

The effects of cage-diving activities on the fine-scale swimming behaviour and space use of white sharks

**Charlie Huveneers, Paul J. Rogers,
Crystal Beckmann, Jayson M. Semmens,
Barry D. Bruce & Laurent Seuront**

Marine Biology

International Journal on Life in Oceans
and Coastal Waters

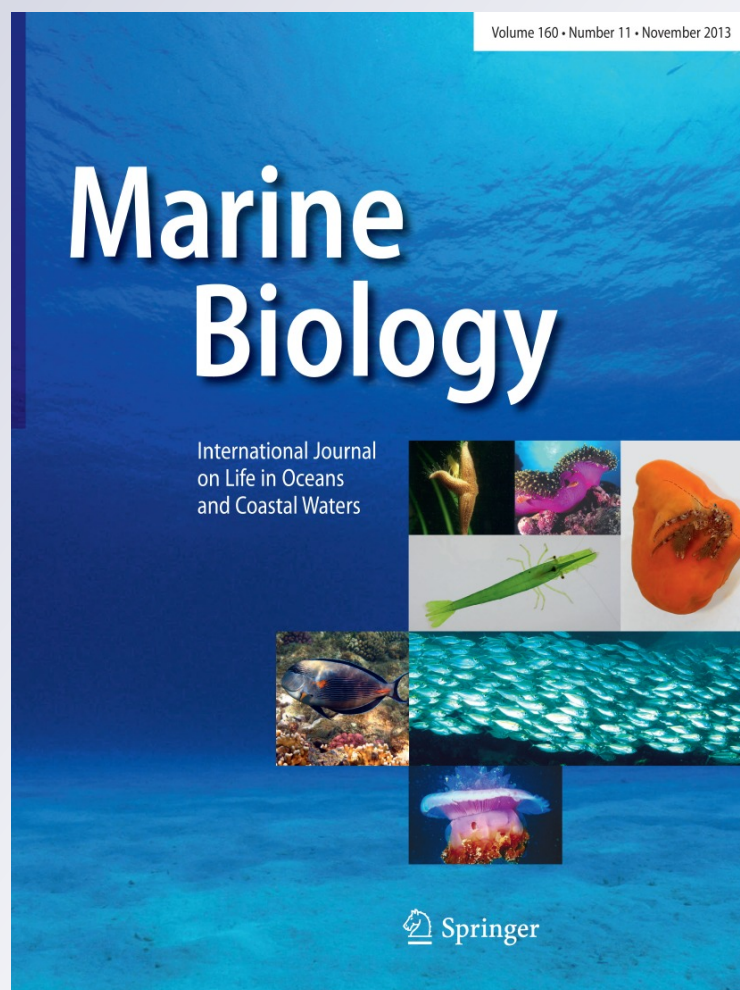
ISSN 0025-3162

Volume 160

Number 11

Mar Biol (2013) 160:2863-2875

DOI 10.1007/s00227-013-2277-6



Your article is protected by copyright and all rights are held exclusively by Her Majesty the Queen in Right of Australia. This e-offprint is for personal use only and shall not be self-archived in electronic repositories. If you wish to self-archive your article, please use the accepted manuscript version for posting on your own website. You may further deposit the accepted manuscript version in any repository, provided it is only made publicly available 12 months after official publication or later and provided acknowledgement is given to the original source of publication and a link is inserted to the published article on Springer's website. The link must be accompanied by the following text: "The final publication is available at link.springer.com".

The effects of cage-diving activities on the fine-scale swimming behaviour and space use of white sharks

Charlie Huveneers · Paul J. Rogers ·
Crystal Beckmann · Jayson M. Semmens ·
Barry D. Bruce · Laurent Seuront

Received: 24 March 2013 / Accepted: 4 June 2013 / Published online: 18 June 2013
© Her Majesty the Queen in Right of Australia 2013

Abstract Wildlife tourism has become increasingly popular and is one of the fastest growing sectors of the tourism industry. A radio-acoustic positioning system was deployed to monitor the fine-scale movements of 21 white sharks (*Carcharodon carcharias*) and investigate the effects of shark cage-diving activities on their swimming behaviour and space use. This study contributes towards improving our understanding of the complex relationship between wildlife tourism and its effects on sharks, and assesses how tourism targeting sharks affects behaviour at a finer spatial scale than previously investigated. Our study demonstrated that shark cage-diving operators (SCDO) influenced the fine-scale three-dimensional spatial distribution and the rate of movement of white sharks at the Neptune Islands. White sharks stayed more than 30 m away from the SCDO on 21 % of the days detected, but

spent a significant amount of time in close proximity to the SCDO on the remaining days. Individual variation was detected, with some sharks behaviourally responding to SCDO more than others. The degree of variation between individual sharks and the different levels of interaction (e.g. presence, proximity to SCDO, and consumption of tethered bait) highlights the complexity of the relationships between SCDO and the effects on sharks. To improve our understanding of these relationships, future monitoring of shark cage-diving operations requires proximity to SCDO to be recorded in addition to the presence within the area. Further work is needed to assess whether the observed behavioural changes would affect individual fitness and ultimately population viability, which are critical information to unambiguously assess the potential impacts of wildlife tourism targeting sharks.

Communicated by S. Connell.

Electronic supplementary material The online version of this article (doi:10.1007/s00227-013-2277-6) contains supplementary material, which is available to authorized users.

C. Huveneers (✉) · P. J. Rogers
Threatened, Endangered and Protected Species Sub Program,
SARDI—Aquatic Sciences, West Beach, SA 5022, Australia
e-mail: charlie.huveneers@sa.gov.au

C. Huveneers · C. Beckmann · L. Seuront
School of Biological Sciences, Flinders University, Bedford
Park, SA 5042, Australia

J. M. Semmens
Fisheries, Aquaculture and Coasts Centre, Institute for Marine
and Antarctic Studies, Hobart, TAS 7001, Australia

B. D. Bruce
Wealth from Oceans Flagship, Commonwealth Scientific
Institute Research Organisation, Hobart, TAS 7001, Australia

Introduction

Globally, wildlife tourism is considered one of the fastest growing sectors of the tourism industry (Scheyvens 1999; Wearing and Neil 2009). One of the main arguments for the continuing development of wildlife tourism is that it helps to secure long-term management and conservation of wildlife (Higginbottom and Tribe 2004; Newsome et al. 2005), by influencing the conservation knowledge, attitudes, and behaviour of tourists (Ballantyne et al. 2007). Wildlife tourism has, however, also been considered a threat to wildlife and ecosystems (Duffus and Dearden 1990; Shackley 1996), for a range of taxa including avian, terrestrial, and marine organisms (Steven et al. 2011; Worlf and Croft 2010; Bejder et al. 2006). 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 to long-term effects, such as increased mortality or reduced breeding success (for review, see: Green and Giese 2004; Orams 2002; Green and Higginbottom 2001).

The conservation benefits of wildlife tourism are possibly greater for potentially dangerous animals, such as sharks, because of the negative public image they suffer from (Driscoll 1995). This is critical as negative perceptions about sharks and shark attack risk have been identified as one of the greatest barriers for global shark conservation efforts (Ferguson 2006). Scientists, conservation societies, policy makers, and even fishers have long expressed concerns about the conservation status of shark populations (Lynch et al. 2010); yet, shark conservation has only relatively recently emerged as a global policy priority (Techera and Klein 2011). Additionally, the logistical difficulties associated with studying large marine predators have led to their responses to wildlife tourism remaining poorly understood. Nevertheless, research on the impacts of tourism on sharks and rays 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 (Laroche et al. 2007; Meyer et al. 2009; Bruce and Bradford 2013; Bruce et al. 2005; Maljković and Côté 2011; Clua et al. 2010; Brunnschweiler and Barnett 2013), changes in vertical activity (Fitzpatrick et al. 2011), and physical impacts of divers Barker et al. 2011a, b; Smith et al. 2010). The effects of wildlife tourism on the fine-scale movements of Elasmobranchs have, in comparison, been overlooked. The lack of a uniform effect across species and populations also suggests that findings cannot be generalised and may vary according to the frequency, location, and type of activities, as well as the targeted species (Meyer et al. 2009; Maljković and Côté 2011; Clua et al. 2010; Bruce and Bradford 2013).

Commercial white shark (*Carcharodon carcharias*) cage-diving is expanding across the species' range and now occurs in Australia, South Africa, the United States of America, Mexico (Guadalupe Island), and New Zealand. This commercial activity is often justified by operators as being beneficial to the conservation of the species through educating participants and increasing levels of public awareness regarding the need for the conservation of sharks. However, the potential for cage-diving activities to negatively impact white sharks represents a concern in some jurisdictions (DEWHA 2010). There is still limited information on the effects of cage-diving operations on white sharks. In South Africa, a study conducted on the effects of provisioning concluded that sharks were found closer to the surface during berleying (Laroche et al. 2007). A trend of decreasing response to berley and tethered baits with time

was also observed in some sharks, suggesting that habituation might be occurring (Laroche et al. 2007). In South Australia, a study using acoustic telemetry presence-absence data examined the residency of white sharks at the Neptune Islands between 2001 and 2003, and concluded that effects were localised, with some evidence that individual sharks remained in shark cage-diving areas for longer periods on days when operations occurred (Bruce et al. 2005). A more recent study was carried out to determine whether there was evidence of behavioural change in white sharks in response to the increase in the South Australian cage-diving operations since 2007 (Bruce and Bradford 2013). 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 2013). These studies, however, used acoustic telemetry that generated presence/absence data, but did not provide information about the fine-scale movements of white sharks or how their behaviour is affected by proximity to cage-diving vessels.

Several 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, however, still 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 (Laroche et al. 2008; Klimley et al. 2001b; Martin et al. 2009; Domeier et al. 2012; Le Boeuf 2004). Several movement patterns have been described in situations when berleying takes place, including downstream circling, island patrolling, and inter-island patrolling (Klimley et al. 2001b; Strong et al. 1992). Yet, a quantitative comparison of white shark fine-scale movement between berleying and non-berleying periods has never been undertaken. Such information is important to consider when determining the effect of wildlife tourism, as changes in behaviour can affect energetic budgets and have long-term effects to the targeted population (Green and Giese 2004; Orams 2002; Lusseau et al. 2009; Kerbiriou et al. 2009).

Using a radio-acoustic positioning system, we estimated the locations of white sharks tagged with acoustic transmitters to determine their fine-scale movements and proximity to cage-diving vessels. Our objective was to compare the vertical and horizontal distribution, as well as rate of movement (ROM) of white sharks during periods of shark cage-diving operations to periods when no operators were present at the dive sites.

Methods

Study site and shark cage-diving operators (SCDO)

The North Neptune Islands group (35°149S; 136°049E) is part of the Neptune Islands located near the approach to Spencer Gulf, about 30 km from the South Australian mainland (Fig. 1). White sharks can be encountered at the North Neptune Island group year-round. Individual sharks, however, are temporary visitors to the site with limited periods of residency (Bruce et al. 2005; Bruce and Bradford 2013). Tracking has also revealed that sharks travel from the Neptune Islands to areas across their Australasian range (Bruce et al. 2006) and that some return on an annual or more frequent basis (Bruce et al. 2005; Robbins 2007). The Neptune Islands have been a site for commercial white shark cage-diving since the late 1970s.

SCDO use a near-constant odour corridor of berley (or chum) comprising mix of minced southern bluefin tuna (*Thunnus maccoyii*) products including offal, oil, and blood to attract sharks present to the cage-diving vessel. Tethered baits of tuna sections or gills and entrails of up to several kilograms are used to improve client experience by keeping sharks within visual range of divers in the cage. Although SCDO are not allowed to deliberately feed sharks, the bait handler is not always fast enough to retract the bait. The frequency of baits being taken is dependent on the speed of shark approach, visibility, and vigilance of the bait handler.

Two cage-diving vessels that release berley and use tethered tuna baits operated independently during the study period (November 2009–September 2011). One operator conducted regular day trips during which they arrived around 9:30 and departed between 14:00 and 17:00 depending on shark activity and day length. Another operator conducted three-day trips during which they arrived around 11:00, stayed for 3 days, and left between 16:00 and 19:00 depending on shark activity and day length. During normal operations, SCDO start berleying and using tethered bait upon arrival and until departure. In the case of the second operator who remains overnight,

berleying and the use of tethered bait are discontinued from ~17:00 until ~8:00. Each operator recorded their arrival and departure time, the times during which they used berley, and their vessel position (latitude and longitude). Operator data were recorded on mandatory daily logbooks and purpose-designed logsheets for this study. A third operator that does not use berley or tethered bait 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. This operator was excluded from the study due to the limited number of detections obtained and different types of attractant used. Although private boats can be present in the area, SCDO are the only vessels allowed to use berley.

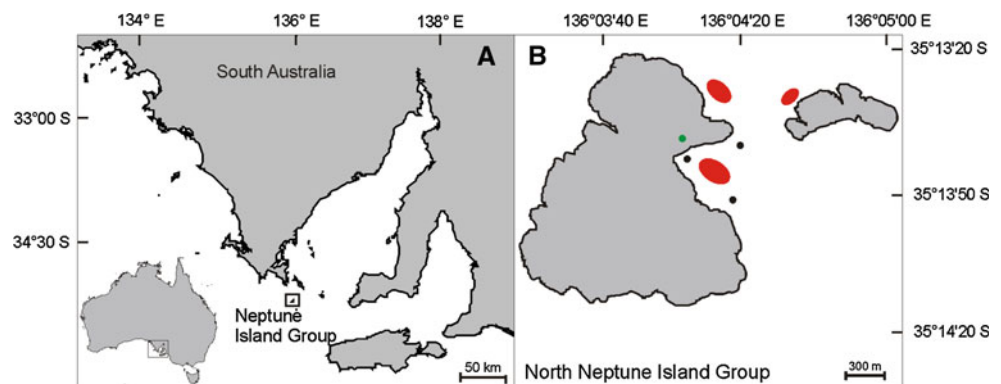
At the time of the study, SCDO were allowed to operate every day and it was not possible to direct them to stay away from the study site. Assessment of the number of operator-free days from previous years suggested that the study period would naturally include sufficient days during which no operator would be present.

Vemco radio-acoustic positioning system

A Vemco radio-acoustic positioning (VRAP) system (Vemco Ltd., Halifax, Canada) was deployed in the bay on the south-east side of North Neptune Island (Fig. 1). The VRAP consisted of three surface buoys deployed in a near equilateral triangle (distances between buoys ranged from 324 to 340 m, area = 52,000 m²) and a shore station in line of sight. Each buoy was equipped with a multi-directional hydrophone that detected the acoustic pulses emitted by the transmitters. The received information was transmitted to the shore station via radio signals, where the geographic position (latitude and longitude) of each shark was triangulated based on the arrival times of the acoustic pulses to each buoy. A detailed description of how the VRAP system estimates the position of tagged organisms is provided by O'Dor et al. (1998) and Klimley et al. (2001a).

The buoy positions were calibrated by the VRAP at the start of each deployment. The VRAP was set to listen to

Fig. 1 Location of **a** the North and South Neptune Island groups and **b** Vemco radio-acoustic positioning (VRAP) system deployment in relation to the North Neptune Island group. The *green 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



each selected frequency for 10 s with the number of frequencies selected at any one time ranging from 1 to 9. 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 moored transmitters showed a similar level of precision of ± 1 m in the middle of our VRAP array, with the precision decreasing outside the triangle formed by the VRAP buoys similarly to Klimley et al. (2001a).

The VRAP system was deployed at North Neptune Islands between late November 2009 and October 2011 for a total of 454 days. The VRAP system was deployed during three monitoring periods ranging from 96 to 188 days (23/11/2009–11/05/2010, 26/06/2010–30/12/2010, and 5/07/2011–8/10/2011) (Fig. 2). 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 3 days of deployment. Technological difficulties with the VRAP system also led to inaccurate estimates of residency due to the date of last detection not necessarily equating to the end of a shark's residency period. Throughout the duration of the study, the VRAP system was operational and transmitters were deployed and active, for a total of 221 days (Fig. 2). Due to tagged sharks leaving the study site prior to the transmitter battery

running out, the total number of monitored days between tagging and last detection was 44 days. SCDO were present during 28 (64 %) of these days with 16 days (36 %) being operator-free days.

Tagging

Twenty-one white sharks were tagged with V16P-5H acoustic transmitters (VEMCO Ltd., Halifax, Canada) between 14 December 2009 and 11 September 2011. Tags were opportunistically deployed throughout the monitoring period depending on the number of sharks reported at the study site by the SCDO. Transmitters recorded depths of tagged sharks via a calibrated pressure sensor (accuracy ± 3.4 m). Transmitters were programmed to transmit every ~ 1 s and had a predicted battery life of ~ 50 days. Transmitters were tethered to an umbrella dart-tag head using a 10- to 15-cm-long stainless wire trace (1.6 mm diameter). Transmitters were implanted in the dorsal musculature of sharks using a tagging pole when sharks were attracted close to the SCDO.

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

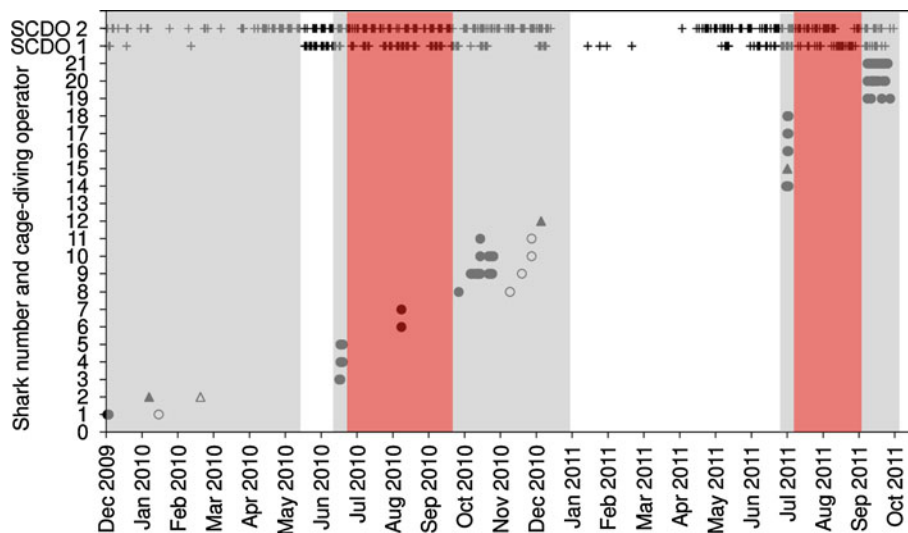


Fig. 2 Summary of deployment periods, shark detections, and presence of cage-diving operators (SCDO) throughout the study. *Filled circles* indicate days when sharks were detected; the first data point represents the date of tagging. *Triangles* represent sharks which were tagged outside the Vemco radio-acoustic positioning (VRAP) array (i.e. berleying sites on the north side of the Islands, see Fig. 1), but which were never detected by the VRAP system. *Empty circles* represent the expected date that transmitter battery would have run

out. *Crosses* indicate days when SCDO were anchored within the VRAP array. The less frequent presence of SCDO during the summer months was not necessarily due to SCDO being absent, but was partly related to SCDO being anchored outside of the VRAP array and using the berleying site north of the Neptune Islands due to prevailing southerly wind often occurring in Summer. Each deployment period is shaded in grey. Areas shaded in red represent periods during which the VRAP system was not operational

Development Core Team, 2011). The time difference, distance, and rate of movement between two consecutive location estimates were calculated using the Eonfusion add-in operator 'Velocity and Acceleration'.

Although the transmitters could be detected further than 500 m from the edges of the triangle formed by the VRAP receivers (hereafter referred to as the VRAP array), the precision of the location estimates is greatly reduced at such distance from the VRAP buoys (>10–20 m, Klimley et al. 2001a). To ensure that the analysis was performed on precise location estimates and to filter erroneous data points, the following filters were applied:

- Position estimates that were on land or outside the VRAP array were removed;
- 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.
- Consecutive location estimates with time differences greater than 5 min were removed. This threshold allowed the shore station to go through two full cycles, while reducing the risk of underestimating the rate of movement from sharks leaving and re-entering the VRAP array.
- 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 was less reliable.
- Rates of movement more than 10 m s^{-1} were excluded due to the physical limits on swimming speed of lunate tail propelled aquatic animals, such as white sharks (Iosilevskii and Weihs 2008).

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, 30–59.9, 60–89.9, 90–119.9, and >120 m. These bins were also used to categorise the level of interaction between white sharks and SCDO as: close (<30 m), medium (30–120 m), and distant (>120 m) interactions.

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

The horizontal distribution and amount of time white sharks were detected 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 $10 \times 10 \text{ m}$ 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 s. 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. Time spent in area was calculated using the make GridTopology and tripGrid.interp tools in the Trip R package.
2. The relative amount of time sharks were present during berleying was expressed as a ratio between the proportion of time 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 proportion of 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 ca. $2,800 \text{ m}^2$, while the area more than 120 m away from SCDO, but within the VRAP array covered ca. $350,000 \text{ m}^2$. 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 the behaviour of each 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 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.

Effect 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, i.e., depth, as well as horizontal distance) were used to calculate the rate of movement (ROM) between each consecutive location. The depth and the calculated ROM 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 ROM when sharks were within each distance bin. Model validity was assessed similarly to the GAMM carried out on the time spent in area. The assumption that SCDO bring sharks close to the surface near SCDO was tested by comparing the proportion of depth records within 5 m of

the surface when sharks were within 30 m and when further than 30 m of SCDO, or when SCDO were absent, using the minlike two-sided Poisson exact test from the *exactci* R package (R statistical software, version 2.13.1) (R Development Core Team 2011) (Fay 2010). The minlike two-sided method was chosen because it is generally more powerful than the central two-sided method (Fay 2010).

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, the time spent in the array during berleying periods, and the time spent within 30 m of the SCDO were tested for correlation with the day number since tagging. These correlations were tested by estimating the Pearson's *r* and the significance of the correlation.

Table 1 Summary of tagged sharks and detections obtained before and after data filters

Shark	Total length (m)	Sex	Date tagged	Date of last detection	Days detected	Location estimate	Filtered location	% filtered
1	3.6	Male	14/12/2009	15/12/2009	2	413	187	55 %
2 ^a	3.5	Male	18/01/2010	18/01/2010	0	0	0	–
3	3.3	Female	26/06/2010	27/06/2010	2	641	282	56 %
4 ^b	3.0	Female	27/06/2010	29/06/2010	3	418	0	100 %
5 ^b	4.5	Female	27/06/2010	29/06/2010	3	182	0	100 %
6 ^c	2.5	Female	17/08/2010	17/08/2010	1	5	0	100 %
7 ^c	4.2	Female	17/08/2010	17/08/2010	1	2	0	100 %
8 ^c	4.0	Male	4/10/2010	4/10/2010	1	7	0	100 %
9	4.0	Male	14/10/2010	1/11/2010	12	3830	1842	52 %
10	3.5	Male	22/10/2010	2/11/2010	5	2714	1427	47 %
11 ^c	3.8	Male	22/10/2010	22/10/2010	1	11	6	45 %
12 ^a	4.2	Male	12/12/2010	12/12/2010	0	0	0	–
13	4.5	Female	5/07/2011	7/07/2011	3	1466	755	49 %
14	2.9	Male	5/07/2011	7/07/2011	3	576	286	51 %
15 ^a	4.0	Male	6/07/2011	6/07/2011	0	0	0	–
16	3.6	Male	6/07/2011	7/07/2011	2	1263	469	62 %
17	3.8	Female	6/07/2011	7/07/2011	2	771	373	51 %
18	2.8	Male	6/07/2011	7/07/2011	2	1339	720	46 %
19	3.5	Female	11/09/2011	30/09/2011	4	798	413	49 %
20	4.0	Male	11/09/2011	26/09/2011	9	1777	885	50 %
21	4.2	Male	11/09/2011	28/09/2011	17	6116	3034	51 %
Total					73	22329	10679	52 %

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; filtered location is the number of location estimates remaining after filters; and % filtered is the percentage of location estimates removed by filters

^a sharks not detected by VRAP array

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

^c sharks removed from further analysis due to small number of location estimates following data filters

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

Results

A total of 21 white sharks were tagged during the study. Two, ten, and nine sharks were tagged and monitored during the first, second, and third deployment periods, respectively. Detection periods (date of first detection to date of last detection) varied between sharks and ranged from 1 to 19 days (mean 5.4 ± 1.5 days; Table 1).

Sharks were detected on 36 of the 221 days monitored. At least one SCDO was present on 25 (69 %) of these days. As multiple tagged sharks could be present within the array at any time, ‘shark-days’ were defined as any day that a specific shark was detected. For example, two sharks detected on the same day represent two ‘shark-days’ in the analyses. A total of 64 shark-days was recorded, of which 45 (70 %) were concurrent with shark cage-diving operations. Six of these days were discarded because cage-diving took place outside the VRAP array.

Tagged sharks did not approach within 30 m of an operator on eight of the remaining 39 berleying days (21 %). This suggested that sharks did not always closely interact with SCDO when present during berleying operations.

Effect 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 from 36,200 to 26,200 m², a reduction of 28 % (Fig. 3). The area where sharks spent 50 % of their time during berleying periods also coincided with the anchoring locations of SCDO (Fig. 3).

The relative amount of time in the array during berleying was highly variable and ranged from 0 to 1 (SE = 0.078); for instance, one shark was only detected when SCDO were absent, while another one was 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 not significantly different to 0.5 (0.56, t test: $t_{10} = 1.70$; $P = 0.12$), indicating that the average amount of time in the array was similar regardless of SCDO being present or absent (Fig. 4).

On average, sharks spent 48 ± 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 within 60 m of SCDO, compared to only 5 % for shark 10 (Fig. 5). Standardising for the different surface areas of the various range bins, 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 each distance bin

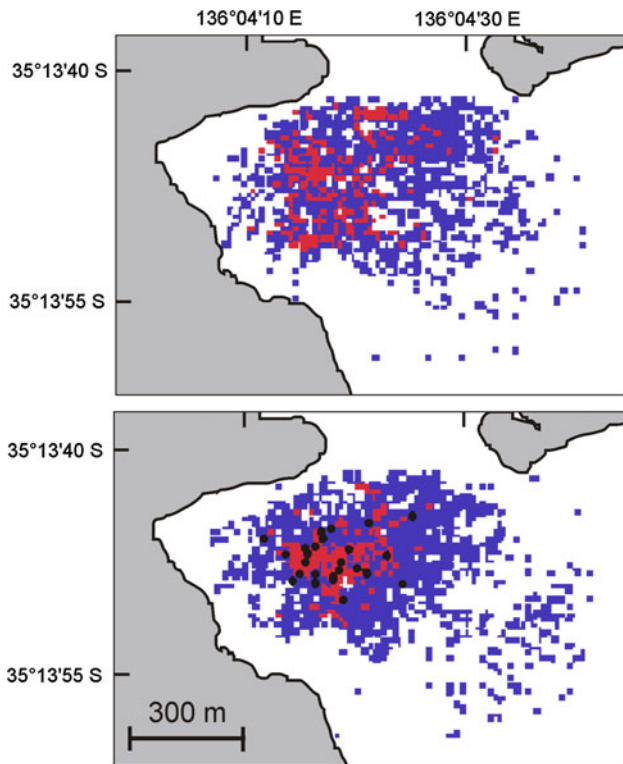


Fig. 3 Time spent in area by white sharks during non-berleying (top figures) and berleying (bottom figures) periods. Blue represents total time spent within the array, while red represents 50 % of time spent within the array. Black circles represent shark cage-diving operators’ locations throughout the monitoring period

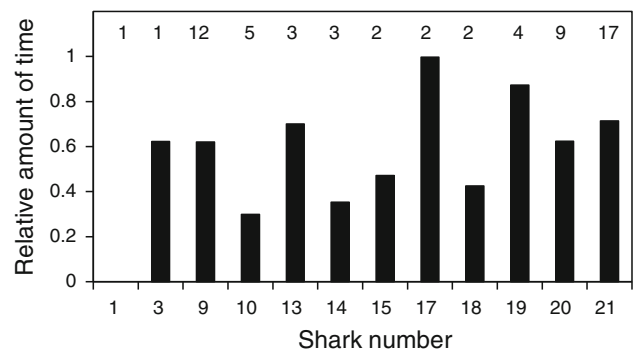


Fig. 4 Relative amount of time spent within the Vemco radio-acoustic positioning array during berleying. Numbers above bars represent the number of days each shark was detected

was significantly different (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 (Fig. 6).

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

The mean swimming depth was significantly shallower when SCDO were present than when no berleying was

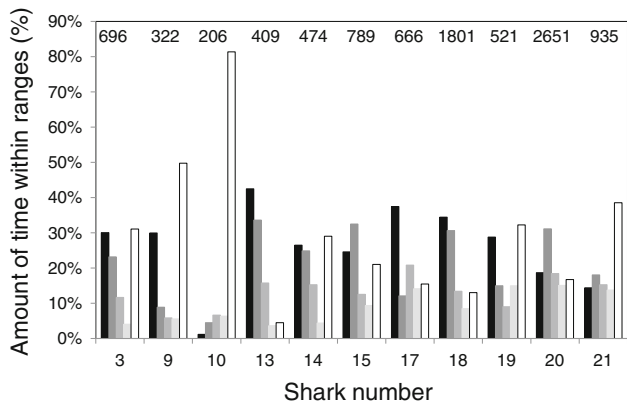


Fig. 5 Proportion of time when white sharks were 0–29.9 (black), 30–59.9 (dark grey), 60–89.9 (medium grey), 90–119.9 (light grey), and more than 120 m (white) away from shark cage-diving operators (SCDO). Numbers above bars represent the number of detections when SCDO were present

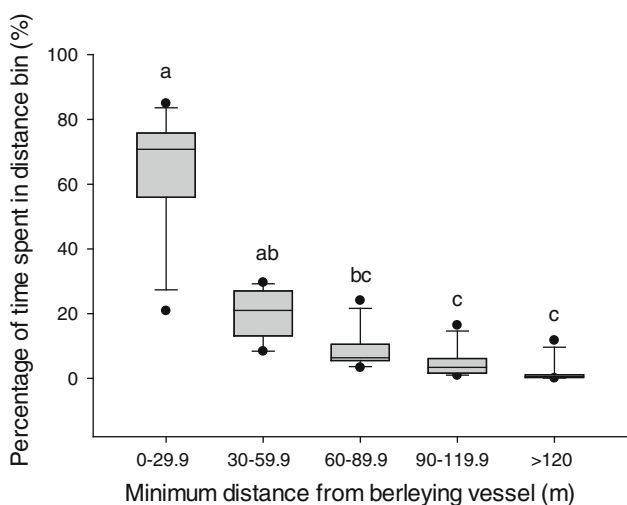


Fig. 6 Percentage of detections obtained within various distances from shark cage-diving operators standardised to take into account the dimensions of the area covered within these distances. Bars with the same letters above represent groups not significantly different. Median values are indicated by the bold horizontal bar; the length of the box is the inter-quartile range; whiskers represent quartiles; and black circles are extreme values

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 (Fig. 7, GAMM: $F = 120$; $P < 0.001$). When sharks were within 30 m of SCDO, 21 % of the depth records were within the top 5 m, which was significantly more than when sharks were further away from the operators, or when SCDO were absent (13 and 10 %, respectively; Poisson exact test: $P < 0.001$). Histograms of swimming depths also confirmed that the observed difference was due to sharks in proximity to SCDO spending more time within the top of the water column rather than due to increasing maximum depths away from the operators (Fig. S1).

The mean ROM of white sharks was not significantly different whether SCDO were present (2.64 m s^{-1}) or absent (2.81 m s^{-1} ; GAMM: $t = 0.10$; $P = 0.921$). The ROM of white sharks was, however, significantly different according to the distance from the SCDO (GAMM: $F = 11.16$; $P < 0.001$). The ROM when sharks were within 30 m of SCDO ($2.4\text{--}2.5 \text{ m s}^{-1}$) was significantly slower compared to when sharks were more than 120 m away from SCDO (3.0 m s^{-1}) (Fig. 7). Histograms of the ROM showed that the decreasing ROM with proximity to SCDO was due to the increasing proportion of slow ROM recorded ($0\text{--}0.4 \text{ m s}^{-1}$) (Fig. S2).

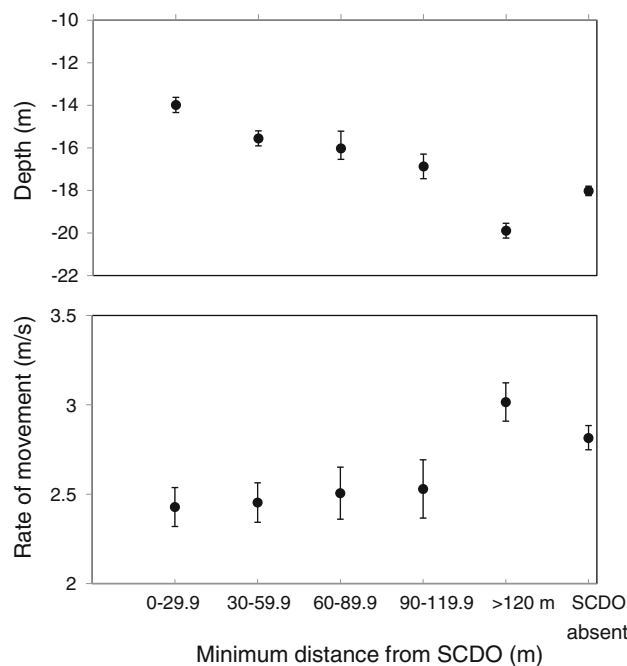


Fig. 7 Mean swimming depth (top) and rate of movement (bottom) in relation to the distance to shark cage-diving operators (SCDO) and when SCDO were absent. Error bars represent 95 % confidence intervals

Temporal correlations

When combining all sharks, a significant negative correlation was apparent between the day number since tagging and the amount of time white sharks were present in the VRAP array, and during berleying. When analysing these correlations for the three individual sharks which were monitored the longest, none of the correlations tested were significant (Fig. 8; Table 2).

Discussion

This study improves our understanding of the complex relationship between wildlife tourism and its effects on sharks, and assesses how tourism affects shark behaviour at a finer spatial scale than previously investigated. The study shows that the space utilisation of white sharks changed

Table 2 Summary of Pearson's *r* between all sharks combined and individual sharks which were detected more than four days between the total amount of time sharks spent in the VRAP array, spent in the array during berleying periods, and within 30 m of a shark cage-diving operator against the day number since tagging

Sharks	Total time	During berleying	Within 30 m
All sharks	-0.412 (0.005)	-0.370 (0.05)	-0.358 (0.06)
Shark 21	-0.418 (0.11)	-0.373 (0.32)	-0.165 (0.61)
Shark 9	0.046 (0.90)	0.004 (0.99)	0.086 (0.91)
Shark 20	0.055 (0.91)	0.089 (0.89)	0.112 (0.86)

Numbers in brackets represent *P* value; numbers in bold represent significant correlations (*P* < 0.05)

when cage-diving vessels were present and depending on the proximity to the SCDO. This is expected, as the use of berley and tethered bait is aimed at temporarily modifying the behaviour of sharks to satisfy the viewing expectation of tourists during the cage-diving experience. The changes were, however, not all consistent, with the level of interaction with SCDO and behavioural responses varying between individual sharks.

The reduction in the area within which white sharks spent 50 % of their time and shallower swimming depth when SCDO were present indicates that SCDO not only affect residency and timing of visitation (Bruce and Bradford 2013), but also the fine-scale spatial distribution of white sharks. The concentrated swimming depth in the surface layer and slower ROM when in proximity to operators further indicate that these effects are not only influenced by the presence of SCDO, but also by the distance to the SCDO. 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 tethered bait is located. Such changes could alter the activity patterns, metabolic requirements, and energy budget of white sharks, as proposed for other species of sharks (Fitzpatrick et al. 2011).

Other factors investigated in our study could also affect the energy budget of white sharks at the Neptune Islands. For example, sharks spent a significant amount of time within the VRAP array, which was deployed close to the highest concentration of pinnipeds of the Island group (Shaughnessy and McKeown 2002). This is consistent with white sharks visiting these islands to feed on pinnipeds (Semmens et al. 2013) and is similar to observations from various other white shark aggregations (Le Boeuf 2004; Laroche et al. 2008; Domeier et al. 2012). Sharks, however, also 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. Based on the estimates of metabolic rates derived from swimming speed, white sharks at the Neptune Islands are predicted to

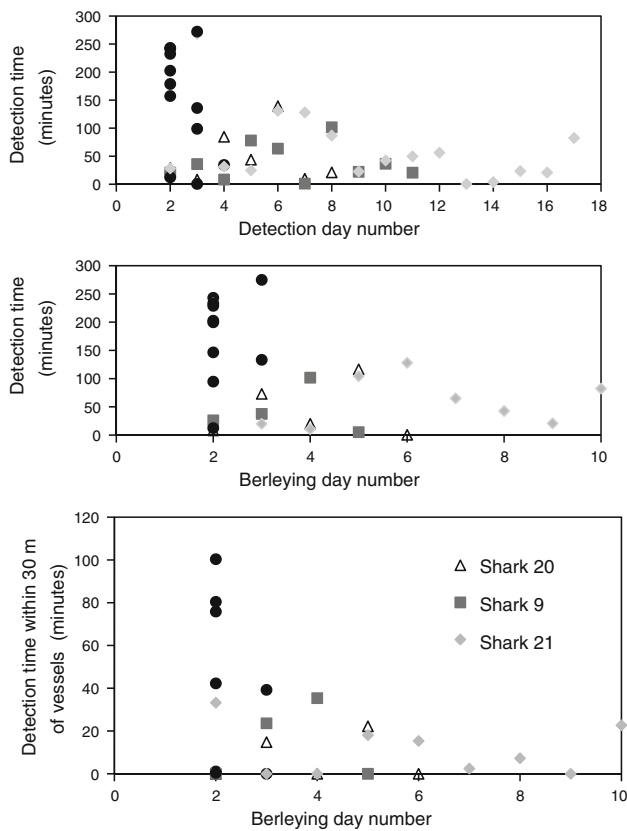


Fig. 8 Scatterplot of the **a** total detection time when sharks were present at North Neptune Island group; **b** detection time during berleying periods; and **c** detection time when sharks were present within 30 m of shark cage-diving operators, against detection day number or berleying day number since tagging. Filled circles represent shark monitored for 4 days or less. Sharks which were monitored for longer than 4 days are represented as different symbols. Note data from the tagging day were removed to account for biases associated with time of tagging and tagging effect

consume 0.3 weaned New Zealand fur seal pups per day, several times higher than previously proposed (Semmens et al. 2013). A reduction in foraging time as a result of wildlife tourism has previously been documented in terrestrial (e.g. Roes et al. 1997; Lott and McCoy 1995; Duchesne et al. 2000), avian (e.g. Steven et al. 2011; Buckley 2004), and marine (e.g. Williams et al. 2006; Lusseau et al. 2009; Christiansen et al. 2010) species and has been shown to affect individual fitness and population viability (e.g. Kerbiriou et al. 2009). The distraction presented by the cage-diving industry could decrease the amount of time white sharks spend foraging and result in reduced foraging success (Bruce and Bradford 2013), hence reducing their fitness, at the individual and population levels.

Changes in the activity levels of white sharks, as observed in the variation of rate of movement (ROM) when in proximity to SCDO, might also have implications for their energy budget. The decreased ROM observed when sharks were in close proximity to the boats may be explained by the increased tortuosity of the tracks and rapid turnarounds when interacting with the tethered bait. The energy requirement to undertake those directional changes could be higher than the routine energy expenditure of 28.2 MJ when patrolling the Neptune Islands at regular swimming speed (Semmens et al. 2013). Increased energy expenditure as a result of human disturbance has been shown to behaviourally and physiologically impact a range of taxa (Knight and Cole 1995; Culik 1994; Giese et al. 1999). The combination of the potential increased energy requirements, due to interactions with tethered baits, and reduced energy intake, due to disrupted natural foraging behaviour, could unbalance the energy budget and has long-term effects on life history traits, such as growth and reproduction (Calow 1979). However, the tethered bait can sometimes be consumed by sharks regardless of the attempts by the SCDO to prevent feeding, and the energy gained from the baits might compensate for the additional activity and disrupted natural foraging incurred by interacting with SCDO. While no data are currently available on the number of baits consumed by individual sharks, or the effects of interacting with SCDO on the energy budget of white sharks, a recent study has estimated the field routine metabolic rate (RMR) at 723 mg O₂ kg⁻¹ (Semmens et al. 2013). The potential impacts on individual fitness and population viability highlight the need to compare the energy expenditure of sharks closely interacting with SCDO to this baseline RMR, and to quantify energy intake from tethered baits.

The ROM obtained in this study (2.7 m s⁻¹) is relatively high compared to previous studies, which range from 0.8 to 1.5 m s⁻¹ (Klimley et al. 2001a; Bruce et al. 2006; Bruce and Bradford 2012, 2013; Strong et al. 1992; Bonfil

et al. 2005; Carey et al. 1982; Strong et al. 1996; Klimley et al. 2002). Most previous estimates of ROM were calculated using positions from conventional acoustic tracking or satellite telemetry and have a propensity to underestimate swimming speed due to errors involved in estimating true position and the two-dimensional point-to-point calculations of distance travelled. The present study suggests that white sharks might be capable of sustained swimming speed higher than previously estimated. Considering that most previous estimates of swimming speed were based on sharks travelling, white shark patrolling seal colonies might also swim on average faster than travelling sharks.

Our study provides evidence that sharks detected within the berleying site vary in their propensity to approach SCDO. This highlights that the presence of sharks on days during which operators are present does not necessarily imply that sharks will come within close proximity of SCDO, or that the presence of the SCDO will lead to direct physiological impacts on all individuals. Situations when sharks do not come in close proximity to SCDO have previously been linked to habituation to berleying exposure (Laroche et al. 2007). Although some evidence suggesting a habituation response was observed when data from all sharks during this study were combined, our ability to further quantify whether habituation occurred was limited as only three sharks were monitored for more than 8 days.

Differences in individual shark's response to SCDO were also observed in the proportion of detections obtained when SCDO were present, 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. For example, some sharks spent more than 60 % of their time within 60 m of the SCDO, while others were mostly detected further than 120 m from the SCDO. These differences are likely to result in the impact from SCDO interactions varying between individuals. This suggests that care should be taken when generalising across individuals and that the findings from a few individuals might not be applicable to all sharks visiting the Neptune Islands. Such individual variability has previously been seen in Caribbean reef sharks (*Carcharhinus perezi*) and sicklefin lemon sharks (*Negaprion acutidens*), where different sharks show opposite residency trends and responses to the tourism industry and associated provisioning (Clua et al. 2010; Maljković and Côté 2011; Brunnenschweiler and Barnett 2013). While sex and size of tagged sharks were recorded, the uneven and relatively small sample size precluded any analysis of sex- or size-related differences. The reasons for the different behaviours observed are potentially numerous and are likely a combination of motivation, different natural feeding histories, dominance hierarchies, individual experiences, previous exposure to berley or number of tethered baits

consumed, environmental conditions, or behavioural syndrome (consistency of responses across situations). 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). The integration of behavioural syndrome, or at least the recognition of individual variability, is recommended in studies of the impact of human disturbance on wildlife (Martin and Réale 2008), and is unambiguously needed to better understand the potential effect of cage-diving on white sharks. The degree of variation between individual sharks and the diverse levels of interactions highlights the complexity of the relationships between wildlife tourism and shark behaviour. The present study suggests that, to improve our understanding of these relationships, future monitoring of wildlife tourism may require further information on both proximity to SCDO and shark presence.

Conclusion

The present study provides quantitative information about the effects of SCDO on the fine-scale swimming behaviour of white sharks and describes significant changes in their short-term spatial distribution and ROM during shark cage-diving operations. Whether these changes will affect population viability of white sharks visiting the Neptune Islands is unknown and was outside the scope of this study. The study, however, also highlighted the need to recognise individual variability in the propensity of sharks to interact with SCDO and emphasised the need to take it into account in future studies and management of the industry. Visitation at the cage-diving site is temporary (Bruce et al. 2005; Bruce and Bradford 2013) and white sharks vary in their level of interactions 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, and should be further investigated.

Acknowledgments This project was carried out under the Department of the Environment and Natural Resources permit number M25738 and M25738-2, and PIRSA Exemption number 9902364. Tagging was undertaken under Flinders University ethics approval number E287, while the VRAP system was operated under the radio licence number 1917458 provided by the Australian Communications and Media Authority. This project was funded by the Winifred Violet Scott Charitable Trust, Neiser Foundation, Wildlife Conservation Fund, Nature Foundation of South Australia, and Solar Online. This research was also partly supported under the Australian Research Council's Discovery Projects funding scheme (project number DP0988554; www.arc.gov.au). Professor Seuront is the recipient of an Australian Professorial Fellowship (project number DP0988554).

The authors would like to thank A. Fox, J. Taylor, and R. Robbins from Rodney Fox Shark Expeditions, and A. Wright and crew from Calypso Star Charters for providing invaluable logistic support and advice during this study. We thank H. Pederson and W. Gillepsie from Eonfusion, Myriax, for their effort and support with the data manipulation and analysis. A. Lowther and S. Kim helped with the time-spent-in-area calculation, GAMM analyses, and statistical interpretation.

References

- Ballantyne R, Packer J, Hughes K, Dierking L (2007) Conservation learning in wildlife tourism settings: lessons from research in zoos and aquariums. *Environ Educ Res* 13:367–383
- Barker SM, Peddemors V, Williamson JE (2011a) Recreational SCUBA diver interactions with the critically endangered Grey Nurse Shark. *Pac Conserv Biol* 16:261–269
- Barker SM, Peddemors V, Williamson JE (2011b) A video and photographic study of aggregation, swimming and respiratory behaviour changes in the Grey Nurse Shark (*Carcharias taurus*) in response to the presence of SCUBA divers. *Mar Freshw Behav Physiol* 44:75–92
- Barnett A, Abrantes K, Stevens J, Bruce B, Semmens JM (2010) Fine-scale movements of the broadnose sevengill shark and its main prey, the gummy shark. *PLoS ONE* 5:e15464
- Bejder L, Samuels A, Whitehead H, Gales N, Mann J, Connor R, Heithaus M, Watson-Capps J, Flaherty C, Krutzen M (2006) Decline in relative abundance of bottlenose dolphins exposed to long-term disturbance. *Conserv Biol* 20:1791–1798
- Bonfil R, Meyer M, Scholl MC, Johnson R, O'Brien S, Oosthuizen H, Swanson S, Kotze D, Paterson M (2005) Transoceanic migration, spatial dynamics, and population linkages of white sharks. *Science* 310(5745):100–103
- Boustany AM, Davis SF, Pyle P, Anderson SD, Le Boeuf BJ, Block BA (2002) Expanded niche for White Sharks. *Nature* 415:35–36
- Bruce BD, Bradford RW (2012) Spatial dynamics and habitat preferences of juvenile white sharks in eastern Australia. In: Domeier ML (ed) *Global Perspectives on the biology and life history of the great white shark*. CRC Press, Boca Raton, pp 225–254
- Bruce BD, Bradford RW (2013) The effects of shark cage-diving operations on the behaviour and movements of white sharks, *Carcharodon carcharias*, at the Neptune Islands, South Australia. *Mar Biol* 160:889–907
- Bruce BD, Stevens JD, Bradford RW (2005) Site fidelity, residence times and home range patterns of white sharks around pinniped colonies. Australian Government Department of Environment and Heritage, Hobart
- Bruce BD, Stevens JD, Malcolm H (2006) Movements and swimming behaviour of white sharks (*Carcharodon carcharias*) in Australian waters. *Mar Biol* 150:161–172
- Brunnschweiler JM, Barnett A (2013) Opportunistic visitors: long-term behavioural response of bull sharks to food provisioning in Fiji. *PLoS ONE* 8:e58522
- Buckley R (2004) Impacts of ecotourism on birds. In: Buckley R (ed) *Environmental impacts of ecotourism*. CAB International, Cambridge, pp 187–209
- Calow P (1979) Adaptive aspects of energy allocation. In: Tyler P, Calow P (eds) *Fish energetics: new perspectives*. Croom Helm, Kent, pp 13–32
- Carey FG, Kanwisher JW, Brazier O, Gabrielson G, Casey JG, Pratt HLJ (1982) Temperature and activities of white shark, *Carcharodon carcharias*. *Copeia* 1982:254–260

- Christiansen F, Lusseau D, Stensland E, Berggren P (2010) Effects of tourist boats on the behaviour of Indo-Pacific bottlenose dolphins off the south coast of Zanzibar. *Endanger Species Res* 11:91–99
- Clua E, Buray N, Legendre P, Mourier J, Planes S (2010) Behavioural response of sicklefin lemon sharks *Negaprion acutidens* to underwater feeding for ecotourism purposes. *Mar Ecol Prog Ser* 414:257–266
- Culik BM (1994) Energy requirements of Pygoscelid penguins: a synopsis. *Rep Polar Res* 150:1–76
- DEWHA (2010) Draft recovery plan for the conservation and management of White Sharks (*Carcharodon carcharias*). Department of the Environment, Water, Heritage and the Arts, ACT
- Domeier ML, Nasby-Lucas N (2008) Migration patterns of white sharks *Carcharodon carcharias* tagged at Guadalupe Island, Mexico, and identification of an eastern Pacific shared offshore foraging area. *Mar Ecol Prog Ser* 370:221–237
- Domeier ML, Nasby-Lucas N, Lam CH (2012) Fine-scale habitat use by white sharks at Guadalupe Island, Mexico. In: Domeier ML (ed) Global perspectives on the biology and life history of the white shark. CRC Press, Boca Raton, pp 121–132
- Driscoll JW (1995) Attitude toward animals: species ratings. *Soc Anim* 3:139–150
- Duchesne M, Cote SD, Barette C (2000) Responses of woodland caribou to winter ecotourism in the Charlevoix Biosphere Reserve, Canada. *Biol Conserv* 96:311–317
- Duffus DA, Dearden P (1990) Non-consumptive wildlife oriented recreation: a conceptual framework. *Biol Conserv* 53:213–231
- Duffy C, Francis MP, Manning MJ, Bonfil R (2012) Regional population connectivity, oceanic habitat, and return migration revealed by satellite tagging of white sharks, *Carcharodon carcharias*, at New Zealand aggregation sites. In: Domeier ML (ed) Global perspectives on the biology and life history of the white shark. CRC Press, Boca Raton, pp 301–318
- Fay MP (2010) Two-sided exact tests and matching confidence intervals for discrete data. *R J* 2:53–58
- Ferguson K (2006) Submerged realities: shark documentaries at depth. *Atenea* 26:115–129
- Fitzpatrick R, Abrantes KG, Seymour J, Barnett A (2011) Variation in depth of whitetip reef sharks: does provisioning ecotourism change their behaviour? *Coral Reefs* 30:569–577
- Giese M, Handsworth R, Stephenson R (1999) Measuring resting heart rates in penguins using an artificial egg. *J Field Ornithol* 70:49–54
- Gosling S (2001) From mice to men: what can we learn about personality from animal research. *Psychol Bull* 127:45–86
- Green R, Giese M (2004) Negative effects of wildlife tourism on wildlife. In: Higginbottom K (ed) Wildlife tourism: impacts, management and planning. Sustainable Tourism Cooperative Research Centre, Gold Coast, pp 81–97
- Green RJ, Higginbottom K (2001) Status assessment of wildlife tourism in Australia series: the negative effects of wildlife tourism on wildlife. Wildlife Tourism Research Report CRC for Sustainable Tourism, Gold Coast, Queensland
- Higginbottom K, Tribe A (2004) Contributions of wildlife tourism to conservation. In: Higginbottom K (ed) Wildlife tourism: impacts, management and planning. Common Ground Publishing, CRC for Sustainable Tourism, Gold Coast, pp 99–123
- Iosilevskii G, Weihs D (2008) Speed limits on swimming of fishes and cetaceans. *J R Soc* 5:329–338
- Jorgensen SJ, Reeb CA, Chapple TK, Anderson SP, Van Sommeran SRF-C, Brown AC, Klimley AP, Block BA (2009) Philopatry and migration of Pacific White Sharks. *Proc R Soc B Biol Sci* 277:679–688
- Kerbiouri C, Le Viol I, Robert A, Porcher E, Gourmelon F, Julliard R (2009) Tourism in protected areas can threaten wild populations: from individual response to population viability of the cought *Pyrhcorax pyrhcorax*. *J Appl Ecol* 46:657–665
- Klimley A, Le Boeuf B, Cantara K, Richert J, Davis S, Van Sommeran S (2001a) Radio acoustic positioning as a tool for studying site-specific behavior of the white shark and other large marine species. *Mar Biol* 138:429–446
- Klimley AP, Le Boeuf BJ, Cantara K, Richert J, Davis SF, Van Sommeran S, Kelly JT (2001b) The hunting strategy of white sharks (*Carcharodon carcharias*) near a seal colony. *Mar Biol* 138:617–636
- Klimley AP, Beavers SC, Curtis TH, Jorgensen SJ (2002) Movements and swimming behavior of three species of sharks in La Jolla Canyon, California. *Environ Biol Fishes* 63:117–135
- Knight RL, Cole DN (1995) Factors that influence wildlife responses to recreationists. In: Knight RL, Gutzwiller KJ (eds) Wildlife and recreationists: coexistence through management and research. Island Press, Washington, pp 71–80
- Koolhaas J, Korte S, De Boer S, Van Der Veegt B, Van Reenen C, Hopster H, De Jong I, Ruis M, Blokhuis H (1999) Coping styles in animals: current status in behavior and stress-physiology. *Neurosci Behav Rev* 23:925–935
- Laroche KR, Kock AA, Dill LM, Oosthuizen H (2007) Effects of provisioning ecotourism activity on the behaviour of white sharks *Carcharodon carcharias*. *Mar Ecol Prog Ser* 338: 199–209
- Laroche KR, Kock AA, Dill LM, Oosthuizen WH (2008) Running the gauntlet: a predator-prey game between sharks and two age classes of seals. *Anim Behav* 76:1901–1917
- Le Boeuf BJ (2004) Hunting and migratory movements of white sharks in the eastern North Pacific. *Memoirs Natl Inst Polar Res* 58:89–100
- Lott D, McCoy M (1995) Asian Rhinos *Rhinoceros unicornis* on the run? Impact of tourist visits on one population. *Biol Conserv* 73:23–26
- Lusseau D, Bain D, Williams R, Smith J (2009) Vessel traffic disrupts the foraging behavior of southern resident killer whales *Orcinus orca*. *Endanger Species Res* 6:211–221
- Lynch A-MJ, Sutton SG, Simpfendorfer CA (2010) Implications of recreational fishing for elasmobranch conservation in the Great Barrier Reef Marine Park. *Aquat Conserv* 20:312–318
- Maljković A, Côté I (2011) Effects of tourism-related provisioning on the trophic signatures and movement patterns of an apex predator, the Caribbean reef shark. *Biol Conserv* 144:859–865
- Martin JGA, Réale D (2008) Animal temperament and human disturbance: implications for the response of wildlife to tourism. *Behav Process* 77:66–72
- Martin RA, Rossmo DK, Hammerschlag N (2009) Hunting patterns and geographic profiling of white shark predation. *J Zool* 279: 111–118
- Meyer CG, Dale JJ, Papastamatiou YP, Whitney NM, Holland KN (2009) Seasonal cycles and long-term trends in abundance and species composition of sharks associated with cage diving ecotourism activities in Hawaii. *Environ Conserv* 36:104–111
- Newsome D, Dowling R, Moore S (2005) Wildlife tourism. Channel View, Clevedon
- O'Dor RK, Andrade Y, Webber D, Sauer W, Roberts M, Smale M, Voegeli F (1998) Applications and performance of Radio-Acoustic Positioning and Telemetry (RAPT) systems. *Hydrobiologia* 371:3721–3728
- Orams M (2002) Feeding wildlife as a tourism attraction: a review of issues and impacts. *Tour Manage* 23:281–293
- Robbins RL (2007) Environmental variables affecting the sexual segregation of great white sharks *Carcharodon carcharias* at the Neptune Islands, South Australia. *J Fish Biol* 70:1350–1364
- Roes D, Leader-Williams N, Dalal-Clayton B (1997) Take only photographs, leave only footprints: the environmental impacts of

- wildlife tourism. International Institute for Environment and Development Wildlife and Development Series, vol 10. International Institute for Environment and Development, London
- Scheyvens R (1999) Ecotourism and the empowerment of local communities. *Tour Manage* 20:245–249
- Semeniuk CAD, Speers-Roesch B, Rothley KD (2007) Using fatty-acid profile analysis as an ecologic indicator in the management of tourist impacts on marine wildlife: a case of stingray-feeding in the Caribbean. *Environ Manag* 40:665–677
- Semmens JM, Payne N, Huvneers C, Sims DW, Bruce BD (2013) Feeding requirements of white sharks may be higher than originally thought. *Sci Rep* 3:1471
- Shackley M (1996) Wildlife tourism. International Thomson Business Press, London
- Shaughnessy PD, McKeown A (2002) Trends in abundance of New Zealand fur seals, *Arctocephalus forsteri*, at the Neptune Islands, South Australia. *Wildl Res* 29:363–370
- Sih A, Bell A, Johnson JC (2004) Behavioral syndromes: an ecological and evolutionary overview. *Trends Ecol Evol* 19:372–378
- Smith K, Scarr M, Scapaci C (2010) Grey nurse shark (*Carcharias taurus*) diving tourism: tourist compliance and shark behaviour at Fish Rock, Australia. *Environ Manag* 46:699–710
- Steven R, Pickering C, Castley JG (2011) A review of the impacts of nature based recreation on birds. *J Environ Manag* 92:2287–2294
- Strong WR, Murphy RC, Bruce BD, Nelson DR (1992) Movements and associated observations of bait-attracted white sharks, *Carcharodon carcharias*: a preliminary report. *Aust J Mar Freshw Res* 43:13–20
- Strong WR, Bruce BD, Nelson DR, Murphy RD (1996) Population dynamics of white sharks in Spencer Gulf, South Australia. In: Klimley AP, Ainley DG (eds) Great white sharks: the biology of *Carcharodon carcharias*. Academic, San Diego, pp 401–414
- Techera EJ, Klein N (2011) Fragmented governance: reconciling legal strategies for shark conservation and management. *Mar Policy* 35:73–78
- Wearing S, Neil J (2009) Ecotourism: impacts, potentials, and possibilities, 2nd edn. Butterworth-Heinemann, Oxford
- Weng KC, Boustany AM, Pyle P, Anderson SD, Brown A, Block BA (2007) Migration and habitat of white sharks (*Carcharodon carcharias*) in the eastern Pacific Ocean. *Mar Biol* 152:877–894
- Williams R, Lusseau D, Hammond P (2006) Estimating relative energetic costs of human disturbance to killer whales (*Orcinus orca*). *Biol Conserv* 133:301–311
- Worlf ID, Croft DB (2010) Minimizing disturbance to wildlife by tourists approaching on foot or in a car: a study of kangaroos in the Australian rangelands. *Appl Anim Behav Sci* 126:75–84
- Zamora L, Moreno-Amich R (2002) Quantifying the activity and movement of perch in a temperate lake by integrating acoustic telemetry and a geographic information system. *Hydrobiologia* 483:209–218