

The effects of shark cage-diving operations on the behaviour and movements of white sharks, *Carcharodon carcharias*, at the Neptune Islands, South Australia

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Abstract The attraction or provisioning of sharks for the purpose of tourism is a lucrative and popular industry that remains controversial regarding its possible risks to target species and impacts on local ecosystems. The long-term impacts of such activities on the behaviour and movement patterns of sharks have typically been difficult to establish as most studies investigate contemporary behaviour concurrent with existing operations and thus have no comparative base from which to compare effects. We compared patterns of residency and behaviour of acoustic-tagged white sharks at the Neptune Islands in South Australia between periods before and after an abrupt and sustained doubling of cage-diving effort that occurred in 2007. The number of sharks reported by cage-dive operators significantly increased after 2007. Comparisons also revealed there were significant increases in sharks' periods of residency, the periods spent within areas where shark cage-diving operations occur and changes in sharks' diel pattern of habitat use. Changes were site-specific with no significant differences in shark behaviour revealed over the same period at an island group 12 km from regular shark cage-dive sites. The results suggest that cage-diving operations can lead to long-term changes in the site-specific behaviour of a highly vagile shark species which may need to be considered in the context of their conservation and in managing the impacts of the industry.

Introduction

Tourism ventures that promote viewing or encountering wildlife in a natural setting have undergone a significant increase in popularity in recent decades (Orams 2002; Tapper 2006). Many such ventures involve provisioning (feeding) or some other form of attracting wildlife, that would otherwise be difficult to view, in order to enhance close encounters and client experience (Kruger 2005). However, tourism that relies on attracting or provisioning wildlife is a controversial activity, particularly when it involves protected species or species that are potentially dangerous to humans.

Various studies have demonstrated that regular provisioning of wildlife or interactions with human activity can lead to changes in the local abundance, behaviour and health status of both target and non-target species at interaction sites. These issues may manifest via the disruption of normal behaviour (Orams 2002; Clua et al. 2010), reductions in activity and home range (Altmann and Muruthi 1988), interference competition between individuals, increased frequency and duration of aggressive behaviours (Orams 2002; Semeniuk and Rothley 2008; Clarke et al. 2011; Fitzpatrick et al. 2011), increased risk of predation (Amo et al. 2006), impoverished body condition and physiological indications of impaired health (Orams 1995; Semeniuk and Rothley 2008; Semeniuk et al. 2009) as well as impacts on local, non-target species (Vignon et al. 2010). In some cases, disturbance from human activity, including tourism and non-tourism related, has been shown to alter species' energy budgets with projected negative effects. Bradshaw et al. (1998) concluded that multiple disturbance events from petroleum exploration activities may cause cumulative changes in energy expenditure by woodland caribou resulting in critical

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changes in over-winter body mass exceeding 15–20 %. Williams et al. (2006) estimated that killer whales disturbed from normal activities by whale watching vessels may suffer up to an 18 % reduction in energy intake through lost feeding opportunities.

Positive benefits may also accrue including local economic and social benefits in populations centres at which tourism operations are based, revenue raising, opportunities for research, benefits via increased public awareness of conservation issues, and education opportunities (Bookbinder et al. 1998; Orams 2002; Tapper 2006; Newsome and Rodger 2008), although not all of these provide direct benefits to the target species.

Marine-based animal tourism is an expanding industry worldwide and shark tourism has shown significant growth over the last few decades (Topelko and Dearden 2005; Hammerschlag et al. 2012). ‘Shark diving’ is a controversial activity that relies on attracting sharks to a viewing site by either berley (=chum), provisioning (=feeding) or both (Burgess 1998). Shark-based tourism ventures can be highly lucrative. Vianna et al. (2012) estimated that shark diving generates US\$18 million to the economy of Palau and similar studies estimate the value of shark diving to the Bahamian economy at up to US\$800 million (Gallagher and Hammerschlag 2011). Such estimates provide strong arguments for shark tourism as an economic alternative to shark fishing and for promoting shark conservation (Vianna et al. 2012). However, the management of such activities must also take into account the impacts on target species and their environment to ensure ecological sustainability. Studies on the impact of shark-based tourism on shark behaviour are few and have provided conflicting results (Laroche et al. 2007; Semeniuk and Rothley 2008; Meyer et al. 2009; Fitzpatrick et al. 2011). A significant limitation for determining the impact on shark behaviour of tourism is a lack of comparative data for sharks at these same sites prior to the commencement or expansion of such activities.

A key target species for shark cage-diving is the white shark (*Carcharodon carcharias*) due to its iconic nature, notoriety as one of the main species responsible for attacks on humans and due to its threatened conservation status. Cage-diving for white sharks is carried out in South Africa, Mexico, California, New Zealand and South Australia (Malcolm et al. 2001; Laroche et al. 2007, M. Francis NIWA, pers. comm.). White shark ecotourism involves a range of operations and stimuli to which sharks may respond including actively berleying, the presentation and consumption of tethered baits, schools of finfish attracted to berley, in-water cages with divers, the general presence of the vessel and the associated physical, electrochemical and acoustic signatures of all of these components combined. Previous studies have concluded that low to moderate levels of ecotourism operations had limited impact on the

behaviour of white sharks and that the changes in behaviour observed were both short-term and localised (Bruce et al. 2005; Laroche et al. 2007). However, as both studies were undertaken at sites where shark cage-dive operations were well established and stable in effort, they suffered from a lack of baseline data from which to compare contemporary behaviour to that prior to sharks’ exposure to operator activities. To investigate the impacts of tourism operations, some studies on elasmobranchs have compared behaviour and indices of health between sites where tourism operations occur and where they do not (e.g. Semeniuk et al. 2009; Maljkovic and Côté 2011). However, such comparisons may similarly be confounded given the propensity for elasmobranchs to show considerable plasticity in their behaviour and site occupancy between different areas (Bruce et al. 2006; Gutteridge et al. 2009; Sims et al. 2012). There are no published studies of which we are aware that compare shark behaviour before and after a tourism operation becomes established as such studies would need to be long-term and the opportunity to undertake research in such areas is often not available until a tourism venture becomes established. An alternative strategy would be to compare the response by target species to significant changes in tourism operations at an existing site before and after such a change. Such an opportunity was provided by an abrupt, sustained and significant increase in shark cage-dive effort at a site in South Australian waters from mid-2007.

The shark cage-diving industry in South Australia is restricted to the Neptune Islands Marine Reserve located 60–70 km south of Port Lincoln, with most cage-diving activities focussed at the North Neptune Island group. Similar to other such operations worldwide, white sharks are attracted to operator vessels by a mix of minced tuna and tuna oil (berley/chum), and the proximity experience for clients is enhanced by drawing attracted sharks in closer to the vessel using tethered baits comprising tuna pieces or tuna gills/entrails of up to several kilograms in weight that are attached to the lengths of rope and retrieved towards the vessel when a shark approaches. Acoustic and satellite telemetry-based tagging at the North Neptune Islands has identified that white sharks may be encountered year-round, but individuals are only temporary visitors to the site with relatively limited periods of residency (Bruce et al. 2005). Tracking has 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 North Neptune Islands have seen an expansion in shark cage-diving activities since 2007, with the mean annual number of days when operations occur rising abruptly from 124 days (2000–2006) to 265 days (2008–2011). This rapid and sustained increase in effort

also coincided with a change from irregular-timed, multi-day trips with irregular operator periods prior to June 2007, to a more regimented, near-daily operation with cage-diving activities occurring over a regular timed daily schedule thereafter.

These significant changes in industry operations, combined with prior data on shark residency patterns and movements at this site (Bruce et al. 2005), provided an ideal opportunity to examine the impact on shark behaviour of this increase in operator activity and the introduction of regular, near-daily shark cage-diving activities which is the more common model in white shark cage-dive industry operations and other shark tourism ventures worldwide (Burgess 1998; Laroche et al. 2007).

The purpose of this study was to examine the current residency and movement patterns of sharks within the Neptune Islands system and to determine whether there was evidence of changed behaviours between two periods of acoustic receiver deployments (2001–2003 and 2010–2011) before and after the increase in operator effort. This study was designed to answer two main questions: What are the current residency patterns and daily patterns

of habitat use at the North Neptune Islands, and how do these compare to the data collected in 2001–2003, prior to the 2007 increase in shark cage-dive operator effort? Our results were integrated to assess the effects on shark behaviour of exposure to shark cage-diving activities, to recommend options to mitigate impacts if required and to ensure that the industry has a sound management plan that promotes the ecologically sustainable, non-extractive use of the species.

Methods

Study area

The Neptune Islands (35°16.72'S; 136°5.48'E) are a series of granite formations rising steeply from approximately 60–100 m depth on the continental shelf some 60–70 km south of Port Lincoln, South Australia. The island system comprises two groups, the North and South Neptune Islands, which are approximately 12 km apart. Each island group comprises two main islands and various small rock

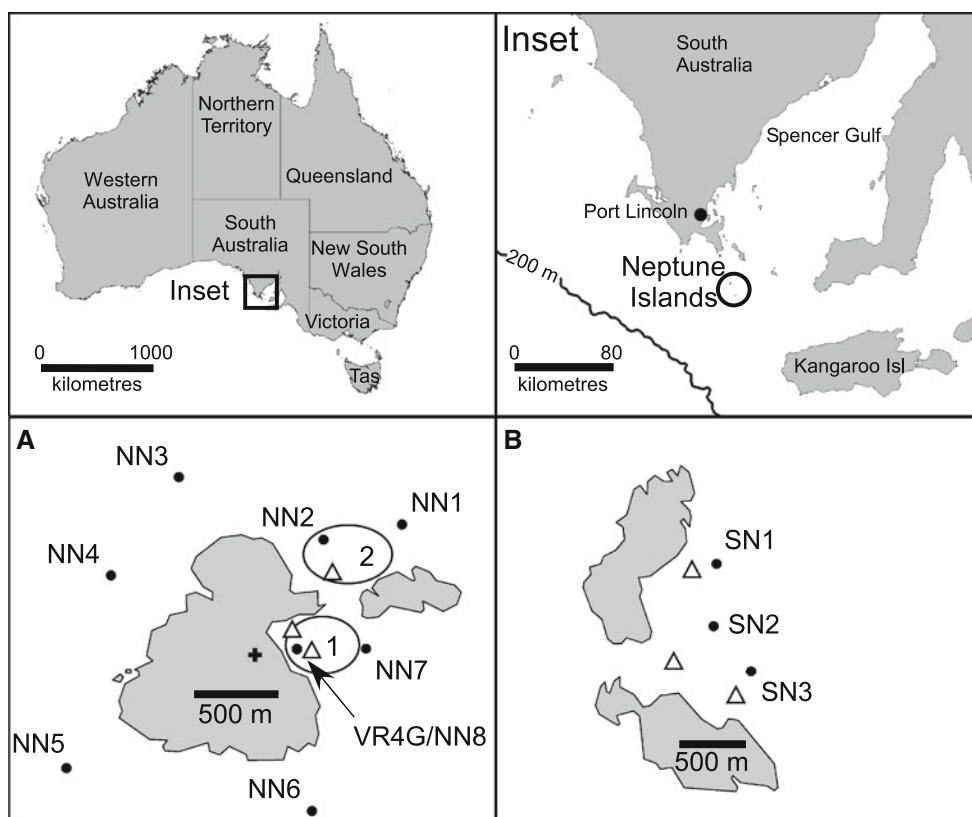


Fig. 1 The location of the Neptune Islands, South Australia (insets). **a** North Neptune Islands; **b** South Neptune Islands. The locations of 2010–2011 acoustic receivers are marked by *solid black dots* and labelled (e.g. NN1); the locations of 2001–2003 receivers are marked by *open triangles*. Shark cage-dive sites at North Neptune Island are

circled; 1 = Operator Site 1; 2 = Operator Site 2. The reference point on North Neptune Island for Centre of Activity analyses is marked by the black cross. Receiver NN8 was positioned on the mooring line of the VR4G receiver

outcrops (Fig. 1). Sub-tidal habitat includes areas of shallow sand and seagrass as well as shallow and deep reef systems (DENR 2010). Both island groups hold breeding colonies of New Zealand fur seals (*Arctocephalus forsteri*) and Australian sea-lions (*Neophoca cinerea*). Combined, the Neptune Islands support the largest aggregations of pinnipeds in Australian waters of which the majority reside on the North Neptune Islands (Shaughnessy and McKeown 2002). Both island groups are included within the Neptune Islands Marine Park. The marine park extends two nautical miles (3.7 km) from the coastline of each island group, covering an area of 146 km² (DENR 2010). Shark cage-diving operations occur at two sites at the North Neptune Islands: Site 1 inside the island's main bay and Site 2 outside and to the north of the bay (Fig. 1). Shark cage-diving operations prior to 2007 were primarily restricted at Site 1, whereas both sites were utilised on a regular basis after 2007. Operator activity at the South Neptune Islands was rare during both study periods.

Acoustic receiver deployments

Acoustic receivers (Vemco-Amirix Ltd, Halifax, NS Canada) were deployed at both North and South Neptune Islands over two time periods, one before and one after the increase in operator effort in 2007. Acoustic receivers log and store the date, time and unique code identity of Vemco RCODE acoustic transmitters fitted to animals that swim within the detection range (typically a 300–500 m radius at these sites—CSIRO unpublished data). The first deployment period, herein referred to as the 2001–2003 study, was part of an initial and separate program investigating the residency patterns of white sharks at the North and South Neptune Island (Bruce et al. (2005)). The second deployment period comprised a more extensive contemporary study of residency patterns and habitat use at the Neptune Island groups from December 2009 to April 2011, herein, the 2010–2011 study.

Acoustic receiver deployments 2001–2003

Data were re-analysed from the 2001–2003 acoustic telemetry study at both North and South Neptune Islands (Bruce et al. 2005). Acoustic receivers (VR2) were deployed from April 2001 to March–April 2003 at both island systems (Fig. 1). Three VR2 receivers were deployed at the North Neptune Islands, two inside the island's main bay at Site 1 where cage-diving operations were primarily undertaken during the period, and one outside and to the north of the bay covering Site 2 where cage-diving operations were rarely undertaken during the period. Three Vemco VR2 units were deployed at South Neptune Islands during the 2001–2003 study on the eastern

side of the island group. Receiver moorings were each anchored to the sea floor attached to a steel post inserted into a concrete-filled truck tyre (approx 120 kg total mass) with each receiver located approximately 1.5 m off the bottom and 10–20 m below the surface, depending on bottom depth. Moorings were located in bottom depths ranging from 12 to 22 m. Receivers deployed during the 2001–2003 study were retrieved, downloaded and replaced by divers using shark-proof cages (see Bruce et al. 2005 for details).

Acoustic receiver deployments 2010–2011

Acoustic receivers (VR2 W and VR3-UWM) were continuously deployed at both North and South Neptune Island sites from December 2009 to April 2011 as part of the 2010–2011 study. Eight receivers were deployed at North Neptune Island and three at South Neptune Island (Fig. 1; Table 1). The array at North Neptune Island complemented an existing, iridium satellite-linked acoustic receiver (VR4-Global [VR4G]; Vemco-Amirix Ltd, Halifax, NS Canada) which has been maintained at Site 1 since April 2008 (Bradford et al. 2011). Receivers NN8 and NN2 approximated the receiver deployment locations of the 2001–2003 study. The two 2001–2003 receivers set inside the bay and the NN8 (2010–2011) receiver provided comparative acoustic coverage of Site 1. The 2001–2003 receiver set outside the bay and the NN2 (2010–2011) receiver provided comparative acoustic coverage of Site 2 over both study periods. Receivers deployed at the South Neptune Islands during the 2010–2011 study approximated the same locations where the 2001–2003 receivers were deployed as described by Bruce et al. (2005) and thus also provided comparative acoustic coverage for this site between both study periods. Data retrieval from VR2 and VR2 W acoustic receivers requires that units are physically recovered and downloaded. Data retrieval from a VR3-UWM is possible via an acoustic communications modem incorporated within each unit which can be remotely activated from a vessel-based hydrophone and deck unit system without retrieving the units. The initial deployment of receivers in December 2009 included both VR2 W and VR3-UWM units. VR3-UWM units were deployed so as to allow for opportunistic retrieval of data via the acoustic modem between full retrieval periods. However, this proved impractical and all VR3-UWM units were recovered, downloaded and replaced with VR2 W receivers in October 2010.

Receiver moorings were anchored to the sea floor using either concrete-filled truck tyres (approx 120 kg total mass) or 20-mm chain moorings each approximately 150 kg total mass, following protocols developed by the Australian Animal Tracking and Monitoring System (AATAMS).

Table 1 Deployment details for acoustic receivers at Neptune Islands (see Fig. 1 for station locations)

Station	Deployment 1					Deployment 2				
	Deploy	Recover	Type	Errors	No. of sharks	Deploy	Recover	Type	Errors	No. of sharks
NN1	09/12/2009	06/10/2010	VR3	Flooded	–	08/10/2010	13/04/2011	VR2 W		14
NN2	09/12/2009	06/10/2010	VR2 W		14	08/10/2010	13/04/2011	VR2 W		16
NN3	09/12/2009	08/10/2010	VR2 W		10	08/10/2010	13/04/2011	VR2 W		14
NN4	09/12/2009	08/10/2010	VR2 W		10	08/10/2010	13/04/2011	VR2 W	Comms	13
NN5	09/12/2009	08/10/2010	VR2 W		10	09/10/2010	13/04/2011	VR2 W		14
NN6	09/12/2009	08/10/2010	VR2 W		13	09/10/2010	13/04/2011	VR2 W		13
NN7	09/12/2009	06/10/2010	VR3		14	08/10/2010	13/04/2011	VR2 W		16
NN8	09/12/2009	06/10/2010	VR2 W		15	08/10/2010	13/04/2011	VR2 W		15
SN1	08/12/2009	07/10/2010	VR3	Flooded	–	07/10/2010	13/04/2011	VR2 W		6
SN2	08/12/2009	07/10/2010	VR3		6	07/10/2010	13/04/2011	VR2 W		5
SN3	08/12/2009	07/10/2010	VR3		6	07/10/2010	13/04/2011	VR2 W		5

Receiver NN8 was attached to the mooring line of the VR4G satellite-linked acoustic receiver moored in the bay at North Neptune Island. The ‘comms’ error indicated that the unit would not communicate on retrieval. Data were successfully downloaded after the unit was returned to the manufacturer

Receivers were fixed to a 14-mm braided line attached to the mooring anchor and suspended under subsurface floats, with the receiver about 20 m below the surface. Moorings were located in bottom depths ranging from 12 to 93 m. Each mooring deployed in 2010–2011 was fitted with a Sub Sea Sonics (www.subseasonics.com) acoustic release and a rope canister which allowed receivers to surface on command and for the complete mooring system to be retrieved.

A large number of acoustic receiver arrays maintained by AATAMS and various other collaborating organizations exist throughout Australia waters (see <http://imos.org.au/aatams.html> for details of receiver locations), and data from these receivers were interrogated for detections of white sharks which had been tagged at the Neptune Islands thus complementing the above data sets and providing information on the broad-scale movements away from the Neptune Islands.

Acoustic tags

The 2001–2003 study included data from 26 sharks tagged with Vemco V16 R256 (4H) coded acoustic transmitters at the North and South Neptune Islands (Bruce et al. 2005). Between December 2009 and March 2011, twenty-one sharks were tagged with Vemco V16 R64K (6H–160 db) coded acoustic transmitters (Table 2). In each study, transmitters were coded with a unique pulse series, operated on a frequency of 69 kHz. Transmitters used in the 2001–2003 study were rated for a battery life of approximately 2.0 years and those used in the 2010–2011 study were rated for approximately 6.5 years. In both studies,

sharks were attracted to the vessel using fish-based berley and tags were attached externally to the dorsal musculature using a tagging pole following the procedures of Bruce et al. (2005).

Data analyses

Analyses were performed using S-PLUS 8.1 (Tibco-Spotfire) and R statistical software, version ‘2.14.2’ (R Development Core Team 2012). Circular statistics were performed using the CircStat package (Berens 2009) developed for Matlab (MathWorks). The significance of all statistical tests was determined at the 0.05 probability level.

Acoustic tag data

Detections recorded by receivers were used to examine the presence and behaviour of tagged sharks at North and South Neptune Islands as well as movements between the two island groups (the study area). Sharks were considered to be present at either North or South Neptune Islands if two or more detections were registered on any receivers on a given day. If a shark was not detected on a given day, then it was assumed not to be present in the study area. Daily detection summaries were plotted to examine the pattern of overall presence of tagged sharks during each study period.

The number of consecutive days individuals were present was calculated each time they entered the study area. Two periods of site occupancy were defined by the acoustic detection data. ‘Residency period’ was defined as the number of days between the first and last detection of a

Table 2 Acoustic tag deployment details for the Neptune Islands, South Australia (2010–2011)

Tag ID	Date	Length (m)	Sex	Location
8561	05/07/2010	3.2	Male	NN-Site 2
8562	19/08/2010	4.2	Male	NN-Site 1
32561	27/10/2010	3.5	Male	NN-Site 1
32562	17/02/2011	4.7	Male	NN-Site 1
32563	09/10/2010	4.3	Male	NN-Site 1
32565	16/01/2011	4.0	Male	NN-Site 1
58068	04/08/2010	3.2	Male	NN-Site 1
58069	08/10/2010	3.5	Male	NN-Site 1
58070	08/08/2010	4.2	Female	NN-Site 1
58071	4/03/2011	4.8	Male	NN-Site 1
62342	24/10/2010	NR ^a	NR	NN ^b
62343	15/12/2010	4.4	Male	NN-Site 1
62344	08/10/2010	4.5	Male	NN-Site 1
62345	08/10/2010	3.5	Male	NN-Site 1
62346	11/06/2010	3.5	Male	NN-Site 2
62347	11/12/2009	4.2	Male	NN-Site 2
62349	19/07/2010	3.5	Female	NN-Site 1
62350	21/06/2010	4.8	Female	SN
62351	27/06/2010	2.8	Female	NN-Site 1
62352	16/06/2010	4.0	Male	NN-Site 1
62353	13/06/2010	4.7	Male	NN-Site 2

Location refers to the Site where sharks were tagged. NN-Site 1 is within the bay at North Neptune Island (Shark cage-dive Site 1); NN-Site 2 is on the northern side of the North Neptune Island (Shark cage-dive Site 2); SN South Neptune Island. See Fig. 1 for site location details

^a NR—data not recorded

^b North Neptune; site not recorded

tagged shark provided gaps between consecutive days of detection did not exceed 5 days. A five-day period was selected on the basis of transit times between the North and South Neptune Islands by individual sharks. The majority (89 %) of return transit times between the island groups during the 2010–2011 study were less than 100 h (median = 15.4 h; range 2.3–504.4 h, SE = 17.4). A period of 5 days was allowed for sharks remaining in the vicinity of the Neptune Islands system but without registering detections at either island. Where sharks were not detected over periods greater than five consecutive days, individuals were assumed to have left the Neptune Islands system and any subsequent return was considered to start a new residency period. ‘Visits’ were defined as the number of consecutive days where detections were registered for any given shark during its residency period.

Detection patterns of acoustic-tagged sharks were compared between the 2001–2003 study and the 2010–2011 study. The 2001–2003 study was undertaken prior to the significant increase in shark cage-dive operator

activity beginning in 2007. The periods of residency and duration of visits between the two study periods were compared using a Mann–Whitney *U* test (Conover 1999). Due to the highly skewed nature of these data, the median was used as the descriptive statistic in preference to the mean.

In addition to the 2001–2003 and the 2010–2011 data sets, data from the VR4G acoustic receiver deployed in the bay at North Neptune Island were used to examine the frequency and nature of shark residency periods and the duration of visits over its period of deployment (2008–2012) using the same analytical techniques. Sharks were tagged at the Neptune Islands from 2007 to 2009 as part of a trial of the VR4G system (Bradford et al. 2011) and a separate, broad-scale study of the movement dynamics of the species in Australian waters utilising receivers deployed by AATAMS and affiliated agencies.

The more extensive acoustic receiver array deployed in the 2010–2011 study enabled a more detailed analysis of the spatial scale of responses to cage-dive operations than the 2001–2003 study. These responses were examined by comparing each shark’s centres of activity between days when operators were present and days when operators were absent, referred to herein as ‘operator’ and non-operator’ days. The centre of activity (COA) for each tagged shark at the North Neptune Islands was estimated from the 2010–2011 acoustic data every 30 min using a weighted mean position algorithm (modified from Simpfendorfer et al. 2002) (Eq. 1);

$$\text{COA} (X_{\text{Rad}30}) = \frac{\sum_i^j (w_i X_i + \dots + w_j X_j)}{\sum_i^j (w_i + \dots + w_j)} \quad (1)$$

where $X_{\text{Rad}30}$ is the mean weighted radian value identifying the centre of activity over each 30-min period, w_i is the number of detections of an individual shark at receiver i during the monitored period (30 min) and X_i is the radian value of the bearing from a central reference point on North Neptune Island to receiver i .

Thirty-minute blocks were chosen to allow for movement to occur between the detection envelopes of adjacent receivers while minimising movement between the reception envelopes of distant receivers. Because our array circled the North Neptune Islands, we converted the latitude and longitude of individual receivers to a bearing from a central reference point on North Neptune Island (see Fig. 1) and then converted that value into radians. The radian value was used in the position algorithm in place of receiver location (latitude/longitude—see Simpfendorfer et al. 2002). The resultant value provided a weighted mean radian estimate identifying the centre of activity as a bearing from the central reference point on the island. COA

bearings were binned into 30° sectors to visualise the distribution of shark activity around the island.

A Watson-Williams test, analogous to a single-factor ANOVA for circular data (Berens 2009), was used to test for differences between the common mean bearing for individual shark's COAs between operator and non-operator days and to test for sharks' responses during periods when cage-dive operators shifted their activities from Site 1 to Site 2 at the North Neptune Islands.

The combined daily patterns in the detections of sharks were examined at the North Neptune Islands Cage-diving Sites 1 and 2 and compared between the 2001–2003 and 2010–2011 study periods. The number of detections of tagged sharks was summed in 30-min bins and χ^2 goodness-of-fit tests were used to compare the frequency of detections to an even distribution. Significant departures from an even distribution were used to identify the presence of diel patterns in shark activity.

Daily logbook data

Data on the long-term number of sharks sighted per operator day, monthly means of these data, and the total number of operator days at the Neptune Islands per year were extracted from daily logbook data filed by shark cage-dive operators (SCDO) over the period from January 2000 to December 2011. Both SCDOs had several years of experience in the industry prior to the introduction of logbooks in late 1999. SCDOs identified the number of individual sharks around the vessel each day by their size, sex, location of tags and natural marks (including shape of the posterior margin of the dorsal fin, colour markings on the flank and lower caudal lobe). Assessments were based on both surface and underwater observations and photographs. Such characters have been successfully used to identify individual elasmobranchs (Marshall et al. 2011) and white sharks in particular (Anderson et al. 2011; Nasby-Lucas and Domeier 2012) at various locations worldwide. An operator day was defined as any day that shark cage-diving operations occurred on site regardless of the number of operators present or the duration of operations on that day. Logbook data were also used to determine and monitor the North Neptune Island shark activity index (NNI shark index). The NNI shark index compares the monthly mean number of sharks sighted by operators per day to the long-term mean for that month over the same 2000–2011 period. The resultant data, as an anomaly, provided a comparative measure of shark activity for any observed period. A Poisson general linear model (GLM) with effects for both month and before/after 2007 was used to determine whether the number of sharks sighted per day had changed after the increase in operator effort and its shift to a regular daily schedule based on these logbook data. Month was retained

as a factor due to the overall seasonal signal in shark abundance at the Neptune Islands (Bruce et al. 2005; Robbins 2007). To compare the number of sharks observed per operator day between months for pre- and post-2007 periods, data were log transformed and a paired *t* test performed.

Shark lengths are reported as total length (TL—see Wintner and Cliff 1999 for definition) unless otherwise stated. The TL for each tagged shark was visually estimated at the time of tagging based on reference to known length measures on the tagging vessel and the in-water dive cage or to graduated one-metre marks on teaser bait lines.

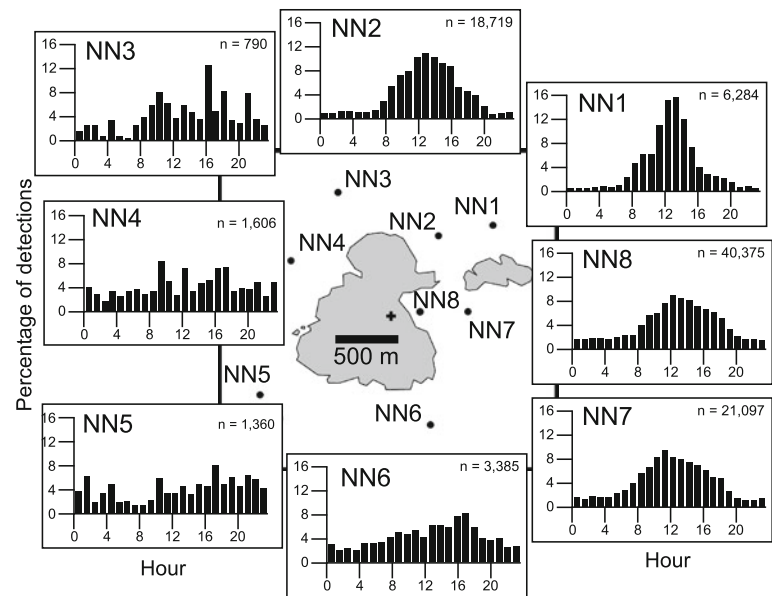
Results

The results of the 2001–2003 study have been previously described by Bruce et al. (2005). Briefly, a total of 81,652 detections were recorded from all 26 sharks tagged at the North and South Neptunes receiver arrays combined. All 22 sharks tagged at the North Neptune Islands were detected by receivers deployed at this island group; 12 of these sharks (54.5 %) were also detected at the South Neptune Islands. All four of the sharks tagged at the South Neptune Islands were recorded at that island group but none of these were detected at the North Neptune Islands. Tagged sharks were detected over the period from 18 June 2001 to 15 December 2002.

A total of 99,957 detections were recorded from all 21 sharks tagged during the 2010–2011 study across the North and South Neptune Islands' receiver arrays combined. All 21 sharks (including the single shark tagged at South Neptune Island) were detected by North Neptune Island receivers. Detections indicated that sharks, at times, utilised the entire area of the arrays including all waters surrounding the North Neptune Islands. However, detections of tagged sharks varied both spatially and temporally (Fig. 2). Receivers NN7 and NN8 near to cage-dive Site 1 and receivers NN1 and NN2 near to cage-dive Site 2 accounted for 92.4 % of all detections. The largest number of detections of tagged sharks (75.8 % of all detections) was recorded inside the Bay at receiver NN8. Data were more limited at NN1 due to flooding of the receiver during the first deployment period. A clear diel pattern in detections was apparent for each of these four receivers with detections generally increasing from 0700 to a peak (1100–1300) followed by a decline to low levels after 1800–1900. A diel pattern was not evident at receivers NN3, NN4 and NN5 although there were comparatively fewer data at these locations.

Eight of the 20 sharks tagged at the North Neptune Islands group (40 %) were detected at the South Neptune Islands group; the single shark tagged at the South Neptune

Fig. 2 Hourly detections of tagged sharks at receiver locations around North Neptune Island (December 2009–April 2011). Data are percentage of total detections by hour for each site; n = total detections registered



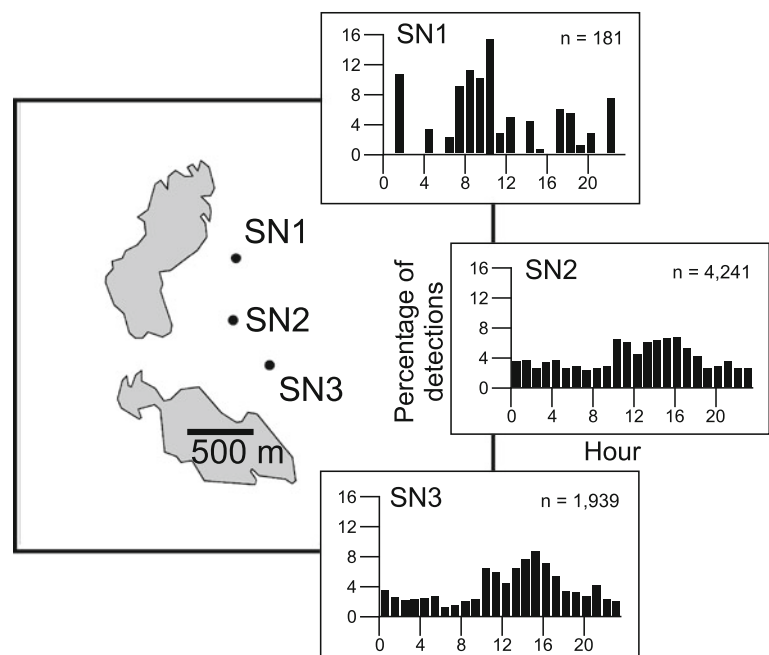
Islands group was also detected at the North Neptune Islands group. However, in each case, sharks spent the majority of their detected time at the island group where they were tagged, with infrequent visits of only short duration to the other island group. Detections of tagged sharks also indicated a diel pattern at South Neptune Island (Fig. 3). Detections generally increased from 1000 to a peak (1300–1600) followed by a decline to stable levels by 1900–2000.

The distribution of shark activity around North Neptune Island was focussed on the eastern side of the island during periods when operators were present and when they were

absent. However, the mean centres of sharks' activity differed significantly (Watson-Williams test, $F_1 = 1280.93$, $p > 0.0001$) depending on which site operators actively engaged in shark cage-dive activities. Sharks focussed their activity between Sites 1 and 2 in unison with the presence of shark cage-dive operations. These data support that the distribution of sharks at the North Neptune Islands was influenced by the presence of operator activity on at least the local spatial and short-term temporal scales (Fig. 4).

With the exception of Shark 62347 (tagged and recorded in December 2009), tagged sharks were detected over the period from 11 June 2010 to 12 April 2011 with up to six

Fig. 3 Hourly detections of tagged sharks at receiver locations around South Neptune Island (December 2009–April 2011). Data are percentage of total detections by hour for each site; n = total detections registered



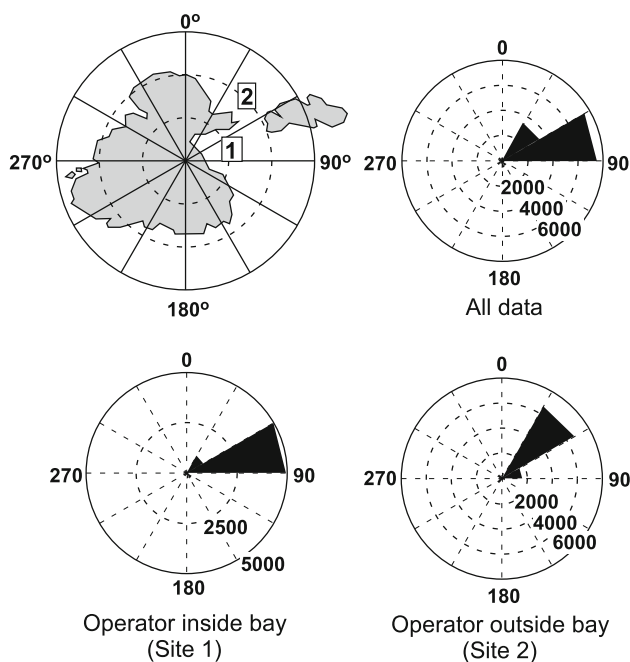
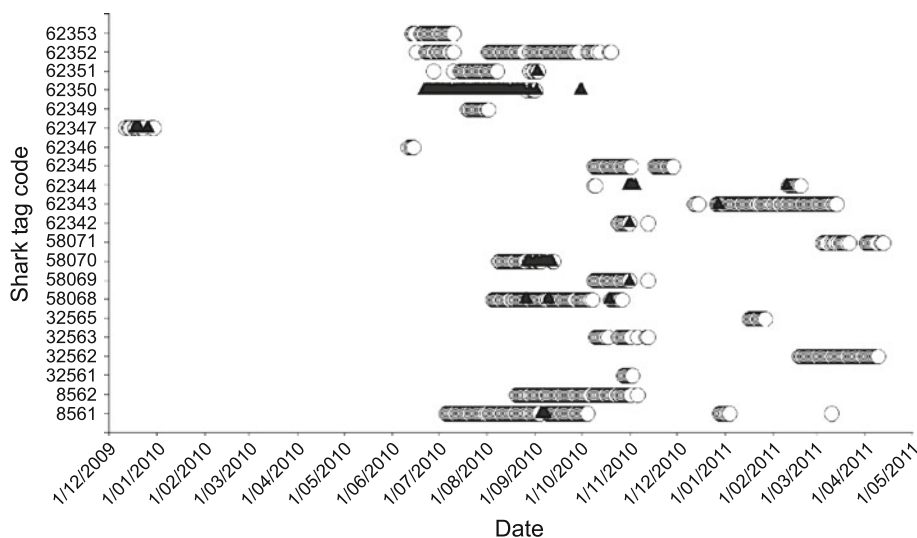


Fig. 4 Distribution of tagged white sharks within the acoustic receiver array at North Neptune Island, South Australia during periods of operator activity at Sites 1 + 2. *Circular scales* indicate number of COA recorded for all sharks combined

sharks present on site at any one time (Fig. 5). Residency periods within the Neptunes Island system ranged from 1 to 92 days (median = 11, SD = 24.2). The number of residency periods ranged from one to five for individual sharks with the majority (57 %) recording multiple residency periods. Most periods (79 %) were separated by 6–10 days and it is thus possible that our residency parameter underestimated actual periods of residency if sharks patrolled areas outside of detection range for >5 days

Fig. 5 Daily presence–absence of acoustically tagged white sharks at the Neptune Islands (2010–2011). Shark numbers refer to unique acoustic tag codes for each shark. *Open circles* indicate that the shark was detected on that day at the North Neptune Islands. *Filled triangles* indicate days when sharks were detected at the South Neptune Islands



while still present within the vicinity of the Neptune Islands system.

Within their overall periods of residency, each shark recorded separate visits of consecutive days to each of the island groups. The duration of visits at the North Neptune Islands ranged from 1 to 52 consecutive days (median = 6.5; SD = 12.5). The duration of visits at South Neptune Island ranged from 1 to 34 consecutive days (median = 2; SD = 6.2).

Sharks made a total of 37 transits between North and South Neptune Islands, representing 18 journeys where they returned to their island group of origin. Only one transit resulted in a shark not returning to its island group of origin. Shark 62351 made the transit from North Neptune Island to South Neptune Island in late September 2010 where it remained for 31 h before again departing. This shark was not detected again on any receiver during the remaining period of the study and was assumed to have departed the region. Movements between North and South Neptune Islands were, in general, relatively rapid indicating directed travel between the two systems. Most transit periods were less than 20 h duration (median 15.4 h) but ranged from 2.23 h to 504.4 h. The shortest duration for travel indicated a minimum sustained rate of movement (ROM) between the two island systems of 5.4 km per hour which is one of the highest recorded for white sharks (see Bruce and Bradford 2012). The longer travel periods (>50 h) suggest that not all travel was direct between the islands, although the incidence of these lengthy transits was few.

Three sharks tagged at the Neptune Islands (Sharks 62342, 62346, and 62349) during the 2010–2011 study were recorded on receivers maintained by other researchers near Chatham Island, Western Australia (35° 2.25' S 116° 29.45' E). These detections occurred, respectively, on 18

April 2011 (Shark 62342), 8 March 2011 (Shark 62346) and 19 December 2010 (Shark 62349). Chatham Island is approximately 1800 km west of the Neptune Islands (approximately 2000 km following a typical on-shelf track). The last detections for each shark at the Neptune Islands were, respectively, 12 November 2010 (Shark 62342), 28 November 2010 (Shark 62346) and 31 July (Shark 62349). No intervening detections of these sharks were registered on other receiver arrays, and these sharks were not re-detected at the Neptune Islands after the above departure dates.

Comparisons between pre-2007 and post-2007 data

Daily logbook data confirmed an increase in operator effort at the Neptune Islands after 2007 (Fig. 6). The mean number of operator days per year from 2000 to 2006 was 124 (range = 108–150, SE = 5.6). The mean number of operator days per year from 2008 to 2011 was 265 (range 241–287, SE = 9.5). This abrupt and sustained increase was initiated in June 2007 on commencement of a daily trip business model by one of the operators. A total of 114 of the 162 operator days in 2007 occurred after the change in business model.

The numbers of sharks sighted per day and recorded in logbooks by each of the two active SCDO were not significantly different over the period 1999–2011 (ANOVA, $F = 1.066059$, $p = 0.3019$). This provided confidence in the veracity of logbook data, and thus, both operators' data sets were pooled for analyses. The GLM point estimate of the before/after 2007 effect (0.4010) suggested an increase in the number of sharks sighted per day after 2007. However, there was clear evidence of year effects, i.e., year-to-year variability (in addition to the before/after 2007 effects), indicating over-dispersion in the data. To test significance in a manner that was robust to such year effects, we used a permutation test, keeping each year's data together, but randomly relabelling the years and then

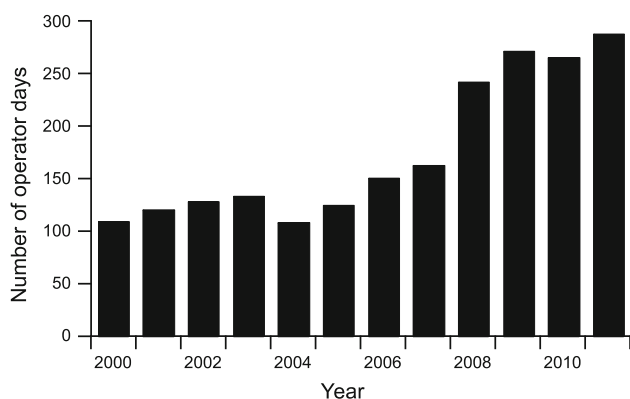


Fig. 6 Annual number of days of shark cage-diving operations at the North Neptune Islands, South Australia, 2000–2011

re-fitting the GLM. Of 100,000 replicates, only 3,386 exceeded the GLM estimate of the before/after 2007 effect in the observed data. The result indicating a significant increase in sharks observed per day after the change in shark cage-dive effort in 2007 ($p = 0.0339$).

Data also indicated that the number of sharks sighted post-2007 increased across the entire year regardless of month (paired t test, $t = 3.667$, $p = 0.0019$; power 5 % significance = 91.47 %); Fig. 7.

Periods of residency and duration of visits by sharks were compared between the 2001–2003 and 2010–2011 data sets. To avoid possible bias generated by the more complete receiver coverage of the North Neptune Islands in 2010–2011, we restricted the data series to detections from those receivers that approximated the spatial deployments of the 2001–2003 study for these comparisons. Detection data from the 2010–2011 NN2 and NN8/VR4G receivers approximated the 2001–2003 receiver deployments and were thus used for these analyses. The resultant median residency period was significantly greater in 2010–2011 than during 2001–2003 (Mann–Whitney U test, median 2001–2003 = 4; median 2010–2011 = 9; $p = 0.0325$). The median duration of visits was also significantly greater in 2010–2011 (Mann–Whitney U test, median 2001–2003 = 2; median 2010–2011 = 4; $p < 0.0001$).

The duration of visits was examined specifically within the bay at North Neptune Island using only the VR4G data set and comparing to the data from the 2001–2003 receiver similarly deployed inside the bay. In this case, the deployment location for both periods was identical. The VR4G receiver was deployed continuously from 2008 providing data over the entire period of increased operator activity. Differences between the duration of visits were

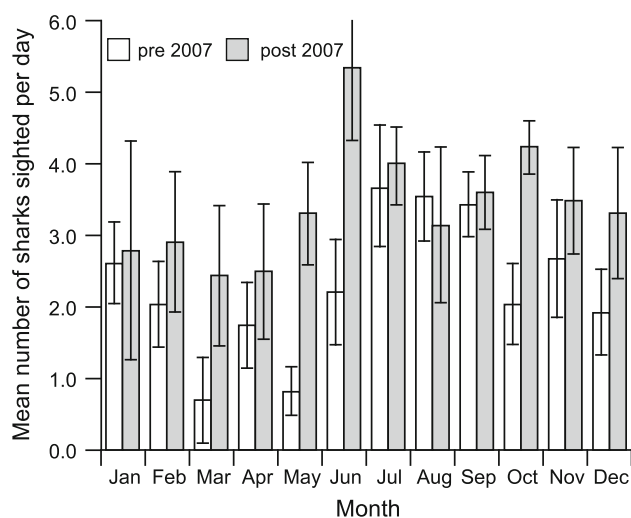


Fig. 7 The mean number of sharks sighted per month at the North Neptune Islands, South Australia by shark cage-dive operators prior to 2007 (2000–2006) and after 2007 (2008–2011). Bars indicate one standard error

again highly significant between the two periods with the VR4G data set recording significantly longer visit durations than those recorded during the 2001–2003 period (Mann–Whitney U test, median 2001–2003 = 2 days; median 2008–2011 = 3 days; $p = 0.0005$).

The periods of residency and duration of visits by sharks to the South Neptune Islands were also compared between 2001–2003 and 2010–2011 periods. Receivers were deployed in nearly the same locations between the study periods and thus were readily comparable. The median period of residency was not significantly different between the two time periods (Mann–Whitney U test, median 2001–2003 = 2.0 days; 2010–2011 = 2.0 days; $p = 0.645$). The median duration of visits was also not significantly different between the two periods (Mann–Whitney U test, median 2001–2003 = 1.0 day; median 2010–2011 = 2.0 days; $p = 0.212$). This, combined with the above analyses, suggested that the increased duration of visits by sharks was an effect restricted to the North Neptune Islands only.

The diel timing of detections of tagged sharks varied between days when operators were present and those when they were absent at the North Neptune Islands during both the 2001–2003 and the 2010–2011 periods. However, the pattern of these detections differed between periods. During the 2001–2003 study, a clear diel pattern in the detections of tagged sharks was observed inside the bay at the North Neptune Islands (Site 1). Detections on both operator days and non-operator days at Site 1 were concentrated during the 0500–2000 period, with a peak in detections around 1100–1200. No such diel pattern was evident in detections north of the bay at Site 2 where cage-dive operations were rarely undertaken during the 2001–2003 study period. Detections at Site 2 were more evenly distributed throughout a 24 h cycle on both operator and non-operator days (Fig. 8).

For the 2010–2011 study, the diel pattern on both days when cage-diving occurred and when operators were absent showed a relatively evenly distributed rise and fall in the detection frequency of tagged sharks over the period 0700–2000 with a peak around 1100–1300. This diel pattern was consistent between sites with a particularly pronounced diel pattern at Site 2 (Fig. 9).

Operator arrivals and departures from 2000 to 2007, a proxy for the start and completion of berleying and other shark cage-dive activities, were generally sporadic with both operators undertaking irregularly timed multi-day trips and poorly defined diel patterns in their activities. The range in number of operator days (108–150) resulted in no operator activity on over 50 % of days each year, and in many cases over extended periods. The timing of arrivals and departures by operators was recorded from 2007 onwards with the introduction of regular daily trips to the

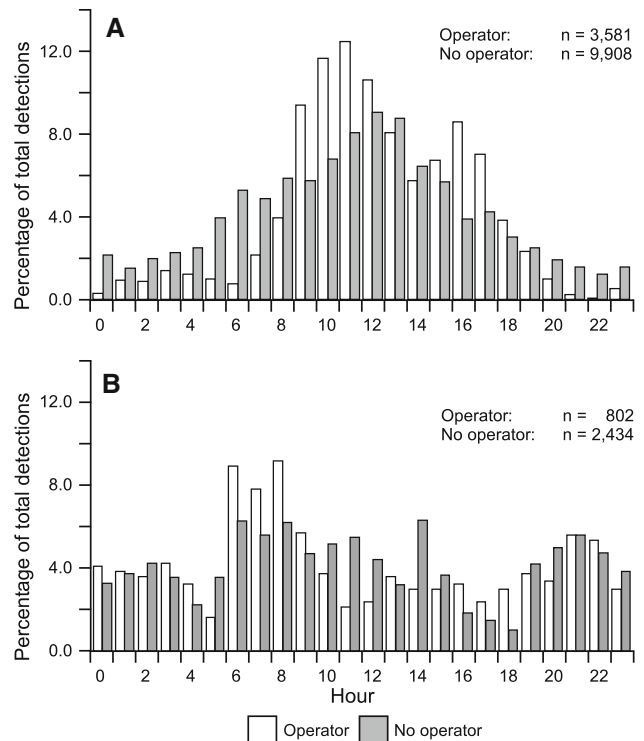


Fig. 8 Hourly pattern of detections of tagged sharks at North Neptune Island 2001–2003 during operator and non-operator periods A: Site 1; B: Site 2; n = number of detections of tagged sharks

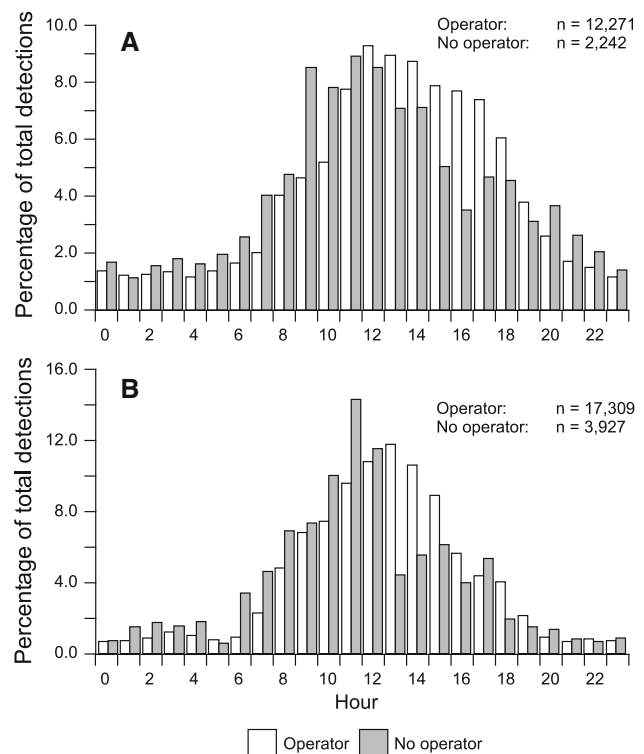


Fig. 9 Hourly pattern of detections of tagged sharks at North Neptune Island 2010–2011 during operator and non-operator periods A Site 1; B Site 2; n = number of detections of tagged sharks

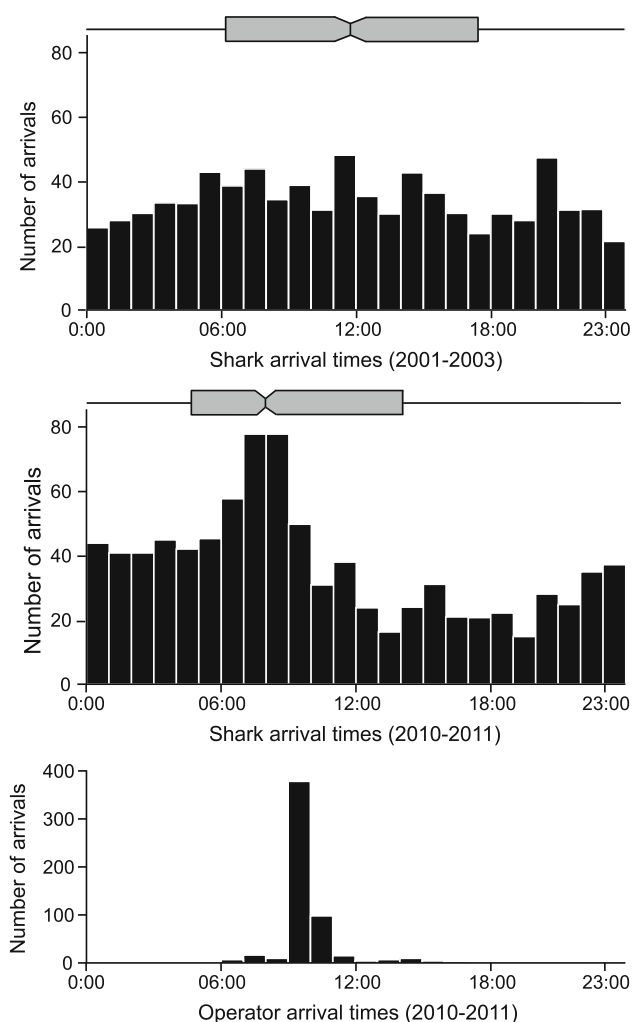


Fig. 10 Hourly distribution of shark arrival times, North Neptune Island in 2001–2003 and 2010–2011; hourly distribution of operator arrival times 2010–2011. Box plots display median; 1st + 3rd quartiles

area. A range of 241 to 287 days of operator effort was recorded annually from 2008 to 2011. Operator arrival times show a clear peak between 0900 and 1000 with departures peaking over the 1500–1700 period (Figs. 10, 11). The arrival and departure times for sharks were calculated based on acoustic detection data. An arrival time was registered when a shark was first detected on any one of the North Neptune Island array receivers, and sharks were deemed to have departed if the period between detections exceeded 3 h. Three hours was chosen on the basis that 75 % of all gaps between detections during visits were less than this period.

A χ^2 goodness-of-fit test indicated no significant departures from a random pattern for the diel distribution of arrival and departure times of sharks for either berley periods or non-berley periods in the 2001–2003 study (Table 3). Arrivals and departures of sharks were evenly

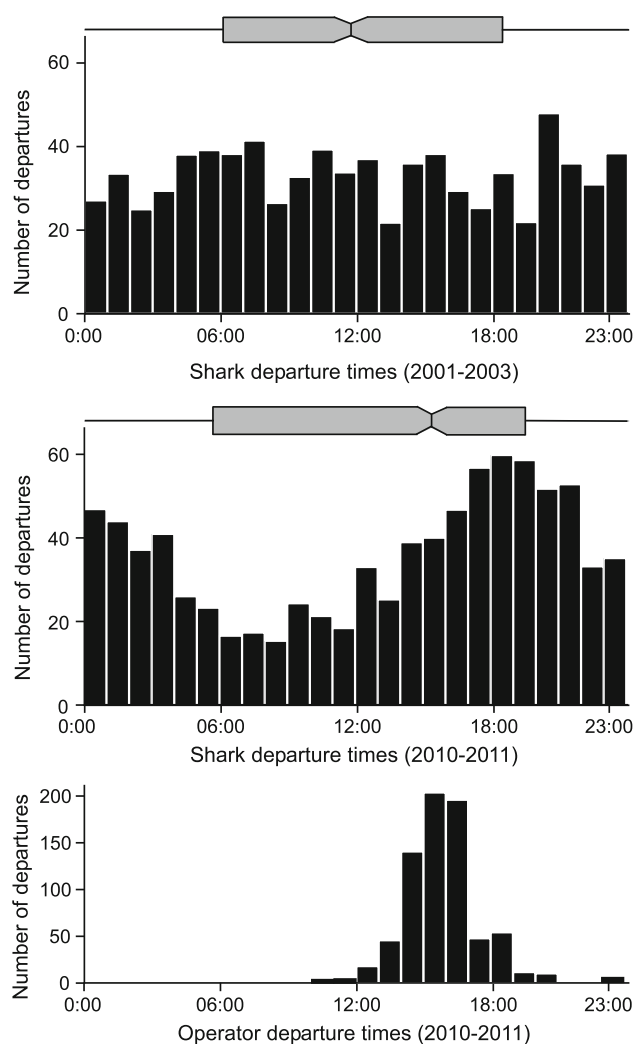


Fig. 11 Hourly distribution of shark departure times, North Neptune Islands in 2001–2003 and 2010–2011; hourly distribution of operator arrival times 2010–2011. Box plots display median; 1st + 3rd quartiles

Table 3 The results of χ^2 goodness-of-fit analyses for diel pattern of arrival and departure times during operator and non-operator periods

Activity and period	χ^2 value	<i>p</i> value
2001–2003		
Operator days—arrival time	50.367	0.342
Operator days departure time	36.500	0.867
Non-operator days arrival time	57.025	0.150
Non-operator days departure time	44.476	0.578
2010–2011		
Operator days—arrival time	164.911	<0.0001
Operator days departure time	136.357	<0.0001
Non-operator days arrival time	110.747	<0.0001
Non-operator days departure time	62.456	0.065

Bold values for *p* indicate a significant variation from an even distribution over a 24 h cycle

distributed over a 24 h period with a median hour for both arrival and departure from 1100 to 1200 (Figs. 10, 11).

A similar χ^2 goodness-of-fit test, however, indicated significant departures from a random pattern for the diel distribution of arrival and departure times during berley periods and for arrival times during non-berley periods but not for departure times during non-berley periods (2010–2011) (Table 3). During the 2010–2011 study, the arrival of sharks showed a clear peak in frequency between 0700 and 0900 (median 0800–0900), Fig. 10. Departures of sharks showed a clear peak in frequency between 1700 and 2100 (median 1500–1600), Fig. 11.

Discussion

Acoustic monitoring at the North Neptune Islands indicated that tagged white sharks change their distribution to align with areas of active shark cage-dive operations over small spatial and temporal scales. Shark cage-dive operators (SCDO) primarily work at two sites at the North Neptune Islands: one inside a small bay located at the larger of the islands and the other to the north of a gap between the two islands that make up the group (see Fig. 1). These sites are separated by approximately 700–800 m and the centre of activity of sharks changed between them corresponding to the presence of operator activity. This was consistent with SCDO observations where visual contact with individual sharks could be readily re-established after moving operations from one site to the other. Strong et al. (1996) concluded that the attracting effects of a berley plume can extend over a scale of several kilometres, and thus, the distance between the two operator sites falls well within the range for attracting sharks from one site to another. This response to shark cage-dive operations is an expected result. The success of tourism ventures designed to view sharks, including white sharks, is often reliant on attracting animals already present in the area to within the visual range of the vessel or clients on site (Burgess 1998; Laroche et al. 2007; Meyer et al. 2009; Hammerschlag et al. 2012). However, this result also demonstrates that the acoustic receiver array deployed at the Neptune Islands was able to adequately monitor the response of sharks to SCDO activities in the area and provides confidence that the arrays also adequately captured the pattern of habitat use by sharks within the Neptunes Islands system in general.

The two cage-dive sites are located off eastern sectors of the North Neptune Islands. These sites are adjacent to the areas where seals and sea-lions are most common (Shaughnessy and Mckeown 2002). Shark activity, regardless of cage-dive operations, was significantly higher in these eastern sectors than in any other areas surrounding

the North Neptune Islands. Similar, uneven distributions of white sharks have been reported around other pinniped colonies, with sharks showing a general preference to occur in areas close to the maximum concentration of pinnipeds, or within the areas of common corridors that pinnipeds use to approach and depart island systems (Klimley and Anderson 1999; Martin et al. 2005). These observations suggest that the uneven distribution of sharks at the North Neptune Islands is likely a result of their natural propensity to reside off the eastern sectors, rather than being driven by shark cage-diving operations alone. However, within this area of naturally focussed shark activity, it is clear that shark cage-diving operations influence the specific areas occupied by sharks on small spatial and temporal scales.

Acoustic monitoring during both the 2001–2003 and the 2010–2011 studies demonstrated that sharks are temporary residents of the Neptune Islands and that individual residency periods commonly comprised a series of visits (consecutive days of detections) interspersed with days when sharks were not detected. This is consistent with acoustic monitoring of tagged white sharks in other areas of the species' range (e.g. California—see Jorgensen et al. 2009). A lack of detections did not necessarily mean that sharks had completely departed the Neptunes Islands system, as sharks had only to move >500 m from the acoustic array for detections to cease. However, periods of extended absence were few when sharks were resident, indicating a propensity for sharks to remain in the close vicinity of the islands when present. Confirmed departures of sharks were apparent when they were detected by acoustic receivers at other sites. Sharks, for example, made several return transits between the North and South Neptune Islands and, in several cases, the transit times indicated rapid and direct travel between these sites. These transits occurred regardless of shark cage-diving operations at the North Neptune Islands, with sharks sometimes departing during an active period of cage-dive operations. Thus, shark cage-diving operations alone did not always maintain a shark on site. The cues for arrival and departure of white sharks from a site are not well established and may relate to interactions with other sharks or other species on site (Strong et al. 1996; Pyle et al. 1999), individual changes in motivation, satiation after a feeding event (Klimley and Anderson 1996), habituation to stimuli (Laroche et al. 2007), a natural search pattern of surrounding waters (Strong et al. 1992) or seasonally mediated movement events (Domeier and Nasby-Lucas 2008). Directed travel between sites of temporary residency has been demonstrated for juvenile, sub-adult and adult white sharks over both small (<10 s km) and large (1000 s km) spatial scales (Bonfil et al. 2005; Bruce et al. 2006; Johnson et al. 2009; Jorgensen et al. 2009; Bruce and Bradford 2012; Domeier 2012; Weng et al. 2012). This behaviour appears to be a

common, and thus presumably normal, feature of white sharks across their range, and in the case of the Neptune islands, this appears to be maintained even in the presence of shark cage-diving operations.

Sharks showed evidence of site preference or fidelity between the North and South Neptune Islands, despite the close proximity of these island groups. Only 52 % of all sharks tagged at North Neptune Island were recorded at South Neptune Island over both study periods combined, and in the 2001–2003 study, none of the four sharks tagged at South Neptune Island were detected at North Neptune. Visits by sharks tagged at North Neptune Islands to the South Neptune Islands were short in duration and followed by a return to the North Neptune Islands or, in one case a departure from the system.

Detection records for many sharks ceased well prior to the end of the study suggesting they had departed the Neptune Islands system. This was confirmed in three sharks which were all detected on acoustic receivers set approximately 2000 km to the west, at Chatham Island (Western Australia), after their last detection at the Neptune Islands. Sharks tagged with acoustic tags at the Neptune Islands prior to the 2010–2011 study were also detected on Western Australian acoustic receiver arrays off Bremer Bay, Albany, Rottnest Island (Perth) and off Ningaloo Reef ranging west in distance from 1,700 to 3,700 km. These observations support the common westerly movement of white sharks after their departure from the Neptune Islands described for satellite-tracked individuals by Bruce et al. (2006). These data also support that although berleying influences the local spatial scale of white shark activity at the Neptune Islands, individuals still undertake broad-scale movements across southern and western Australia consistent with other studies of their behaviour. Hammerschlag et al. (2012) similarly concluded that tiger sharks (*Galeocerdo cuvier*) exposed to provisioning for ecotourism in the Bahamas continued to range over extensive distances (1000 s of km) and were not more site attached than conspecifics in areas where ecotourism operations did not occur.

Previous studies on the effects of shark cage-diving operations on white shark behaviour have concluded that impacts are localised and relatively minor (Bruce et al. 2005; Laroche et al. 2007). However, both studies suffered from a lack of baseline or control data with which to compare results and, in both cases, the amount of operator activity relative to the current situation at the Neptune Islands was relatively low, albeit, effort in each case had been ongoing for many years. The previous study of white shark residency and habitat use at the Neptune Islands by Bruce et al. (2005) was prior to the increase in operator effort subsequent to 2007.

Temporarily altering the behaviour of sharks is one of the key elements of a successful and economically viable

shark cage-diving operation and an essential element for client satisfaction. Sharks are attracted to the vessel and contact time is encouraged so as to enable clients to view sharks that would otherwise not be reliably seen. However, wildlife tourism that involves provisioning (feeding), attraction or some form of reward for the animals involved can often result in changes to behaviour in target species that last over varied time-scales and may give rise to unintentional effects on those species and the ecosystem within which they reside (Orams 2002). Behavioural changes in the context of provisioning or attraction as a result of cage-dive operations may manifest as an acceleration in response time and/or increased contact time between target species and the tourism operation (Laroche et al. 2007; Maljkovic and Côté 2011), arrival at the 'provisioning' site in anticipation of vessel arrival (Meyer et al. 2009), changes in the duration that target species remain in specific areas, and/or changes in diel activity, depth-swimming behaviour, changes in the frequency of intra-specific aggression and local increases in the abundance of target species (Semeniuk and Rothley 2008; Clarke et al. 2011; Fitzpatrick et al. 2011).

Comparisons between the behaviour of sharks acoustically monitored during the 2001–2003 and the 2010–2011 periods, as well as data from the VR4G mooring and SCDO daily logbooks, all detected significant changes in shark behaviour and residency at the North Neptune Islands since operator effort and its regularity increased from 2007. It is not possible to unequivocally isolate the impacts of shark cage-diving from the natural underlying seasonal and interannual variability in shark behaviour due to the lack of true baseline data prior to cage-diving operations being established. However, there are several lines of evidence that support the significant post-2007 increase in operator effort and its daily regularity as being a key factor in these observed behavioural changes.

Daily logbook data recorded since August 1999 indicated that there has been a significant increase in the number of sharks sighted per day at North Neptune Island specifically since 2007. Long-term monitoring of shark activity from the same logbook data indicates that the pattern of shark activity varies with season and between years (Fig. 12), with periods of below, or of no, shark activity occurring at the North Neptune Islands both pre- and post-2007, regardless of an overall average increase in shark sightings. It is unclear what drives these variations in shark activity, but it is likely that they relate to environmental influences and manifest over far broader areas than the North Neptune Islands site alone. An increase in shark sightings at the North Neptune Islands would be consistent with an increase in population size in response to the species protection in Australian waters in the late 1990s (Malcolm et al. 2001); however, there are currently no

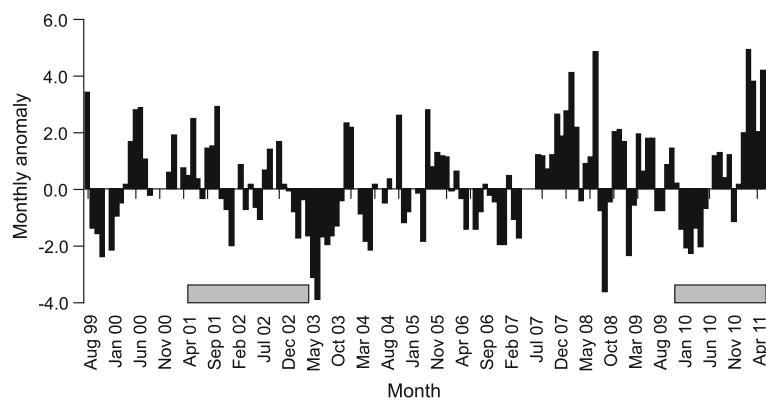


Fig. 12 Long term (1999–2011) aggregated monthly data of shark activity (sharks sighted per day) at the North Neptune Islands. Data represent deviations (anomaly) from the long-term average for each month. Monthly anomalies are calculated by subtracting the mean

annual cycle from each individual month. *Positive* values indicate an above average number of sharks sighted during the month; *negative* values indicate a below average number of sharks sighted during that month. *Shaded horizontal bars* indicate the two study periods

effective population metrics in Australian waters from which to assess population trends or status. The lack of available measures of population size combined with these interannual variations makes it difficult to conclude population-level changes in abundance from these data.

Concurrent with the increase in recorded shark sightings since 2007, sharks have significantly increased their residency periods and the duration of visits at the North Neptune Islands. Increases in the population size of sharks may naturally increase shark residency times if animals were competing for access to the same resource (e.g. pinnipeds) and if sharks were required to adequately provision on pinnipeds prior to their departure from the Neptunes system. This process is referred to as competitive interference (Case and Gilpin 1974; Krause and Ruxton 2002). Longer residence times may ensue if competition between sharks resulted in some animals taking longer to capture sufficient pinniped prey to adequately provision themselves, hence requiring an extension of their visits to do so. The temporary residency of sharks to the Neptune Islands system followed by departure, long distance travel to other feeding sites where prey different to seals are targeted and then return to the Neptunes (Bruce et al. 2006) is consistent with provisioning on seal prey being an important, but only part, component of each shark's annual diet. Although not conclusive, this is consistent with a scenario that may lead to competitive interference at the Neptune Islands when shark numbers increase. However, an increase in shark sightings is also a predictable consequence of an increase in the duration of visits, even in the absence of an overall increase in population size or competitive interference. An increase in the duration of visits results in sharks temporarily accumulating on site, and thus, the probability of encountering (=sighting) any one particular shark is increased. Notably, the duration of visits by sharks to the South Neptune Islands was not

significantly different between the 2001–2003 and 2010–2011 data sets, suggesting that changes in shark behaviour have been exclusive to the North Neptune Islands where SCDO activities occur. It is reasonable to expect that if the increase in the duration of visits was in response to a general and more widespread increase in population size, then a similar increase in the duration of residency periods and duration of visits would be apparent at the South Neptune Islands. The increase in duration of visits, exclusive to the North Neptune Islands, is consistent with other studies where localised responses have been documented in sharks exposed to shark-based tourism that employ forms of attraction and provisioning (Laroche et al. 2007; Clarke et al. 2011; Maljkovic and Côté 2011).

Acoustic monitoring also recorded changes in the daily pattern of occupancy by sharks at the North Neptune Island operator sites. In the 2001–2003 study, sharks showed a distinct diel pattern in detections at Site 1 inside the bay where, at that stage, most cage-diving operations occurred. Detections at Site 2, where cage-diving operations were infrequent, showed no evidence of a diel pattern. Post-2007, the number of days when cage-diving occurred at Site 2 increased substantially, concomitant with the overall increase in operator effort. In excess of 400 days of operator effort was registered at Site 2 from 2007 to 2011 with the frequency of activities also increasing at Site 1 (Shark cage-dive operator logbook data, CSIRO). Operator activity at both sites followed a more regimented daily timing post-2007, occurring during daylight hours between 0600 and 1600. Sharks monitored in the 2010–2011 study showed distinct diel patterns of detections at both Sites 1 and 2, indicating the maintenance of the 2001–2003 diel pattern at Site 1 and a substantial change to a similar diel pattern at Site 2. The change at Site 2 was concomitant with an increase in operator effort at that site, with the presence of sharks aligning with the overall daily timing of

cage-dive operations. The diel pattern in shark detections at both Sites 1 and 2 was maintained even on days when cage-dive operations did not occur. Diel patterns in habitat use by sharks are well documented for a variety of species (Klimley et al. 1988; Holland et al. 1993; Clarke et al. 2011) and have been suggested for white sharks as being part of a natural diel cycle in hunting behaviour around seal colonies (Bruce et al. 2005; Martin et al. 2005). The presence of a diel pattern in occupancy as indicated by acoustic detections inside the bay during both study periods thus cannot be attributed to the effects of cage-diving operations alone and likely represent a natural propensity for daily activity levels in the bay where pinnipeds are most common, against which SCD operations follow a similar pattern. However, the change to a marked diel occupancy in sharks at Site 2, where pinnipeds are less common, and which was not apparent prior to 2007, aligned with a substantial increase in SCD effort at that site, is consistent with a response to provisioning/berleying similar to that observed in other elasmobranch species exposed to such activities (Semeniuk and Rothley 2008; Fitzpatrick et al. 2011). Furthermore, the maintenance of this pattern on days when cage-diving did not occur, suggests a conditioned or anticipatory response by sharks to SCD operations on site. Arrival of sharks at ‘provisioning’ sites in anticipation of vessel arrival has been observed or suggested in a number of studies (e.g. Meyer et al. 2009; Fitzpatrick et al. 2011 and references therein), but has not previously been demonstrated in white sharks.

Acoustic monitoring in 2010–2011 demonstrated a marked change in the timing of arrival and departure of sharks at both Sites 1 and 2 at the North Neptune Islands compared to the 2001–2003 study. Shark arrival and departure times showed no diel pattern on either operator or non-operator days during the 2001–2003 study. However, in the 2010–2011 study, sharks showed a distinct diel pattern with arrivals peaking between 0700 and 0900 with a slightly more diffuse peak in departures between 1400 and 2200 at both sites. The peak in arrival times of sharks was immediately prior to the peak in arrival times of SCDO vessels which occurred between 0900 and 1000. Departure of SCDO vessels occurred over a more extensive time window that fell within the peak window of shark departures. Strong et al. (1996) observed that white sharks may remain in the vicinity of a site where berleying occurs for periods up to several hours after this activity ceases, undertaking a swim behaviour they described as ‘downstream circling’. Downstream circling was regarded as a response by sharks to the presence of the berley plume until it dissipated, a process dependant on local conditions at the time. The broader peak in shark departures relative to the cessation of cage-dive operations is consistent with the responses to a dissipating berley plume and as described by

Strong et al. (1996). The shift from no daily pattern to a distinct daily peak in arrivals and departures by sharks that was in phase with the arrival and departure of SCDO vessels and that propagated through to non-operator days is consistent with both a change in diel activity and an anticipatory response by sharks to SCDO activities as observed in other elasmobranch species exposed to provisioning and forms of attraction (Semeniuk and Rothley 2008; Meyer et al. 2009; Fitzpatrick et al. 2011).

Previous studies of white shark responses to shark cage-dive operations (e.g. Bruce et al. 2005; Laroche et al. 2007) have been ambiguous and have focussed on the activities of berleying and provisioning. Berley by itself does not constitute provisioning, the latter referring to feeding of the target species. Berley attracts sharks by providing an odour corridor over distances of up to several kilometres and visual cues over smaller spatial scales close to its source (Strong et al. 1996). The berley used by SCD operators is a mix of tuna oil and minced fish products; mammal products are banned in South Australia for use as shark attractant. While it may provision finfish in the area, berley is comprised of particles too small for white sharks to feed on. Floating (‘tethered’) baits used to lure sharks closer to the vessel, thereby increasing the proximity experience between sharks and tourists, provide the only provisioning opportunity for sharks during SCD operations at the Neptune Islands. Tethered baits are generally pieces of tuna in the form of head, trunk, tail sections, or gill and gut remains. Normal SCD operating procedures limit the number of tethered baits taken by sharks, but does not prevent this completely. It is unclear whether the current level of inadvertent provisioning provided to sharks by them occasionally intercepting tethered baits is sufficient to generate a conditioned response. However, this cannot be ruled out and the consumption of such baits by individual sharks should be monitored. The size of tethered baits should be minimised and the consumption of such baits by sharks should also be limited as much as is practical.

Even without the consumption of tethered baits, it is possible that white sharks are sufficiently programmed to respond to the odour corridor that berley produces to maintain an interaction and thus become conditioned to respond to SCD operations. Under natural circumstances, odour corridors comprising biological products provide cues for sharks to locate marine animal carrion that may represent critical feeding opportunities (e.g. dead cetaceans—Curtis et al. 2006). Response to such stimuli, even in the case where no reward is achieved, may be an overriding behaviour in white sharks. If this is the case, sharks may forgo feeding and thus provisioning opportunities on pinnipeds when present at the Neptune Islands in preference to responding to a suboptimal cue and feeding opportunity in the form of berley and occasional tethered

baits. Such a distraction response to SCD operations would have the potential to come at an energetic cost to sharks in the form of lost feeding opportunities and increased swimming activity in the vicinity of operator vessels. Such impacts have been recorded for other species. Williams et al. (2006) concluded that distraction caused by tourist vessels may reduce energy intake in killer whales by up to 18 %. Such changes to behaviour may have impacts on other species in the area. If sharks are distracted from natural feeding opportunities, occupy areas or undertake swimming patterns that are not conducive to normal predatory behaviour, then these may result in changes to their overall predatory success and changes in predatory pressure on pinnipeds in the area as suggested by Laroche et al. (2007) for shark-seal interactions in South Africa.

Although all parameters examined suggest behavioural changes have occurred in white sharks at the North Neptune Islands that are consistent with those observed in other shark and ray species in response to tourism operations, this study was not designed to determine whether they represent long-term costs to white sharks visiting the area. Understanding the repercussions to white sharks of altered behaviours attributable to the effects of cage-dive operations is complicated as sharks are only temporary visitors to the North Neptune Islands where such activities occur and thus are only exposed to this activity for the periods during which they reside there. Various negative effects have been documented in other situations where wildlife, including elasmobranchs, are attracted for the purpose of tourist viewing including dependence on provisioning, overfeeding, malnourishment, increased aggression, altered behaviour, disrupted ecological relationships and an unbalancing of energetic budgets (Orams 2002; Newsome et al. 2004; Semeniuk and Rothley 2008; Semeniuk et al. 2009; Clua et al. 2010).

The results of this study demonstrate that cage-diving may lead to long-term, albeit localised, changes in the behaviour of a highly vagile shark species. Given that white sharks are a listed threatened species under various jurisdictions worldwide (including all Australian waters and under both CITES and CMS), a process to minimise the impacts of shark cage-dive operations on shark behaviour at the North Neptune Islands is warranted, and further research is required to understand the implications of the observed changes in behaviour. It also suggests that monitoring elements of shark behaviour should be used as a common approach to managing this industry worldwide. The challenge for managing agencies and the shark cage-dive industry will be to find a balance between reducing these impacts on shark behaviour and the ecosystem within which they reside, while maintaining a successful, economically viable and world-class shark cage-diving experience that fulfils client expectations, continues to contribute

significantly to local economies and provides a platform for education and research on white sharks and their conservation into the future.

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