects of berleying on the residency of white sharks between 2001–03 found that they appeared to be localised, with some evidence that individual sharks were attracted to the immediate vicinity of cage-diving operations (Bruce *et al.*, 2005). A more recent study was carried out to determine whether there was evidence of a change in the behaviour of white sharks in response to the increase in the South Australian cage-diving operations since 2007 (Bruce and Bradford, 2011). This study showed increases in residency and duration of visits (defined as the number of consecutive days with detections for any given shark during its residency period), average number of sharks, and changes in the temporal distribution of visits to match cage-diving operations (Bruce and Bradford, 2011). These previous studies, however, used acoustic telemetry that generated presence/absence data, but did not provide information about the fine-scale movements of sharks or whether they are directly interacting with cage-diving vessels.

Previous studies have investigated the large-scale movements of juvenile and adult white sharks and reported long-distance migrations between temperate, subtropical, and tropical habitats, as well as some temporal residency within oceanic regions (Boustany *et al.*, 2002; Bonfil *et al.*, 2005; Bruce *et al.*, 2006; Weng *et al.*, 2007; Domeier and Nasby-Lucas, 2008; Jorgensen *et al.*, 2009; Duffy *et al.*, 2012). The fine-scale movements of white sharks are more poorly understood, with research mostly focusing on predator-prey interactions in the vicinity of seal colonies in the Northern Hemisphere and on the South African coastline (Klimley *et al.*, 2001b; Laroche *et al.*, 2008; Martin *et al.*, 2009; Domeier *et al.*, 2012). The fine-scale spatio-temporal distribution of white sharks is often related to the habitat use of

their prey such as the Guadalupe fur seal around Guadalupe Island, Mexico (Domeier *et al.*, 2012), or Cape fur seal around Seal Island, South Africa (Laroche *et al.*, 2008). Several movement patterns have also been described in situations when berleying had taken place, including downstream circling, island patrolling, and inter-island patrolling (Strong *et al.*, 1992; Klimley *et al.*, 2001b).

We present a complementary study to the broad-scale analysis of the effect of the cage-diving industry on the residency times, site use, and behaviour by Bruce and Bradford (2011). We used continuous tags and a radio-acoustic positioning system that enabled modeling of the position of tagged sharks with precision of up to 1 m to infer the fine-scale movements of white sharks and the level of direct interactions with cage-diving vessels. We aimed to examine the behaviour of sharks when exposed to the cage-dive industry and assess the effects of the cage-diving industry on the vertical and horizontal distribution, and rate of movements (ROM) of white sharks. The effects of cage-diving operations on sharks can arise from a range of factors including the presence of the vessel, cage and divers in the water, or the use of berley, teaser baits or other means to attract and interact with sharks. The relative importance of these individual components is difficult to assess and could not be addressed in this study. As such, this report will refer to shark cage-diving operators (SCDO) to encompass all the possible causal factors related to the activities of the cage-diving industry.

2 METHODS

2.1 Study site

The Neptune Islands are located near the approach to Spencer Gulf, about 30 nautical miles south-southwest of Port Lincoln and about 15 nm from the Australian mainland (Figure 1). The Neptune Islands are part of the Neptune Islands Conservation Park and have recently been included within the South Australian marine park network. The Neptune Islands have been a site for commercial cage-diving with white sharks since the late 1970s. While other areas were previously also used for cage-diving, all commercial operations were restricted to the Neptune Islands Conservation Park in 2002. While the waters surrounding the South and North Neptune Island groups are open to cage-diving operations, the North Neptune Islands group ($35^{\circ}149\text{ S}$; $136^{\circ}049\text{ E}$) is most frequently used by the current operators.

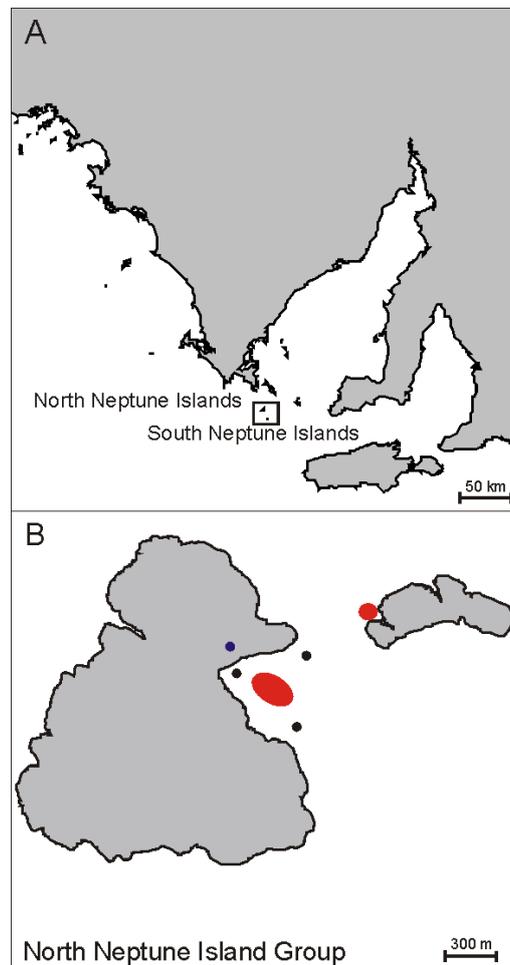


Figure 1. Location of (A) the North and South Neptune Island groups and (B) VRAP system deployment in relation to the North Neptune Island group. The blue circle represents the location of the shore station; black circles represent the location of the three VRAP buoys; and red circles represent the main areas where shark cage-diving operators anchored.

Water depth rapidly increases to 80 m within 200 m of the western shoreline of the North Neptune Islands and about 60 m on the southern and northern shores. The bay in which the radio-acoustic positioning system was deployed is relatively shallow, averaging 20 m, with a maximum depth of about 30 m. Benthic substrate is mostly sand with seagrass patches, rocky reef outcrops and ledges.

2.2 Shark cage-diving operators (SCDO)

Two cage-diving vessels that release berley and use tuna teaser baits operated during the study period (14/12/2009 to 30/09/2011). Calypso Star Charters conducted regular day trips during which they arrived around 09:30 and departed between 14:00 and 17:00 depending on shark activity and day length. Rodney Fox Shark Expeditions conducted three-day trips during which they arrived around 11:00, stayed for three days and left between 16:00 and 19:00 depending on shark activity and day length. Each operator recorded their arrival and departure time, the times during which they used berley and the vessel position (latitude and longitude) (Figure 1). A third operator that does not use berley or teaser bait (Adventure Bay Charters) conducted a small number of trips during the study period, but only operated within the monitored area when tagged sharks were present on two occasions. Subsequently, the third operator was excluded from the study due to the limited number of detections obtained and different type of attractant used.

2.3 Vemco radio-acoustic positioning system

A Vemco Radio Acoustic Positioning (VRAP) system (Vemco Ltd., Halifax, Canada) was deployed in the bay on the southeast side of North Neptune Island (Figure 1). The deployment location of the VRAP system was chosen to take into account the most frequent site where cage-diving vessels used berley and where shark abundance has historically been the highest (winter/spring months from about June–September) (Bruce and Bradford, 2011).

The VRAP consisted of three surface buoys deployed in a near equilateral triangle (distances between buoys ranged from 0.324 to 0.340 km, area = 0.052 km²) and a shore station in line-of-sight. The locations and distance between the buoys were chosen to ensure that all three hydrophones could detect sharks located in the middle of the array, taking into account environmental noise caused by adverse weather or natural biological noise, and to minimise exposure to extreme weather. O'Dor *et al.* (1998) and Klimley *et al.* (2001a)

provide a detailed description of how the VRAP system estimates the position of tagged organisms. In summary, each buoy is equipped with a multi-directional hydrophone which detects pulses emitted by the transmitters. The received information is transmitted to the shore station via radio signals where the geographic position (latitude and longitude) of each shark fitted with a transmitter is triangulated based on the arrival times of the acoustic pulses to each buoy. As the transmitters were also fitted with a pressure sensor, the depths of the tagged sharks were also recorded by the buoys.

The shore station was installed on North Neptune Island and was powered by a 167Ah gel battery and two Solar-E 80W solar panels installed with a Powerstar 12 V 20A regulator. Buoys were powered by one Solar-E 20W solar panel installed with a Morningstar 4.5A regulator. The buoy positions were calibrated by the VRAP at the start of each deployment. Further calibration of the buoy positions after the initial calibration was unnecessary as the buoys were securely moored. The VRAP was set to listen to each selected frequency for 10 seconds with the number of frequencies selected at any one time ranging from one to nine. As a result, and taking into account the time necessary for the buoys to send the data to the shore station, the ten-second listening period was repeated every 15 to 150 seconds.

The VRAP system has previously been used for a range of species including lobster (Lucieer and Pederson, 2008), cephalopods (O'Dor *et al.*, 2002), fish (Løkkeborg *et al.*, 2002; Jadot *et al.*, 2006), and sharks (Klimley *et al.*, 2001b; Barnett *et al.*, 2010). Previous studies have indicated that the precision of the locations estimated by the VRAP system can be up to ± 1 m (Zamora and Moreno-Amich, 2002; Barnett *et al.*, 2010). The deployment of sentinel transmitters showed a similar level of precision in the middle of our VRAP array.

2.4 Tagging

Twenty-one white sharks were tagged with continuous V16P-5H acoustic transmitters (VEMCO Ltd., Halifax, Canada) between 13 December 2009 and 11 September 2011. Transmitters recorded depths of tagged sharks via a calibrated pressure sensor (accuracy ± 3.4 m). Transmitters were programmed to transmit every ~ 1 second and had a predicted battery life of ~ 50 days. Transmitters were glued to a small anti-fouled net float with waterproof Araldite to ensure that transmitters would remain above the shark's skin and reduce the likelihood of any potentially harmful effects from abrasion. The net float was tethered to a plastic umbrella dart using a 10–15 cm long stainless wire trace (1.6 mm diameter). Sharks were attracted to the boat with berley and a section of tuna tied to a rope

teaser line. Transmitters were implanted in the dorsal musculature of sharks using a pole and stainless steel applicator.

2.5 Data analysis

Data visualisation and analysis was carried out using Eonfusion version 2.2 and 2.3 (Myriax, Hobart, Australia), IBM SPSS Statistics version 19 (IBM Corporation, New York, USA), and R statistical software version 2.15.0 (R Development Core Team, 2011).

Data processing and filtering

Positions estimated by the VRAP were filtered using a six-step process to remove erroneous and inaccurate data points. The data were filtered as follows:

1. Six days were removed from the analysis due to faulty hydrophones on the VRAP buoys and to the presence and/or location of SCDO not being recorded by the operators.
2. As the intervals between transmissions were sometimes slightly shorter than one second and the VRAP system did not record milliseconds, two location estimates were sometimes provided for the same time stamp (duplicates). When this occurred, the duplicates were removed and replaced with an averaged location estimate;
3. Position estimates that were on land or greater than 700 m from the edge of the VRAP array were removed.

The time difference, distance, and rate of movement between two consecutive location estimates were calculated using the Eonfusion add-in operator 'Velocity and Acceleration'. Additional filters based on the estimates obtained were then applied as follows:

4. Consecutive location estimates with time differences greater than 5 minutes were removed. This threshold allowed the shore station to go through two full cycles, while reducing the risk of under-estimating rate of movement from sharks leaving and re-entering the VRAP array;
5. Consecutive location estimates with distances larger than 200 m were removed. Such distances would have likely resulted from location estimates at the edge of or outside the VRAP array, where precision is the worst;
6. Rates of movement more than 10 ms^{-1} were also excluded due to the physical limits on swimming speed of lunate tail propelled aquatic animals, such as white sharks (Iosilevskii and Weihs, 2008).

Following filters 1–3, location estimates were categorised by the presence or absence of SCDO. For each 'SCDO-present' location estimate, the distance between the white shark

and each SCDO was calculated. Based on these calculations, location estimates were binned into one of the following groupings: 0–29.9 m, 30–59.9 m, 60–89.9 m, 90–119.9 m, and >120 m.

Data analysis

Impact of cage-dive operations on timing of detections

The percentage of detections for each hour of the day was compared between when SCDO were present and when they were absent using a Kolmogorov-Smirnov (K-S) test (Massey, 1951) to determine whether cage-diving operations had an effect on the timing of detections of white sharks. Time of initial detection within 30 m of SCDO was also compared to the time of initial detection once an SCDO was present. This provided an estimate of how long sharks took to approach within 30 m of SCDO.

Impact of cage-dive operations on horizontal distribution and time spent in the area

The horizontal distribution and amount of time white sharks spent in the VRAP array between berleying and non-berleying periods was investigated using several metrics:

- 1) The spatial distributions of the sharks between berleying and non-berleying periods were compared using 'time-spent-in-area' analysis within a 10x10 m grid of the study site. Locations were interpolated, based on equal-time spacing between records and binned to a grid of cells with the time spacing of 1,000 seconds. The cells with the highest relative proportion of time spent and accounting for 50% of total amount of time spent in the area were then plotted in relation to the position of the SCDO, and compared for non-berleying and berleying periods.
- 2) The relative amount of time sharks were present during berleying was expressed as a ratio between the probability of being detected within the VRAP array when SCDO were present and absent. The likelihood of white sharks spending more time within the VRAP array when SCDO were present was tested by comparing the relative amount of time present against 0.5, which represents equal time spent in the VRAP array regardless of SCDO presence. Only time periods between 08:00 and 19:00 were included to avoid biases introduced by potential diel differences (i.e. low rate of detections at night).
- 3) During berleying, the time spent within each distance bin of the SCDO was also calculated.
- 4) Time spent within these distances was then standardised for all sharks to take into account the different surface areas of the various ranges. For example, the circular area within 30 m of an SCDO was ~2,800 m², while the area more than 120 m away covered ~354,800 m². The difference in time spent within each distance bin was

assessed using a Generalised Additive Mixed-Model (GAMM) to account for the lack of independence in behaviour within each identified shark and because the relationships between the dependent and independent variables were not linear. Individual sharks were included in the model as the 'random effect' and the distances from the boat as the 'fixed effect'. The error structure of GAMM corrects for non-independence of statistical units due to shared temporal structure, and permits the 'random effects' variance explained at different levels of clustering to be decomposed. The most appropriate statistical family, error distribution, and validity of the model were determined through an examination of the distribution of the response variable, a visual inspection of the residuals for the saturated models, and an ANOVA test between the fitted and residual values of the model. Modelling was undertaken using the 'gamm' function and restricted maximum likelihood approach of the 'mgcv' R package.

Impact of cage-dive operations on swimming depth and rate of movement

The time interval between consecutive detections and three-dimensional distance between the estimated locations (taking into account vertical distance (depth) as well as horizontal distance) were used to calculate the rate of movement between each consecutive location estimates in Eonfusion. The depth (provided by the VRAP system), and the calculated rate of movement of white sharks, were compared between berleying and non-berleying periods using a GAMM with individual shark as the 'random effect' and the presence/absence of SCDO as the 'fixed effect'. Since the swimming behaviour of white sharks might only be impacted by SCDO when within a certain distance from the vessels, a similar analysis was undertaken comparing the depth and rate of movement when sharks were within each distance bin. Model validity was assessed similarly to the GAMM carried out on the time spent in area.

Time partition between SCDO

The VRAP array enabled the comparison of time spent by sharks that were moving between the two operators. When both SCDO were present simultaneously, the percentage of detections within each distance bin from each SCDO was calculated for each shark to assess whether sharks spent most of their time interacting with one SCDO only, or if sharks were partitioning their time between vessels.

Temporal correlations

Temporal correlations were assessed to test whether the effects of SCDO were influenced by the number of days exposed to berleying. The total amount of time sharks spent in the

VRAP array, spent in the array during berleying periods, and within 30 m of the SCDO, were tested for correlation with the day number since tagging. Additionally, the time difference between vessel and shark arrival (following vessel arrival) and between shark arrival and the time at which sharks were within 30 m of SCDO for the first time, were also tested for correlation with the day number. These correlations were tested by estimating the Pearson product-moment correlation coefficient (PPMCC). PPMCC of $\pm 0.9-1$, $0.7-0.9$, $0.5-0.7$, $0.3-0.5$, and $0-0.3$ were considered as very strong, strong, moderate, weak, and little if any correlation, respectively.

For all statistical analyses, $P < 0.05$ was considered statistically significant. Values provided in the results are mean \pm standard error, unless stated otherwise.

3 RESULTS

Between November 2009 and September 2011, the VRAP system was deployed at the same location for three monitoring periods ranging from 96 to 187 days. The three deployments were necessary to gather a large enough sample size due to the lack of white sharks around the Neptune Islands during the first deployment and technological difficulties with the VRAP system during the second and third deployments, including hydrophones that failed within three days of deployment. Throughout the duration of the study, the VRAP system was operational, and tags were deployed and active, for a total of 178 days.

A total of 21 white sharks were tagged. Two, ten, and nine sharks were tagged and monitored during the first, second, and third deployment periods, respectively (Table 1). The monitored period varied between sharks and ranged from 1 to 19 days (mean 5.4 ± 1.5 days). During these monitored periods, sharks were detected an average of 3.5 ± 0.9 days (range 1–17). No locations were estimated for three of the 21 tagged sharks (shark 2, 12, and 15). A total of 22,329 location estimates were obtained, with the number of estimates per shark averaging $1,063 \pm 334$ (range 0–6,116).

Twenty-four percent of the data were removed following filters 1–3 (range for individual sharks 14–100%). Although sharks 4 and 5 provided a total of more than 180 and 400 location estimates, respectively, faulty hydrophones throughout their monitoring periods led to the exclusion of these sharks. Four sharks (6, 7, 8, and 11) were also removed due to the low number of location estimates remaining after applying these filters. Data from the remaining 12 sharks were used to analyse the effects of cage-diving operations on white sharks at the Neptune Islands. Following filters 4–6, another 28% of positions were removed, leaving 48% of estimated positions (range 0–55%) (Table 1).

Out of the 178 days of the study period, sharks were detected on 36 days, during which at least one SCDO operated on 25 days (69%). The proportion of detections during berleying days was higher, with 84% of the detections obtained when at least one SCDO was present. Throughout the study period, there were several days during which more than one shark was detected by the VRAP system, increasing the sample size of the study. For example, two sharks detected in one day represented two replicates. Accounting for individual sharks, a shark was detected on 64 days, during which berleying took place on 45 days (70%). Out of these, six days were removed from further analysis as berleying took place outside the range of the VRAP array. Out of the remaining 39 days when berleying took place, there were five days (13%) when white sharks were not present concurrently with an SCDO, with

an additional eight days (21%) when sharks never approached within 30 m of an SCDO. Combined, white sharks did not directly interact with an SCDO on 34% of the days in which both operators and white sharks were present.

Table 1. Summary of tagged sharks and detections obtained before and after data filters. Total length was estimated using the length of the marlin board as a reference; location estimate is the number of location estimates recorded by the VRAP system prior to any filters; Clipped location is the number of location estimates remaining after filters 1–3; % clipped is the percentage of location estimates clipped by filters 1–3; Filtered location is the number of location estimates remaining after filters 4–6; % filtered is the percentage of location estimates filtered by filters 4–6.

Shark	Total length (mm)	Sex	Date tagged	Last transmission	Days detected	Location estimate	Clipped location	% clipped	Filtered location	% filtered
1	3600	Male	14/12/2009	15/12/2009	2	413	320	23%	187	32%
2 [*]	3500	Male	18/01/2010	18/01/2010	0	0	0	-	0	-
3	3300	Female	26/06/2010	27/06/2010	2	641	497	22%	282	34%
4 ^{**}	3000	Female	27/06/2010	29/06/2010	3	418	0	100%	0	0%
5 ^{**}	4500	Female	27/06/2010	29/06/2010	3	182	0	100%	0	0%
6 ^{***}	2500	Female	17/08/2010	17/08/2010	1	5	3	40%	0	60%
7 ^{***}	4200	Female	17/08/2010	17/08/2010	1	2	1	50%	0	50%
8 ^{***}	4000	Male	4/10/2010	4/10/2010	1	7	6	14%	0	86%
9	4000	Male	14/10/2010	1/11/2010	12	3830	2964	23%	1842	29%
10	3500	Male	22/10/2010	2/11/2010	5	2714	2085	23%	1427	24%
11 ^{***}	3800	Male	22/10/2010	22/10/2010	1	11	8	27%	6	18%
12 [*]	4200	Male	12/12/2010	12/12/2010	0	0	0	-	0	-
13	4500	Female	5/07/2011	7/07/2011	3	1466	1103	25%	755	24%
14	2900	Male	5/07/2011	7/07/2011	3	576	423	27%	286	24%
15 [*]	4000	Male	6/07/2011	6/07/2011	0	0	0	-	0	-
16	3600	Male	6/07/2011	7/07/2011	2	1263	916	27%	469	35%
17	3800	Female	6/07/2011	7/07/2011	2	771	554	28%	373	23%
18	2800	Male	6/07/2011	7/07/2011	2	1339	988	26%	720	20%
19	3500	Female	11/09/2011	30/09/2011	4	798	617	23%	413	26%
20	4000	Male	11/09/2011	26/09/2011	9	1777	1330	25%	885	25%
21	4200	Male	11/09/2011	28/09/2011	17	6116	4608	25%	3034	26%
TOTAL					73	22329	16423	24%	10679	28%

^{*} sharks not detected by VRAP array

^{**} sharks removed from further analysis due to location estimates obtained on days with faulty hydrophones

^{***} sharks removed from further analysis due to small number of location estimates following filter 1–3

3.1 Impact of cage-dive operations on the timing of detections

Tagged white sharks were mostly detected during the day, with more than 50% of the location estimates obtained between 10:00 and 15:00. The comparison between days when SCDO were present and absent shows that tagged sharks were mostly detected during the day regardless of the presence of SCDO. However, the peak in the percentage of detections was lower, broader, and started and finished earlier when SCDO were not present (07:00–14:00 vs. 10:00–15:00, when SCDO were absent and present, respectively), leading to a significant difference in the distribution of detection times (K-S test: $t_5=12.42$; $P<0.001$) (Figure 2). On average, it took 90 minutes (range 1–371 minutes) from the arrival of a SCDO for sharks to be detected within the array, with an additional 44 minutes (range 0–212 minutes) for sharks to approach within 30 m of the SCDO.

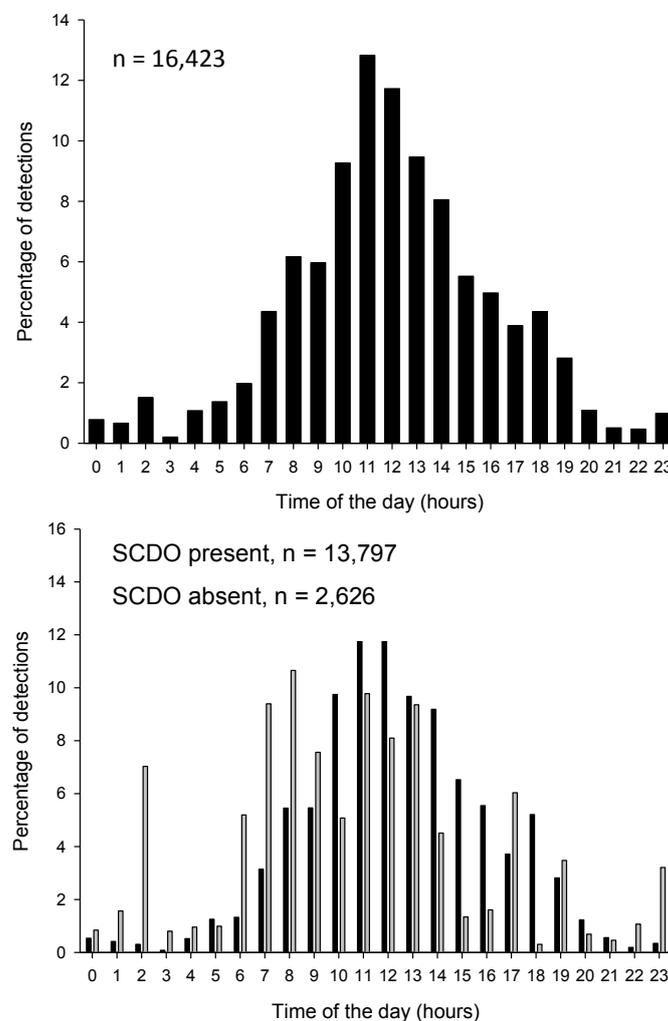


Figure 2. Hourly percentage of detections for (a) all sharks and days combined, and (b) during days when SCDO were present (black bars) and absent (grey bars). 'n' represents the number of detections.

3.2 Impact of cage-dive operations on horizontal distribution and time spent in the area

The horizontal distribution of sharks was affected by SCDO, with the area in which they spent 50% of their time decreasing 28% from 0.0362 to 0.0262 km² (Figure 3). Most of the time spent by sharks during berleying periods was in close proximity to SCDO. Although sharks were still within the same area when berleying was not occurring, sharks were less concentrated in one area (Figure 3).

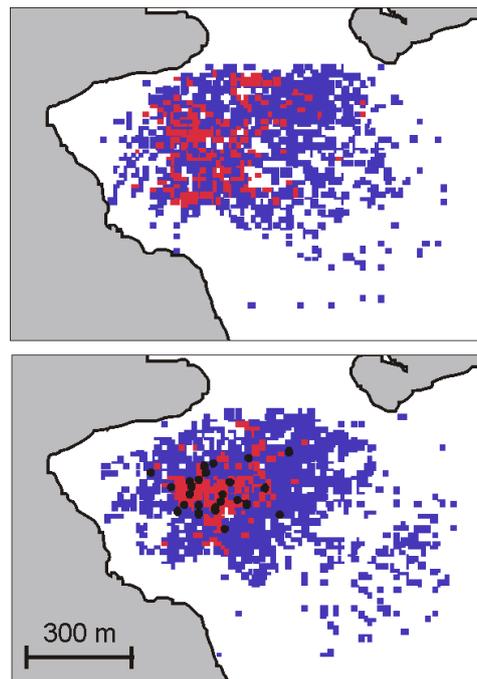


Figure 3. Time spent in area by white sharks during non-berleying (top figures) and berleying (bottom figures) periods. Blue represent total amount of time spent with red representing 50% of time spent. Black circles represent SCDO locations throughout the monitoring period.

The amount of time between 08:00 and 19:00 that sharks spent in the VRAP array varied between sharks and in response to the presence of vessels. For example, sharks 19 and 20 were only detected between 08:00 and 19:00 for about 15% of the time (only counting days on which they were detected at least once). On the other hand, sharks 13 and 15 were detected more than 60% of the time (albeit they were only detected for three and two days, respectively). The relative amount of time in the array during berleying was highly variable and ranged from 0 to 1, with some sharks only detected when SCDO were absent, while others were only detected during berleying operations. Four sharks were in the array more than twice as long when SCDO were present compared to when SCDO were absent (i.e. relative amount of time > 0.7). The average relative amount of time spent within the array during berleying was 0.56. This was not significantly different to 0.5 (t-test: $t_{11}=0.75$; $P=0.47$),

indicating that the average amount of time in the array was similar regardless of SCDO being present or absent (Figure 4).

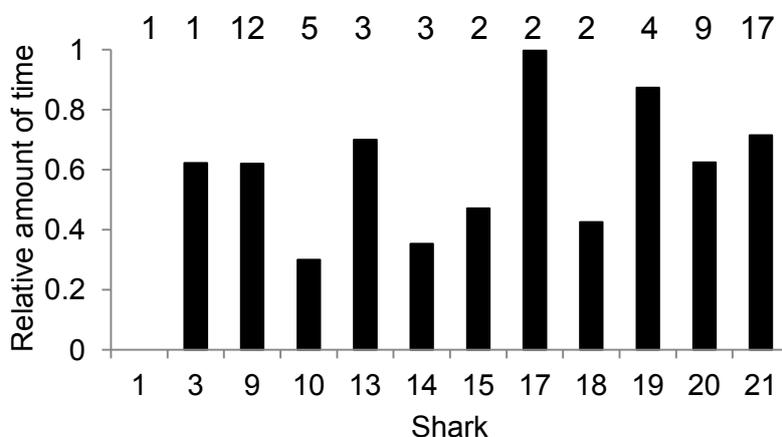


Figure 4. Relative amount of time spent within the VRAP array during berleying. Numbers above bars represent the number of days each shark was detected.

When an SCDO was present, sharks spent more than 65% of the time that they were detected within 30 m of an operator. Following results from the GAMM showing that the time spent in area was significantly different between distance bins (GAMM: $F=274.1$, $P<0.001$), pairwise comparison showed that sharks spent more time within 0–29.9 and 30–59.9 m from SCDO than within 60–89.9 m or more than 90 m from SCDO (Figure 5).

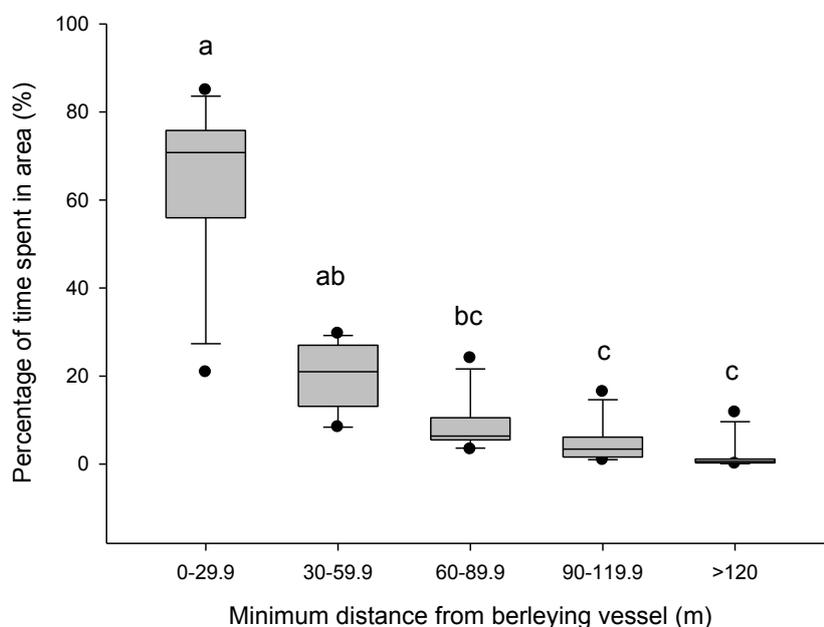


Figure 5. Percentage of detections obtained within various distances from SCDO standardised to take into account the dimensions of the area covered within these distances. Bars with the same letters above represent groups not significantly different. Median values are indicated by the bold horizontal bar; the length of the box is the inter-quartile range; whiskers represent quartiles; and black circles are extreme values.

On average, sharks spent $48 \pm 5.5\%$ of the time within 60 m of the SCDO. While most sharks spent a large amount of time within 60 m of SCDO, there was significant variation between individuals. For instance shark 13 spent ~70% of the time in proximity to SCDO, compared to only 5% for shark 10 (Figure 6).

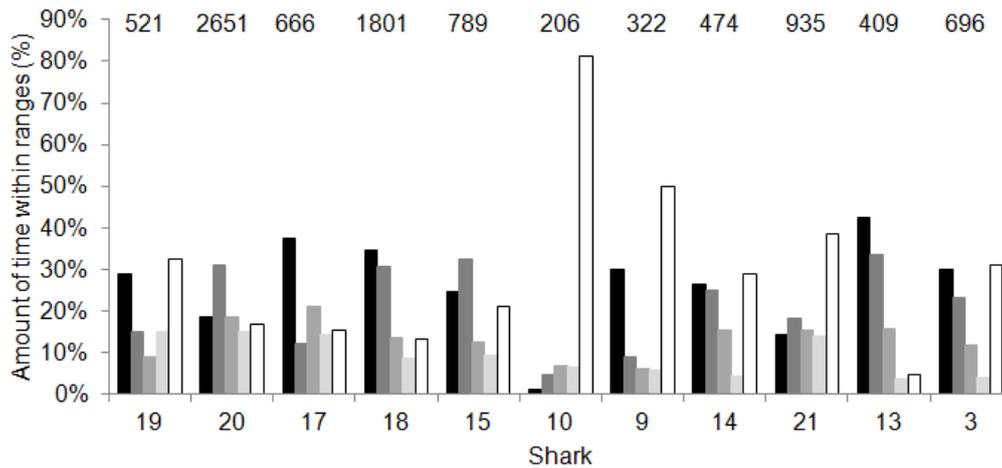


Figure 6. Proportion of time when white sharks were 0–29.9 (black), 30–59.9 (dark grey), 60–89.9 (medium grey), 90–119.9 (light grey), and more than 120 m (white) away from SCDO. Numbers above bars represent the number of detections when SCDO were present.

3.3 Impact of cage-dive operations on swimming depth

The mean swimming depth was significantly shallower when SCDO were present than when no berleying was taking place (GAMM: $t=-3.16$; $P=0.002$). The swimming depth of white sharks was also significantly different according to the distance from the SCDO, with a mean depth of 14 m within 30 m increasing to 20 m when greater than 120 m from SCDO (Figure 7, GAMM: $F=120$; $P<0.001$).

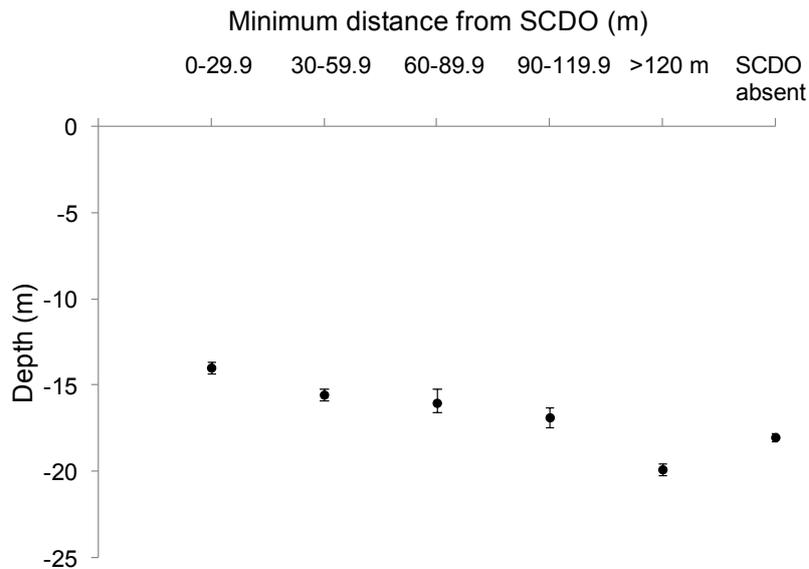


Figure 7. Mean swimming depth in relation to the distance to SCDO and when SCDO were absent. Error bars represent 95% confidence intervals.

3.4 Impact of cage-dive operations on rate of movement

The mean rate of movement of white sharks was not significantly different whether SCDO were present or absent (2.64 and 2.81 ms^{-1} , respectively) (GAMM: $t=0.10$; $P=0.921$). The rate of movement of white sharks was, however, significantly different according to the distance from the SCDO (GAMM: $F=11.16$; $P<0.001$). The rate of movement when sharks were greater 120 m away from SCDO (3.0 ms^{-1}) was faster compared to when sharks were in closer proximity ($2.4\text{--}2.5 \text{ ms}^{-1}$) (Figure 8).

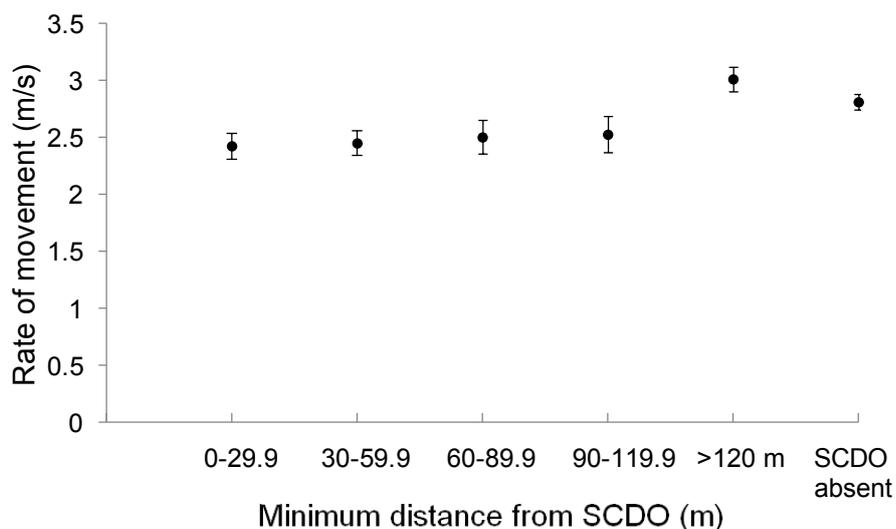


Figure 8. Mean rate of movement of tagged shark in relation to its distance to SCDO and when SCDO were absent. Error bars represent 95% confidence intervals.

3.5 Time partition between SCDO

When both SCDO were present, white sharks partitioned their time between the operators (Figure 9). While all but one shark visited both vessels (e.g., shark 3 was detected in equal percentages between the two SCDO), shark 21 was only detected in proximity to Calypso Star (32% within 60 m), and was never detected closer than 60 m to Princess II, with 90% of detections more than 120 m away from Princess II. Overall, sharks spent more time near Calypso Star (44% within 60 m) than Princess II (19% within 60 m). However, this trend was highly variable between sharks, with some spending more time in proximity to Princess II overall (e.g., shark 13 and 17 which spent 40% within 60 m of Princess II), while others spent more time in proximity to Calypso Star (e.g., shark 9 and 18 which spent ~45% within 30 m of Calypso Star).

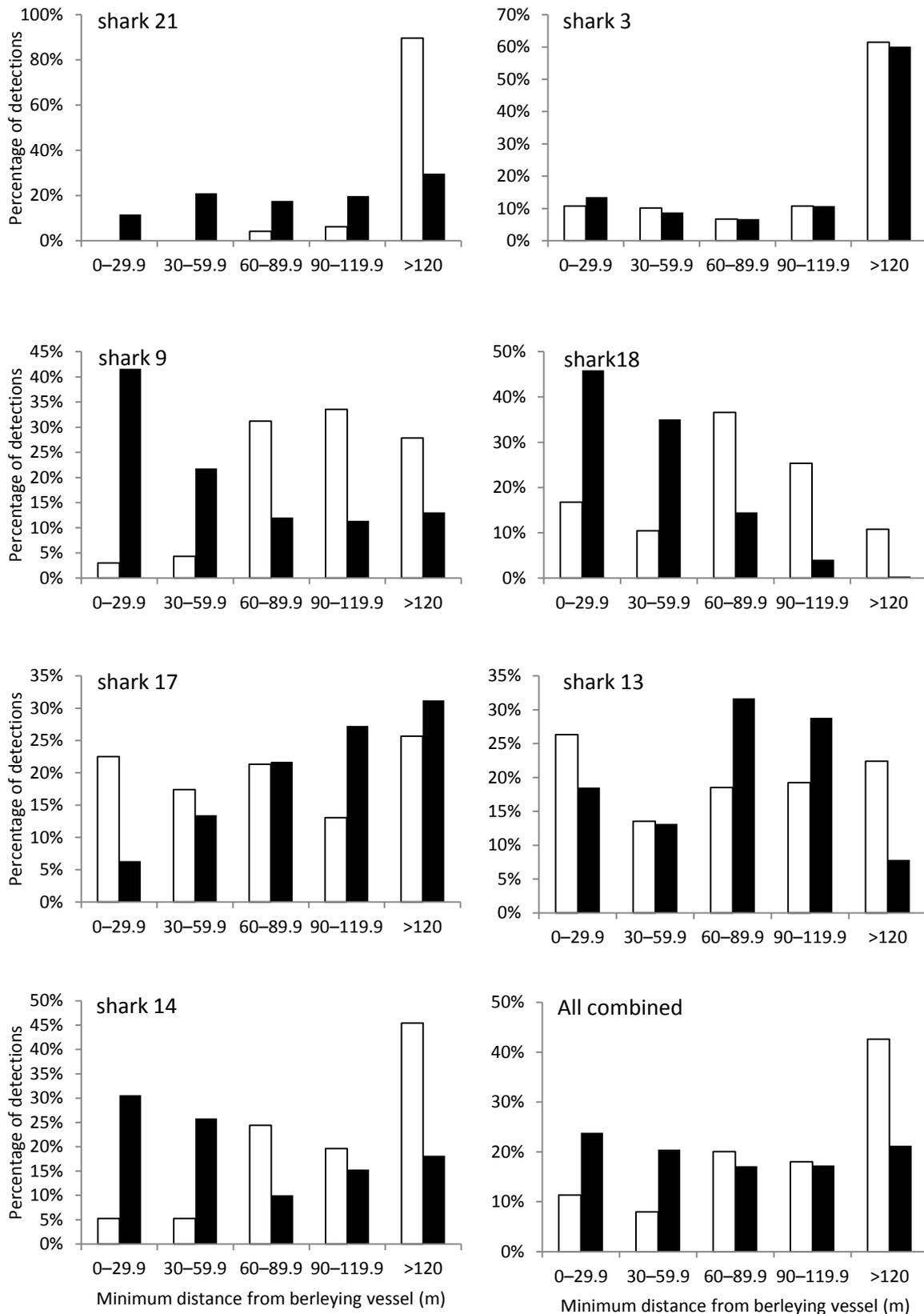


Figure 9. Percentage of detections obtained within various distances from Princess II (white bars) and Calypso Star (black bars) for each shark and all sharks combined.

3.6 Temporal correlations

The amount of time white sharks spent in the VRAP array in a day ranged from 7 seconds to nearly 5 hours. There was a weak negative correlation between the amount of time white sharks were present in the VRAP array and the day number since tagging (Figure 10a; PPMCC = -0.412). When analysing this correlation by individual shark for those which were monitored the longest, shark 21 also had a weak negative correlation (PPMCC = -0.418). The two other sharks with long monitoring periods showed little if any correlation between the amount of time they were present in the VRAP array and the day number since tagging (shark 9: PPMCC = 0.046; shark 20: PPMCC = 0.055). The same patterns were observed for the correlation between the amount of time sharks were present during berleying periods and the number of days sharks had been exposed to berleying (Figure 10b). Combining all sharks, there was a weak negative correlation between the amount of time sharks were present during berleying periods and the number of days sharks were exposed to berleying (PPMCC = -0.370; Figure 10b). Similarly to above, shark 21 also had a weak negative correlation (PPMCC = -0.373), but the other two sharks with long monitoring periods showed little if any correlations (shark 9: PPMCC = 0.004; shark 20: PPMCC = 0.089).

While the amount of time white sharks spent within 30 m of the SCDO varied from 0 to ~1.5 hours, there was a weak negative correlation between the amount of time white sharks were in close proximity to the SCDO and the number of days sharks were exposed to berleying (PPMCC = -0.358) (Figure 11). In this instance, all three sharks with long monitoring periods showed little if any correlation between the amount of time they were within 30 m of SCDO and the number of berleying days (shark 21: PPMCC = -0.165; shark 9: PPMCC = 0.086; shark 20: PPMCC = 0.112).

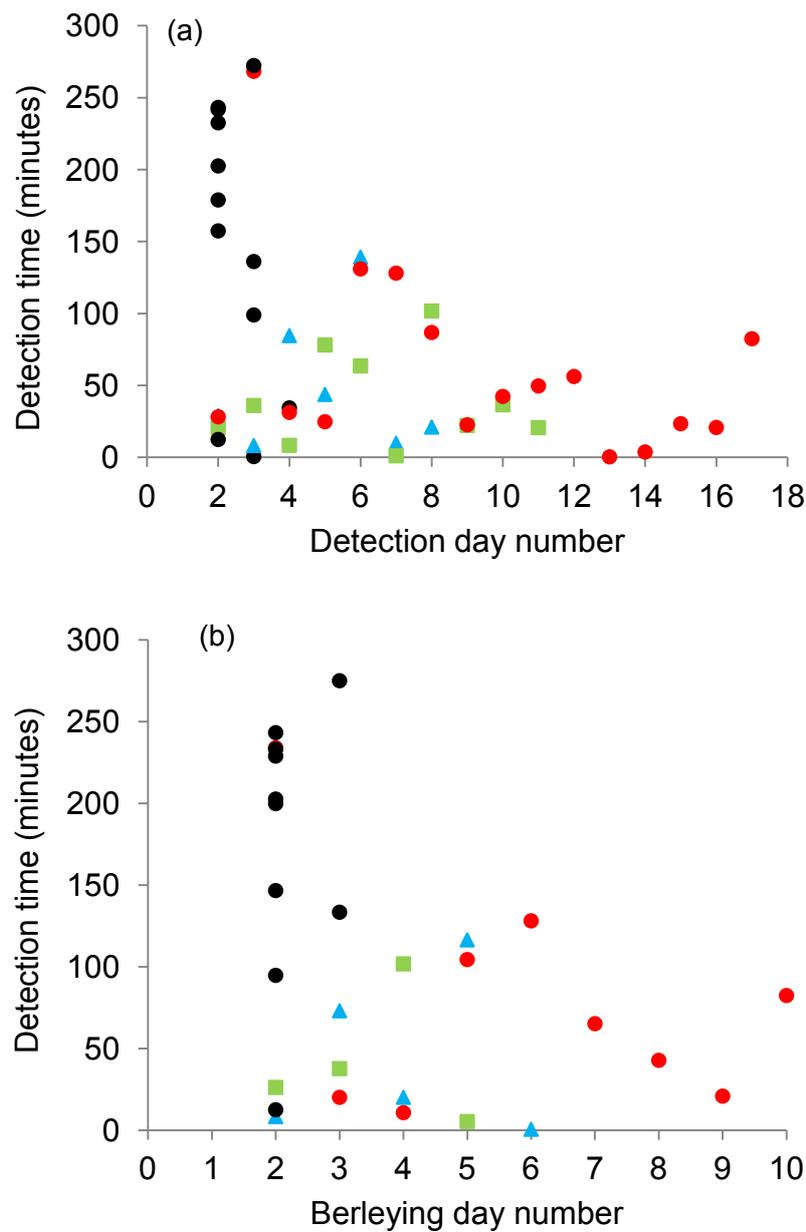


Figure 10. Scatterplot of the total detection time when sharks were (a) present at North Neptune Island group and (b) during berleying periods, against detection day number since tagging. Sharks which were monitored for longer than four days are represented as different symbols. Blue triangles are shark 20; green squares are shark 9; and red circles are shark 21. Black circles are all other sharks. Note: data from the tagging day was removed to account for biases associated with time of tagging and tagging effect.

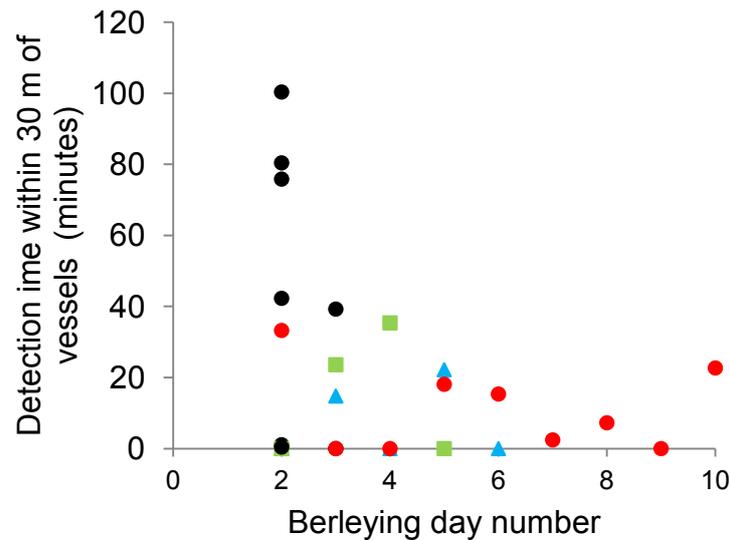


Figure 11. Scatterplot of the detection time when white sharks were present within 30 m of SCDO against berleying day number since tagging. Sharks which were monitored for longer than four days are represented as different symbols. Blue triangles are shark 20; green squares are shark 9; and red circles are shark 21. Black circles are all other sharks. Note: data from the tagging day was removed to account for biases associated with time of tagging and tagging effect.

There was no or little correlation between the time it took sharks to be first detected and the number of days sharks were exposed to berleying (PPMCC =0.214) (Figure 12). When analysing the individual sharks monitored for the longest periods, two different trends became apparent. The time it took shark 21 to be detected within the VRAP array once SCDO arrived was positively correlated to the number of days exposed to berleying (shark 21: PPMCC =0.686). On the other hand, the time it took the other two sharks with long monitoring periods to be detected within the VRAP array was negatively correlated to the number of days exposed to berleying (shark 9: PPMCC =-0.623; shark 20: PPMCC =-0.341).

Once present within the array, the amount of time it took sharks to approach the SCDO within 30 m was positively correlated to the number of days exposed to berleying (PPMCC =0.457) (Figure 13). When sharks which were monitored the longest were analysed individually, the shark with the longest monitoring period was positively correlated (shark 21: PPMCC=0.643). The other two sharks most commonly monitored only approached the SCDO within 30 m on two to three days preventing a PPMCC from being estimated.

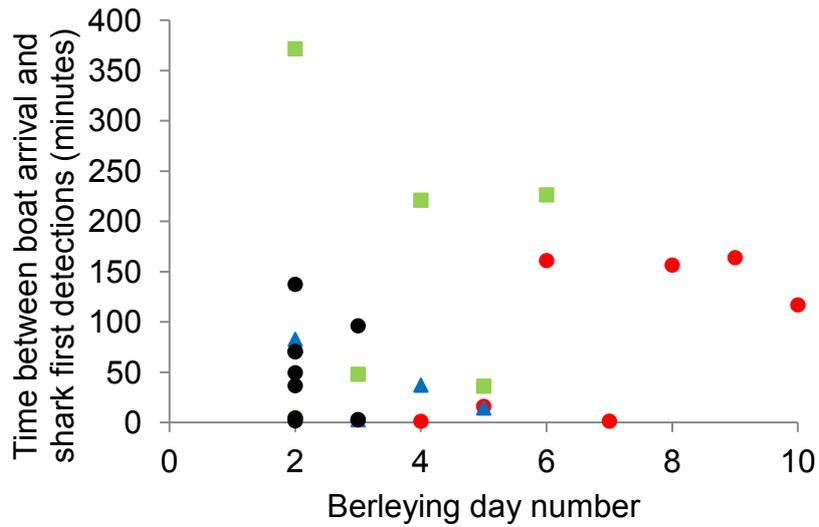


Figure 12. Plot of the detection time difference between SCDO arrival and first shark detection since SCDO arrived against berleying day number since tagging. Sharks which were monitored for longer than four days are represented as different symbols. Blue triangles are shark 20; green squares are shark 9; and red circles are shark 21. Black circles are all other sharks. Note: data from the tagging day was removed to account for biases associated with time of tagging and tagging effect.

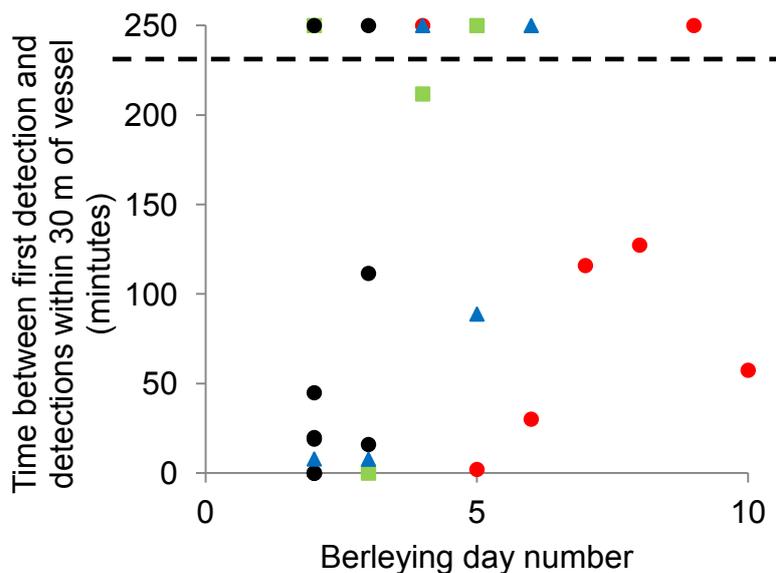


Figure 13. Plot of detection time difference between the first shark detection following SCDO arrival and first detection of shark within 30 m of SCDO against berleying day number since tagging. Data points above dashed line represent occasions when sharks did not approach within 30 m of SCDO. Sharks which were monitored for longer than four days are represented as different symbols. Blue triangles are shark 20; green squares are shark 9; and red circles are shark 21. Black circles are all other sharks. Note: data from the tagging day was removed to account for biases associated with time of tagging and tagging effect.

4 DISCUSSION

Our study is the first to document the effects of wildlife tourism on the fine-scale horizontal movements of an elasmobranch species, and shows that sharks interact with cage-diving activities in complex ways. In general, the space utilisation of white sharks changed when cage-diving vessels were present. The changes were not all consistent, with the level of interaction between SCDO and white sharks varying between individuals. The response of white sharks to SCDO shown in our study leads to implications for assessing the nature and effects of the undesirable impacts previously documented in Bruce and Bradford (2011).

Regardless of the presence of SCDO, peak detection of white sharks at the Neptune Islands was between 10:00 and 15:00. Although a similar peak was found in previous studies at the Neptune Islands (Bruce *et al.*, 2005; Bruce and Bradford, 2011), white shark detections around the seal colony of False Bay (Cape Town, South Africa) peak between sunrise and noon (Laroche *et al.*, 2008). This is likely related to the dusk and dawn peak of in-water seal activity in South Africa (Laroche *et al.*, 2008). Although seal activity has not been measured at the Neptune Islands, movements of New Zealand fur seals off Kangaroo Island, 60 nm southeast from North Neptune Island, peaked between 12:00 and 18:00 (Goldsworthy, 2006). This is similar to the day time peak of white shark detection off South Australia. As such, the timing and peak of detections are consistent with white shark relative abundance being highest when seals are most active in the water in both South Australia and South Africa. The timing of shark presence was affected by SCDO, with the peak of detections being earlier during non-berleying days. This is similar to the findings of Bruce and Bradford (2011).

The reduction of the area within which white sharks spent 50% of their time when SCDO were present indicates that SCDO not only affect residency and timing of visitation (Bruce and Bradford, 2011), but also fine-scale spatial distribution. The increased concentration of sharks within a small area could lead to intra-species competition and result in aggressive behaviour between individuals, as shown previously for a range of taxa (Orams, 2002), including sharks (Clua *et al.*, 2010a) and rays (Semeniuk and Rothley, 2008). Further research should be undertaken to monitor evidence of aggressive behaviour between individuals (e.g., agonistic display, biting scars).

The vertical distribution of sharks is also affected by SCDO, with sharks swimming at shallower depths during berleying periods and as sharks get closer to the SCDO. This suggests that the cage-diving industry is concentrating the three-dimensional spatial

distribution of white sharks into a small area around the berley source and at the surface where the teaser bait is located. This is expected, as the use of berley, teaser bait, or any other attractants, is aimed at temporarily modifying the behaviour of sharks to satisfy the viewing expectation of tourists during the cage-diving experience (Bruce and Bradford, 2011). The impact of tourism activity and berleying on the vertical distribution of sharks has previously been observed on the whitetip reef shark, *Triaenodon obesus* (Fitzpatrick *et al.*, 2011), with the authors of this study suggesting that such changes in vertical distribution may alter the activity patterns and/or metabolic requirements of these sharks. The changes observed in our study could also impact the energy partitioning of white sharks at the Neptune Islands, which ultimately dictates the expression of life history traits (e.g. life span, growth rates, reproductive scheduling).

Sharks spent a significantly greater amount of time in close proximity to the SCDO (up to 60% of their time within 60 m of the vessels) than expected by chance. Although it is unknown whether direct interactions with SCDO reduce individual fitness through increased energetic demands, the time spent interacting with SCDO is likely to distract sharks from other natural behaviours. White sharks are believed to aggregate at the Neptune Islands to feed and provision on the pinnipeds hauling out and breeding on the Islands. The distraction presented by the cage-diving industry could decrease the amount of time spent foraging and result in reduced foraging success (Bruce and Bradford, 2011). The reduction of foraging time as a result of wildlife tourism has been observed in terrestrial (e.g. Lott and McCoy, 1995; Roes *et al.*, 1997; Duchesne *et al.*, 2000), avian (e.g. Buckley, 2004; Steven *et al.*, 2011), and marine (e.g. Williams *et al.*, 2006; Lusseau *et al.*, 2009; Christiansen *et al.*, 2010) species. In the case of white sharks, the overall effect could be a reduction in either or both the quality or quantity of food consumed. If the timing of the interaction with SCDO coincides with the natural predation times, sharks are likely to spend less time foraging, subsequently reducing the quantity of food consumed. Additionally, if sharks are successful at taking the teaser bait used by cage-diving operators, the quality of the food consumed might also be reduced, as sharks would be feeding on tuna instead of pinnipeds. The calorific value of tuna (Topic Popovic *et al.*, 2012) is likely to be less than of pinnipeds (Arnould *et al.*, 1996; Williams *et al.*, 2004) because of the blubber in the latter. However, this might not be the case in weaned pups, which are assumed to be the targeted prey of white sharks at the Neptune Islands. The nutritional requirements of white sharks at the Neptune Islands and the differences in energy input from various food sources based on amount ingested and nutritional value should be investigated to assess the potential impact of the SCDO further. When the disturbance of natural foraging behaviour coincides with important periods in the

life cycle of individuals, there is potential for longer-term, negative effects on survival (Green and Giese, 2004).

Changes in the activity levels of white sharks, as seen by the variation of rate of movement (ROM) when in proximity to SCDO, might also have implications for the energy budget of white sharks. The decreased ROM observed when sharks were in close proximity to the boats, is potentially the result of increased tortuosity of the tracks and rapid turnarounds when interacting with the teaser bait. The energy requirement to undertake those directional changes could be higher than the energy used when patrolling the Neptune Islands at regular swimming speed. Increased energy expenditure as a result of human disturbances has been shown to behaviourally and physiologically impact a range of taxa (Culik, 1994; Knight and Cole, 1995; Giese *et al.*, 1999).

The ROM obtained in this study (2.7 ms^{-1}) is relatively fast compared to previous studies, which range from $0.8\text{--}1.5 \text{ ms}^{-1}$ (Carey *et al.*, 1982; Strong *et al.*, 1992; Strong *et al.*, 1996; Klimley *et al.*, 2001a; Klimley *et al.*, 2002; Bonfil *et al.*, 2005; Bruce *et al.*, 2006; Bruce and Bradford, 2011; Bruce and Bradford, 2012). Most previous estimates of ROM were calculated using positions from conventional acoustic tracking or satellite telemetry and have a propensity to underestimate true swimming speed because of the errors involved in estimating true position and the two-dimensional point to point calculations of distance travelled. In contrast, although the VRAP method takes into account three-dimensional movement, it is known to overestimate the true swimming speed, especially when the tracked organism is outside the triangle formed by the VRAP buoys (Klimley *et al.*, 2001a). This potential for overestimation was reduced through data processing by ignoring estimates over 10 ms^{-1} , obtained from positions over 200 m apart, or with more than 5 minutes between position estimates. Our study suggests that white sharks might be capable of sustained swimming speed higher than previously estimated. Although the absolute values of the ROM might still be overestimated, the relative differences of ROM obtained between berleying and non-berleying periods, and between the distance bins are still valid.

Our study provides evidence that sharks detected within the berleying site do not always directly interact with SCDO. White sharks remained away from the operators, or left the area before the operators arrived, on about a third of the days on which both operators and white sharks were detected. In South Africa and South Australia, acoustically tagged sharks that are not sighted by the cage-diving operators can still be regularly detected within the berleying site by acoustic receivers (Laroche *et al.*, 2007; Bruce, unpublished data). In these situations, sharks do not directly interact with cage-diving operators and are, therefore, less

likely to be physiologically impacted. This highlights the benefits obtained from using complementary approaches. Data obtained from presence/absence acoustic telemetry allows for the assessment of changes in habitat use and residency as a result of increases in shark cage-diving effort (Bruce and Bradford, 2011). However, a combination of photo-identification and fine-scale positioning is necessary to define the nature and variability of direct interactions between white sharks and the SCDO.

The extent of interaction between sharks and SCDO was also variable within individuals. For example, some sharks spent a large amount of time in close proximity to an SCDO one day, but did not approach within 30 m of any SCDO the next. The potential reasons for such change of behaviour are many and could be a combination of different natural feeding histories, dominance hierarchies, individual experiences, behavioural syndrome (consistency of responses across situations), or environmental conditions. The motivation for sharks to decide whether or not to interact with SCDO is unknown and would be extremely difficult to quantify and analyse (Gruber, 1988). A study assessing the effects of berleying in South Africa has shown evidence of habituation (decrease in the strength of a response; Mazur, 2006) rather than conditioning (association between a stimulus and a behaviour; Laroche *et al.*, 2007). Such a level of habituation has previously been observed in other taxa exposed to wildlife tourism for prolonged periods (Ellenberg *et al.*, 2009; Knight, 2009; Higham and Shelton, 2011). Our study attempted to look at the potential change in response to berleying through time and found some evidence suggesting habituation in the shark monitored for the longest period of time. This was not observed across all sharks, with the opposite trend or no temporal correlation found in the three other sharks recorded on more than four days. The potential for habituation has previously been shown to be influenced by various factors including gender and behavioural syndrome (Ellenberg *et al.*, 2009). In the present study, most sharks were not monitored for long enough to assess whether habituation was taking place. Additionally, factors other than the number of days exposed to SCDO may also influence the likelihood of sharks being impacted by the cage-diving industry. For example, the amount of berley used or the number of teaser baits obtained by white sharks may be more likely to impact their behaviour than the number of days present within the berleying site, especially considering that sharks do not always directly interact with SCDO. As a result, the level of habituation at the Neptune Islands could not be ascertained.

The sharks monitored were not equally affected by the SCDO, with some sharks interacting with operators more than others. This was observed in the proportion of detections obtained when SCDO were present, but also in the proportional amount of time spent in close proximity to the SCDO, swimming depth, rate of movement, and correlations with number of

days exposed to berleying. Some sharks spent more than 60% of their time within 60 m of the SCDO, while others actively avoided SCDO, departing soon after the vessels arrived and returning a short period after the vessels had left. Although it is possible that this is a result of social interactions between sharks or a reaction to a more dominant individual, the reason for such behaviour is unknown. This suggests that care should be taken when generalising across individuals and that the findings from one individual might not be applicable to all sharks visiting the Neptune Islands. Such differences have previously been seen in Caribbean reef sharks (*Carcharhinus perezii*) and sicklefin lemon sharks (*Negaprion acutidens*), where different groups of sharks were observed and showed opposite residency trends and responses to the tourism industry and associated provisioning (Clua *et al.*, 2010a; Maljković and Côté, 2011). The response of individual animals to human disturbance can also be influenced by behavioural syndrome (Martin and Réale, 2008). Although the existence of behavioural syndrome has not yet been recorded in elasmobranchs, evidence has been shown in many other species across a range of taxa (Koolhaas *et al.*, 1999; Gosling, 2001; Sih *et al.*, 2004).

White sharks have also been found to exhibit different predatory strategies across individuals (Holman, 2012), potentially explaining the differences in observed responses. Presence/absence evidence also suggests that the Neptune Islands are visited by two different types of white sharks. Some white sharks visit the Neptune Islands for short periods of time (1–3 days), while others remain within the Neptune Islands for periods up to 92 days (Bruce and Bradford, 2011), and are considered 'temporary residents'. As temporary residents spend longer at the Neptune Islands, they are more likely to be exposed to and interact with SCDO, resulting in the potential impact from SCDO being greater for these individuals compared to visitors. Differences were, however, also observed between sharks monitored the longest, with some sharks more likely than others to come into close proximity to cage-diving operators (e.g., shark 20 and 9). The integration of behavioural syndrome, or at least the recognition of individual differences, is recommended in studies of the impact of human disturbance on wildlife (Martin and Réale, 2008), and is needed to better understand the potential effect of cage-diving on white sharks.

In situations when two SCDO were present simultaneously, white sharks were observed to partition their time between the two operators. From the cage-diving industry perspective, this reduces the incentive for the operators to attempt over-berleying each other as white sharks are likely to visit each vessel. However, it also means that the more operators that are present at the berleying site at any one time, the more they will have to share shark interactions amongst each other. For example, a shark present at the Neptune Islands for

one hour could result in one hour of interaction with one SCDO, or 20 minutes of interactions at each of three SCDO. Individual sharks did not partition their time uniformly, with some sharks spending more time in proximity to one or other of the vessels present. The variation suggests that the differences observed might be due to individual preferences rather than to a physical characteristic of the vessel or behaviour of the cage-diving operators.

The effects of the cage-diving industry are currently confined to one location so that only a fraction of the Australian white shark population is potentially currently impacted. A better understanding of white shark population structure and the fraction of the Australian population visiting the Neptune Islands would provide a better understanding of the extent of the population impacted. Prior to any expansion of the cage-diving industry to new areas, which has previously been proposed, it should first be determined whether different sharks than those frequenting the Neptune Islands are likely to be exposed to wildlife tourism, potentially affecting a larger fraction of the population, or whether sharks from the Neptune Islands will be exposed to an additional level of disturbance at new sites. This could be undertaken through the combination of a genetic study investigating the fine-scale stock structure of the Australian white shark population along with a photo-identification study cataloguing individuals visiting the Neptune Islands and any other area proposed to host wildlife tourism. A recent study on the fine-scale spatial structure of Australian white sharks identified female reproductive philopatry and that males may also exhibit some degree of reproductive philopatry (Blower *et al.*, 2012). This suggests that the stock structure of white sharks might be more complex than previously thought. The low sample size and wide temporal distribution of the samples collected, combined with a likely high proportion of pre-dispersal juveniles, precluded to test for the extent of sex-biased dispersal, with the study concluding that further investigation is required to clarify whether the levels of philopatry differ between genders in this species (Blower *et al.*, 2012).

5 CONCLUSION AND IMPLICATIONS

Our study demonstrated that wildlife tourism within the Neptune Islands Marine Park can influence the fine-scale horizontal and vertical distribution, and rate of movement, of white sharks at the Neptune Islands. Visitation at the cage-diving site is temporary and white sharks do not always interact with SCDO. As such, the effects of the cage-diving industry are unlikely to be uniform, and would be limited to periods when white sharks visit the Neptune Islands. The observed effects could, however, lead to physiological impacts and potentially decrease individual or population fitness if elicited frequently or repetitively, or within important habitats (e.g., breeding, nursery, or foraging areas), as might be the case for white sharks returning to the Neptune Islands on a yearly basis to provision on pinnipeds.

Sharks detected within the monitored area did not interact with cage-diving vessels a third of the time. We also found a large amount of variation in the response to SCDO between individual sharks. These differences might have been due to a range of factors including motivation, natural feeding history, dominance hierarchies, individual experience, behavioural syndrome, exposure to berley, or number of teaser baits consumed. The degree of variation between individual sharks and the diverse levels of interaction highlight the complexity of the relationships between the SCDO and effects on white sharks. To improve our understanding of these relationships, future monitoring of the cage-diving industry may require recording information at a fine level of detail, which might not currently be achieved by solely recording the number of days SCDO are present in relation to data obtained from presence/absence acoustic telemetry. Our study highlights the need to use complementary approaches and ensure that information about the amount of interaction between sharks and cage-diving vessels is being collected. Future monitoring should also record the effects on white sharks in relation to a more detailed measure of the SCDO effort (e.g., number of teaser baits taken by each shark, amount of berley) in addition to the, currently collected, number of days SCDO are present.

The impacts of the changed behaviour on the dynamics and viability of the white shark population visiting the Neptune Islands remains unknown and should form the focus of future research. The potential effects on individual fitness and population viability as a result of disturbed foraging behaviour have previously been hypothesised in killer whales (*Orcinus orca*) (e.g. Lusseau *et al.*, 2009) and documented in chough (*Pyrrhocorax pyrrhocorax*) (e.g. Kerbiriou *et al.*, 2009). The combination of the potential increased energy requirements due to interactions with teaser baits, and reduced energy intake due to disrupted natural foraging behaviour, could unbalance the energy budget and physiological requirements of white

sharks. While no data are currently available on the energy budget of white sharks and effects from interacting with SCDO, potential impacts on individual fitness and population viability highlight the need to investigate this further.

6 REFERENCES

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