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

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The Grey Nurse Shark (*Carcharias taurus*) is a popular attraction for shark eco-tourism using SCUBA. The species is also 'globally Vulnerable' (IUCN 2008. List of Threatened Species. www.iucnredlist.org/). Magic Point (off Maroubra) in Sydney is favoured by recreational SCUBA divers wishing to observe these sharks. The objective of this study was to experimentally test the level of the activities of recreational SCUBA divers on shark behaviour. This study assessed the shark responses to diver group size (4, 8 and 12), time of day (am, noon and pm) and diver distance from the sharks (3 m and 6 m). The study found that diver activity does affect the aggregation, swimming and respiratory behaviour of sharks at this site, albeit at short-term levels. Diver group size had no significant effect on shark aggregation, but the proximity of divers to the sharks was crucial. Shark distribution in the cave changed significantly in the presence of divers at 3 m distance from the cave, but stayed unchanged at 6 m. This was particularly apparent in the presence of large groups of 12 divers at 3 m distance when sharks increased their swim speed and ventilation mechanism from 'active' to 'RAM' ventilation. Such change coincided with a sudden decrease in ventilation frequency. Our research suggests that these effects are short-term and that sharks resume their behaviour once the divers retreat. If divers abide by the current code of practice for diving at this site, it is unlikely that their activities will substantially impact Grey Nurse Sharks in the long term.

Keywords: Grey Nurse Shark; *Carcharias taurus*; SCUBA divers; behaviour, aggregation; swimming; ventilation rate

Introduction

Grey Nurse Sharks, *Carcharias taurus* (family Odontaspididae), are large (up to 318 cm in total length) and predominantly coastal, occurring in warm-temperate and tropical waters in the north and south Atlantic, Indian, and western Pacific Oceans (Last and Stevens 2009). Once widely distributed, populations of *C. taurus* have been severely depleted throughout its range and is now considered globally Vulnerable according to the International Union for the Conservation of Nature (IUCN 2008).

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Populations have been severely depleted in Australia and the north-western Atlantic due to various anthropogenic activities, particularly since the 1950s (Reid and Krogh 1992; Musick et al. 1993; Pollard et al. 1996; Bradshaw et al. 2008).

Carcharias taurus are often observed just above the sea bed near sandy-bottomed gutters or rocky caves in the vicinity of inshore rocky reefs and islands (Pollard et al. 1996). Caves or overhangs in Australia and South Africa, and to a lesser extent ship wrecks in North Carolina USA, appear to be preferred habitats for *C. taurus* (Dicken et al. 2006; Martin 2007). Aggregations of individuals are reported to occur at these sites for feeding, courtship, mating and birth (Compagno 2001). This aggregation behaviour, together with their rather slow moving and docile nature, made them particularly vulnerable to spearfishing (skin diving) activities in Australia during the 1950s and 60s (Cropp 1974; Environment Australia 2002). Ongoing anthropogenic impacts, along with their low fecundity and genetic isolation have led to *C. taurus* on the east coast of Australia becoming Critically Endangered as classified by the Environmental Protection and Conservation Act (EPBC ACT 1999). Consequently, the east coast population for Australia is deemed as being one of the most threatened populations globally, with several models suggesting eminent danger of extinction (Otway et al. 2004; Bradshaw et al. 2008).

Although human-induced fishing mortalities are considered the greatest threat to *C. taurus* globally (IUCN 2008), several concerns have been raised about non-fatal activities, such as recreational diving at apparently biologically important aggregation sites (Environment Australia 2002; Lynch et al. 2004). These sharks are the focus of dive tourism activities in South Africa, Australia, the east coast of the USA, the Mediterranean Sea, and Malpelo Island in the eastern Pacific (Compagno 2001). The young-of-the-year, juveniles and pregnant females can remain in the geographical distinct nursery areas for extensive periods in waters off South Africa and the east coast of Australia (Dicken et al. 2006; Bansemer and Bennett 2009; Barker and Williamson 2010). Therefore, this type of recreational activity has the potential to adversely impact the population of *C. taurus* (Cavanagh et al. 2003; Lynch et al. 2004). Furthermore, earlier studies have highlighted that in some cases recreational SCUBA diving has exceeded the limits of ecological sustainability and has had variable impacts on marine ecosystems (Hawkins and Roberts 1996; van Treeck and Schumacher 1998).

Recreational diving to encounter sharks at a close range as part of the growth in shark-based tourism has grown exponentially since the 1990s due to shifts in attitudes towards these animals. Globally, there are over 300 shark dive sites offering opportunities to view sharks (Topelko and Dearden 2005). There are approximately 19 known popular dive sites in Australia providing economic benefits. The whale shark industry at Ningaloo Marine Park in Western Australia, for example, is estimated to be worth $13 million AUD annually (Meizlish et al. 2005).

Carcharias taurus diving at their aggregation sites provides substantial income for several communities along the east coast of Australia. These sites are generally well marketed to tourist divers – based on the amount of photographic opportunities; the size of the animals; visibility; bottom profile and accessibility to the site (Topelko and Dearden 2005). *Carcharias taurus* is considered harmless to divers, thus representing an attractive SCUBA diving experience for the tourist market. This is reflected in the ranking amongst the top dive sites in Australia for two *C. taurus* aggregation sites: Magic Point (Maroubra) and Fish Rock Cave (South West Rocks) (Hockton 2003; Meizlish et al. 2005).

Codes of conduct for shark diving have been implemented in several countries, but conservation management solutions such as in situ SCUBA diver impact assessments have not been thoroughly explored. In Australia, a Code of Practice for diving with *C. taurus* was enacted in 2002 by the Commonwealth Government of Australia (Environment Australia 2002). Although this may reduce the numbers of visiting divers, there has been no assessment of the efficacy of implementing such a voluntary code of practise in reducing shark responses to divers. Along the east coast of Australia, approximately 85% of the known *C. taurus* aggregation sites have substantial reef features such as caves, caverns and overhangs (Environment Australia 2002; Otway et al. 2003). Determining shark responses to divers in these environments would provide baseline data for environmental managers and tourism companies to ensure sustainable environmental tourism. Parameters such as increases or decreases in shark abundance and/or distribution, and changes in the swimming and ventilation rate may be expected in response to divers and may therefore be used as behavioural measures to evaluate any visual signs of a potential impact (Barreto et al. 2003; Hannon and Crook 2004; Brown et al. 2005).

This study focussed on a representative aggregation site of *C. taurus* off Sydney. Using data accumulated during an earlier study of the natural behaviour of SCUBA divers in relation to the sharks present at this aggregation site (Barker et al. 2011), we determined whether there was a critical time, particular distance or number of divers that change the aggregation or distribution behaviour of these sharks. The following three questions were addressed: (1) does the number of recreational divers and the distance from the site of refuge for the sharks, in this instance a cave, significantly impact shark distribution within the cave; (2) does the presence and number of recreational divers change the swimming and ventilation behaviour of the sharks; and (3) does the intensity of that response increase with either an increase in the number of divers present and/or their distance from the sharks?

Materials and methods

Study area

Magic Point

Magic Point is on the southern headland of Maroubra Beach, approximately ten km south of Sydney Harbour (33°57′29″S, 151°15′51″E) (Figure 1a), Australia. The main features of Magic Point are an overhang and nearby gutter-like formation at approximately 16 m water depth that form part of the reef system extending from Maroubra headland (Byron 1999). The underwater terrain also features a number of caves and reefs, including the main shark cave used as our primary study site (Figure 1b). The cave is approximately 20 m long, 2 m in depth and 1–2 m in height.

Observations of natural shark and diver behaviour suggest that *C. taurus* prefer the main 'shark cave' and that the cave could be divided into two distinct regions to the left and right of a large boulder located centrally to the cave entrance (Barker et al. 2011). The propensity of sharks to aggregate inside the cave and overhang enables divers to approach the aggregations at close distances (Figure 1b). As per other aggregation sites around the world, *C. taurus* at Magic Point also occur at other nearby features such as gutters and overhangs close to the main shark cave (Barker et al. 2011). Since dive charter operators rarely visit these other areas,
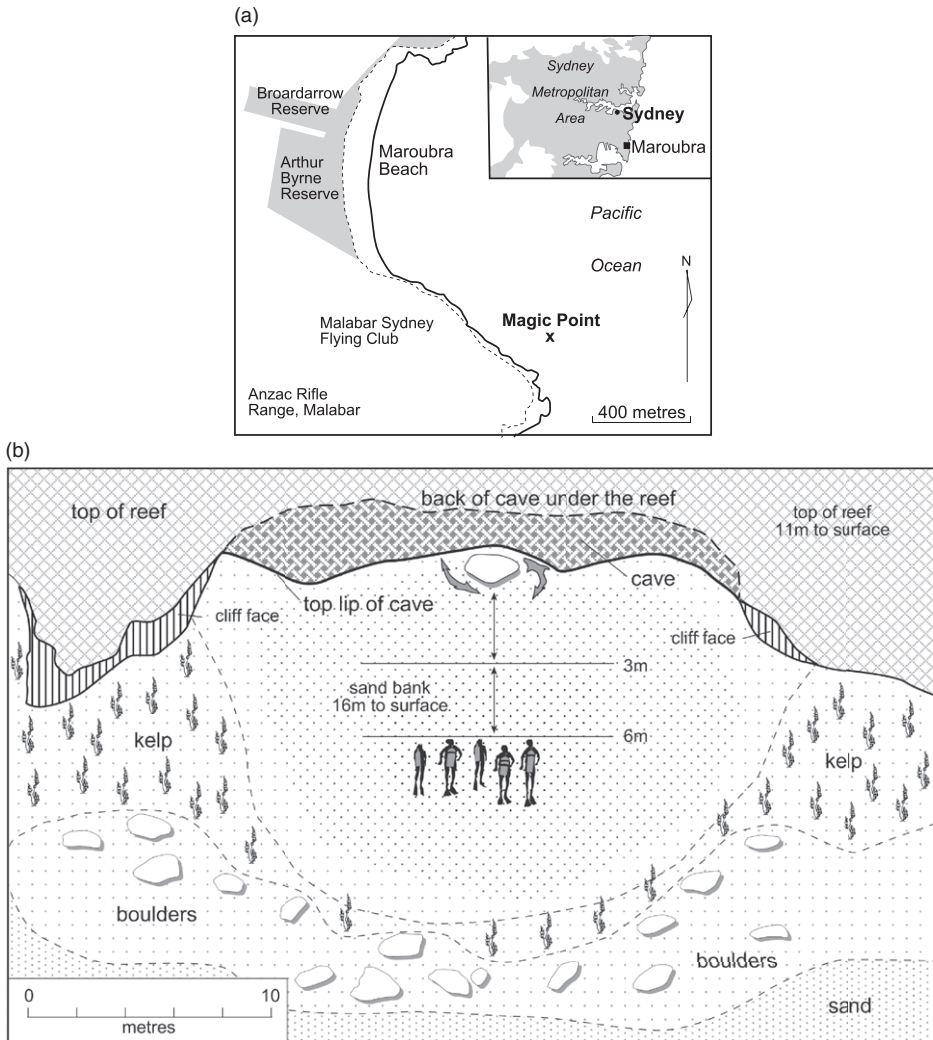
Figure 1. (a) Location of Magic Point, situated at the south end of Maroubra Beach, off the coast of Sydney, Australia. (b) The underwater terrain at Magic Point highlighting the position of diver groups on the sand at 3 m and 6 m in front of the cave occupied by *C. taurus*. For analysis, the cave was divided into left and right sides in relation to the natural boulder positioned approximately midway along the length of the cave (shown).

however, only the main shark cave was likely to be substantially impacted by divers and was thus the focus of this study.

Fish Rock

Fish Rock Cave at South West Rocks (30°56′25″S, 153°06′05″E), Australia, is another common aggregation site for *C. taurus*. It has three major gutters that are subjected to tidal conditions, along with a shallow-water (~depth 16 m) and a deep-water (~depth 24 m) entrance to a large underwater cave, with individuals often aggregating at either or both of these entrances (Figure 2) (Pollard et al. 1996). The
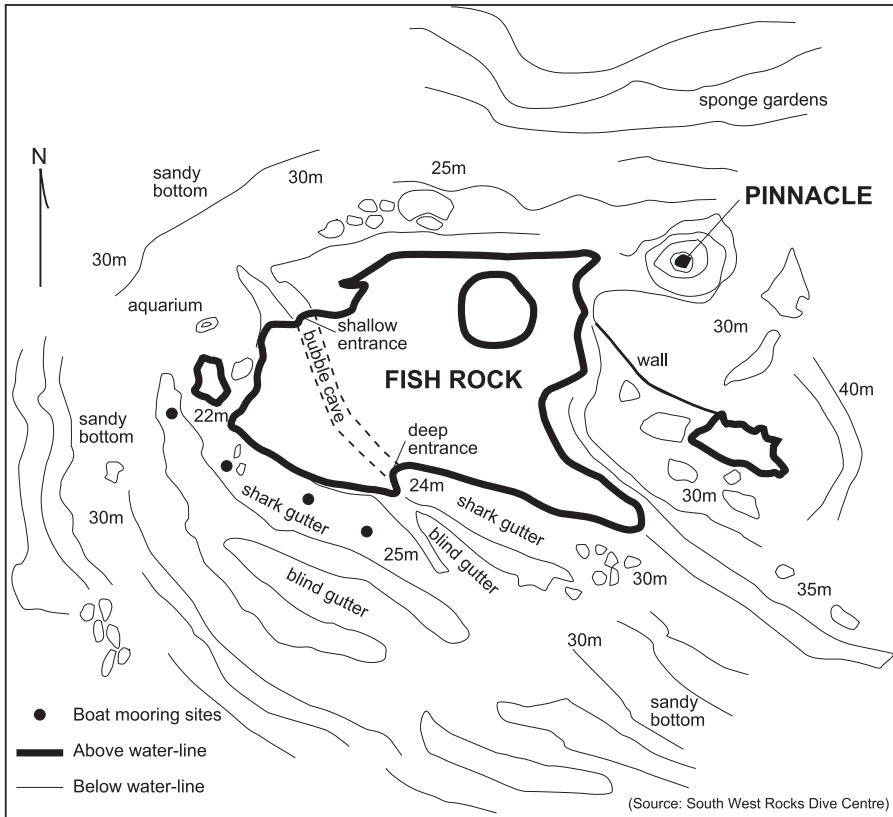
Figure 2. Fish Rock, a *C. taurus* aggregation site on the New South Wales mid-north coast. Data were collected for ventilation and swimming behaviour of *C. taurus* at both the shallow and deep water entrances to the cave, and in the gutters off the south east of the site.

cave itself runs approximately 100 m through a large rock pinnacle (Fish Rock). This site was used to gather baseline ventilation frequency rates of *C. taurus* to assess the effect of depth on ventilation and to obtain information on the relationship between swimming and ventilation rate. These data are analysed to ensure our findings were relevant to other dive sites where *C. taurus* aggregate.

Sampling methodology

Sampling was undertaken using SCUBA (Self Contained Underwater Breathing Apparatus) at the main shark cave at Magic Point. To counteract any effects of shark habituation towards the experimental team of divers, field visits were spaced at least 24 hours apart and undertaken during 17 dives in May 2008 and May 2009. All experiments were filmed using a Cannon MV200i video camera and Amphibico housing set on a tripod near the cave entrance (see supplementary video clip 1, available online at http://dx.doi.org/10.1080/10236244.2011.569991). This allowed detailed analyses of both diver and shark behaviour, including assessment of swimming speeds and ventilation rates. Two calibrated laser pointers were attached

to the video camera to assist in size determination for all sharks encountered as per Barker and Williamson (2010).

The video camera was set up fifteen minutes prior to the arrival of the diver groups to allow a ten minute control period of recording shark abundance, behaviour and distribution in a non-diver-affected state. This was achieved by the videographer retreating to a nearby reef after setting up the camera and waiting for five minutes for sharks to settle down following the presence of the diver (Barker et al. 2011).

The experimental groups of divers were based on teams of 'buddy pairs' in groups of: (1) small groups of four divers; (2) medium-sized groups of eight divers; and (3) larger-sized groups of 12 divers. Group sizes were based on the average sizes of recreational diver groups that visit the site to view the sharks (Barker et al. 2011).

A 10 m length of rope was secured at both ends with lead weights and placed either 3 m or 6 m from the cave entrance, allowing a visual reference line for diver positioning that was parallel to the cave (Figure 1b). All data could therefore be standardised to this reference line. Divers were subsequently requested to position themselves in their predetermined diver groups and appropriate positions in front of the cave. The order for the placement of diver groups and their respective distances were determined using a Latin Square design, with treatments (diver groups, cave distance) assigned within rows and columns.

To assess the affect of time of day on shark responses to divers, dives were conducted during the morning (~9 am), at midday (~12 pm) and in the afternoon (~3 pm). This temporal spacing also allowed for settlement of the sharks between experiments, and enabled a natural exchange of sharks within the study site, thereby enhancing independence of data.

The behaviour of both sharks and divers was sampled every 60 seconds using the Martin and Bateson (1993) instantaneous sampling technique. The exact position of divers and sharks was recorded for each successive sample interval period. Data recorded at each sample interval included the number of divers, their position (3 m or 6 m) and the number of sharks positioned within the two regions inside the cave (e.g. region 1 = left and region 2 = right side of the cave from the central boulder). As the cave is relatively shallow (~2 m, Figure 1b), the number of sharks within each of the two regions of the cave could easily be distinguished.

Carcharias taurus *abundance*

Information on shark abundance was collected using a visual census at the start of every dive as per Barker et al. (2011) but analysis was undertaken using a one-way ANOVA to explore seasonal differences in the number of sharks at Magic Point from data collected for four consecutive years (Barker and Williamson 2010; Barker et al. 2011). Comparative analysis of the number of sharks was then undertaken using a one-way ANOVA for data taken from the month of May in surveys from 2006 to 2009 (data pooled with Barker et al. 2011). Analysis then focused on data collected for the current study only. To determine natural shark abundance within the cave, a one-way ANOVA was conducted using non-diver control data with number of sharks as the 'response' and two regions with the cave as the fixed factors (Figure 1b). A separate analysis was done for non-diver control versus diver

treatments, with total number of sharks (within the cave) as the 'response' and non-diver (1), 4-diver (2), 8-diver (3) and 12 divers (4) as fixed factors.

Carcharias taurus *distribution*

Sixty second sample intervals were recorded for 180 individual observations of *C. taurus*, during the research dives. Data were analysed for any effects relating to diver group size using a linear model or 'gee' (generalised estimating equation, Murrell 2006) in 'R' (Version 2.8.0, 2008) that was fitted to the left and right differences in shark frequencies (analogous to their position in the cave). A repeated measures analysis was subsequently performed to adjust for correlation between successive observations using the 'geepack' software package. This assessed whether the first-order factor (i.e. any differences in the frequencies of shark) was significant for treatments of diver group size (non-diver control vs. 4 divers, 8 divers and 12 divers), distance (3 m and 6 m), and time of day (morning, midday and afternoon). Whenever the first-order auto-correlation coefficient was non-significant, further analyses were conducted without adjusting for correlation (Murrell 2006; Kuning and McNeil 2008). Gee results showed no evidence of correlation in repeated measures during the same observation sessions, with either exchangeable (P-value $= 0.317$) or first-order auto-correlation structure (P-value $= 0.271$). Given this outcome, the data were retrofitted to only graph the basic linear regression model coefficients with 95% confidence intervals based on the 'sum contrast', taking the categories 'non-diver' control, 3 m distance, and morning period, respectively, as reference levels for the three factors. These gave a confidence interval for each level of each factor. An 'adjusted analysis' (with adjust $= T$) was done, which considered each treatment correlation separately after adjusting for the other two determining factors (Murrell 2006; Kuning and McNeil 2008).

Carcharias taurus *physiological responses*

Individuals were separated into two size categories: (1) young-of-the-year and sexually immature individuals ≤ 120 cm precaudal length (PCL), and (2) sexually mature adults >120 cm in PCL using the two calibrated laser scaling devices (Barker and Williamson 2010). Adult sharks were subsequently divided into male and female categories.

The video footage was assessed to determine the swimming and ventilation rate of sharks, as per previously published methods (Hannon and Crook 2004). Swimming rate was defined by the position of the tail in relation to the shark's mid-line to the extreme left or right and back to the mid-line during normal locomotion and observed per 60 seconds, or flick's per minute (FPM) (Hannon and Crook 2004) (see supplementary video clip 2, available online). Ventilation rate (active ventilation) was defined as the number of single ventilation cycles (i.e. mouth opening and closing, or 'mouth gapes') observed per 60 seconds, or ventilations per minute (VPM) (Roberts 1975; Hannon and Crook 2004) (see supplementary video clip 3, available online). 'Passive' (RAM) ventilation was recorded when the shark no longer exhibited 'mouth gaping' (Hannon and Crook 2004) (see supplementary video clip 4, available online).

Data were transformed using $\ln(x+1)$ to 'normalise' the data considering the RAM ventilation rate was zero. A one-way ANOVA was used to compare the observed data for swimming and ventilation rates as the 'response' and diver group size (i.e. non-diver control and 4, 8 and 12 divers) as the fixed factor. A separate analysis was done for juveniles, as well as male and female adult sharks. There were insufficient data to compare diver distances for juvenile sharks, thus any distance data for juveniles was pooled and only their response to diver group sizes assessed. A post hoc Scheffe test was applied against any significant results to determine where the differences lay for distance and diver group size variables, respectively.

Relationship of increased swimming and RAM ventilation

Additional data on physiological responses were obtained during 14 dives at Fish Rock between October 2008 and March 2009. Data from 37 observations of *C. taurus* at Magic Point and Fish Rock were pooled to estimate the threshold at which active ventilation switched to passive ventilation (RAM) with increased swimming.

Data from 30 individuals filmed at Magic Point and Fish Rock were used to assess the impact of depth on shark physiological response to divers. Data were collected at the two *C. taurus* aggregation sites (16 m and 25 m depth) at Fish Rock to the cave at Magic Point (16 m depth). Rates per minute were calculated and analysed using a one-way ANOVA with the observed data for ventilation rates as the 'response' and site location (i.e. Magic Point, Fish Rock Gutter and Fish Rock Cave) as the fixed factor.

Carcharias taurus *agonistic displays*

A variety of agonistic displays have been described for sharks (Martin 2007). As these may often represent reactive behaviour to the presence of perceived threats such as divers, two previously described agonistic behaviours for *C. taurus* were recorded when observed: 'tail popping' and 'pectoral fin depression' (Martin 2007). Tail popping has been described by Martin (2007) as 'Loud shotgun-like sounds generated by exaggerated tail beats during rapid withdrawal, often performed in conjunction with pectoral fin depression', and pectoral fin depressions as a 'Sustained bilateral lowering of the pectoral fins from their usual position during swimming'.

Results

Carcharias taurus *abundance*

The number of *C. taurus* varied seasonally at Magic Point during 2006, 2007, 2008 and 2009 surveys, with a general increase in late summer and early autumn, but lower numbers in the winter months (one-way ANOVA, $F_{3,27} = 3.28$, $P = 0.036$) (pooled data). As the month of May represented peak shark abundance, with no significant difference in shark numbers for the consecutive May survey periods (one-way ANOVA, $F_{3,2} = 0.59$, $P = 0.677$), all further analyses were conducted for this month.

Comparison across the non-diver control periods throughout the study showed no significant difference in the number of sharks in the two regions (left vs. right)

within the cave at Magic Point (one-way ANOVA, $F_{1,18} = 0.00$, $P = 1.00$) prior to diver appearance. This indicated that non-diver-affected shark numbers and their distributions were stable throughout the period that the research was conducted. These data facilitated further comparison on the position of sharks in the cave against data collected in the presence of divers. There was no significant difference in the total number of sharks for the non-diver control, 4-diver, 8-diver and 12-diver group (one-way ANOVA, $F_{3,8} = 2.22$, $P = 0.163$; Table 1).

Carcharias taurus distribution

Throughout all treatments, slightly more sharks occupied the right side of the cave compared to the left side (as represented by the overall mean in Figure 3). Overall,

Table 1. *Carcharias taurus* abundance at Magic Point cave, Sydney, during the experimental diver group treatments. Each treatment comprised 30 instantaneous counts conducted during experiments.

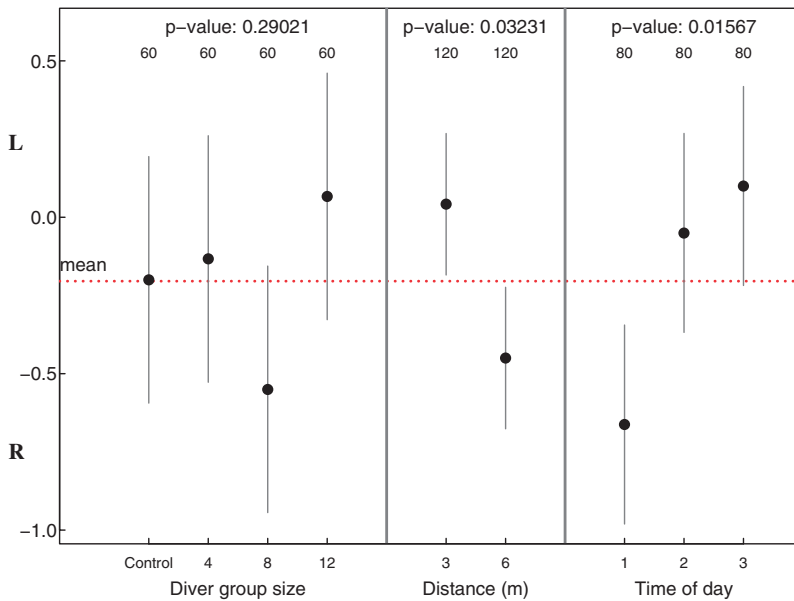| Time of day	Control Mean (S.D.)	4 Divers Mean (S.D.)	8 Divers Mean (S.D.)	12 Diver Mean (S.D.)
Morning	5.3 (0.6)	4.8 (0.8)	4.6 (1.1)	4.8 (0.6)
Midday	5 (1)	4.9 (0.7)	5 (1.6)	5 (1.2)
Afternoon	5 (0)	4.7 (1.1)	5 (1.4)	4.6 (0.9)

Figure 3. Distribution of *C. taurus* within the Magic Point cave in response to variations in diver group size, their distance from the cave, and the time of day. Values with Confidence Intervals (C.I. = 95%) that do not intersect the mean line are significantly different. Note differences in scale of y-axis.

the group size of divers had no significant impact on the distribution of *C. taurus* within the cave (gee test, $P = 0.290$; Figure 3). Diver group size became more influential, however, when assessed in relation to diver distance from the cave, with sharks substantially changing their position within the cave in response to groups of 8 and 12 divers (Figure 3). Assessment of the effect of diver distance on shark distribution indicated a significant shift in distribution by *C. taurus* to the left of the cave when divers approached to 3 m (gee test, $P = 0.032$; Figure 3). A significant shift to the right of the cave by the sharks was determined between morning and the later observations (gee test, $P = 0.016$; Figure 3).

Carcharias taurus *physiological responses*

Comparison across the 'non-diver' control periods throughout the study showed that there was no significant difference in the swimming (one-way ANOVA, $F_{2,6} = 2.22$, $P = 0.190$) and ventilation (one-way ANOVA, $F_{2,6} = 0.766$, $P = 0.506$) rate of sharks. This indicated that shark swimming and ventilation rates in the absence of divers were stable throughout the period that this research was conducted. These data facilitated further comparison against data collected in the presence of divers.

The swimming rate of adult female sharks changed significantly in response to the number of divers (one-way ANOVA, $F_{3,8} = 5.753$, $P = 0.021$, Figure 4), with sharks exposed to the presence of 12 divers at 3 m having significantly higher rates of swimming than those in the controls (non-diver treatment) (post hoc, $P = 0.038$) (see supplementary video clip 5, available online). The ventilation rate of adult female sharks also changed significantly in response to the number of divers present (one-way ANOVA, $F_{3,8} = 4.567$, $P = 0.038$, Figure 4), with sharks exposed to the presence of 12 divers at 3 m having significantly lower rates of ventilation than those in the 'controls' (non-diver) (*post hoc*, $P = 0.036$, Figure 4). Although a significant result had not occurred for the swimming rate of adult female sharks in response to the number of divers positioned at 6 m (one-way ANOVA, $F_{3,8} = 1.685$, $P = 0.247$), the
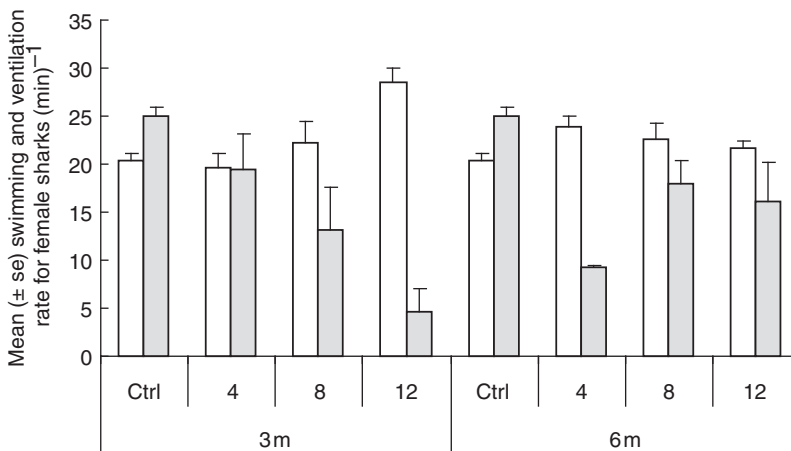

Figure 4. Mean ($1 \pm SE$) swimming (white bar = number of tail flicks per minute) and ventilation (grey bar = ventilations per minute) rates for female *C. taurus* in response to variations in diver group size and their position at 3 m or 6 m from the cave.

ventilation rate changed significantly (one-way ANOVA, $F_{3,8} = 4.130$, $P = 0.048$, Figure 4), with sharks exposed to the presence of 4 divers at 6 m having significantly lower rates of ventilation than those in the controls (*post hoc*, $P = 0.041$).

The swimming rate and ventilation of adult male sharks did not differ significantly from the control for diver treatment groups at 3 m (one-way ANOVA, $F_{3,8} = 0.245$, $P = 0.862$ and one-way ANOVA, $F_{3,8} = 0.917$, $P = 0.475$, respectively), or 6 m (one-way ANOVA, $F_{3,8} = 1.329$, $P = 0.331$ and one-way ANOVA, $F_{3,8} = 1.584$, $P = 0.268$, respectively) (Figure 5). The swimming rate and ventilation of juvenile sharks did not differ significantly from the control for either the 4- or 8-diver treatment groups (one-way ANOVA, $F_{2,6} = 2.637$, $P = 0.151$, and one-way ANOVA, $F_{2,6} = 1.973$, $P = 0.220$, respectively) (Figure 6) (see

Figure 5. Mean ($1 \pm SE$) swimming (white bar = number of tail flicks per minute) and ventilation (grey bar = ventilations per minute) rates for male *C. taurus* in response to variations in diver group size and their position at 3 m or 6 m from the cave.
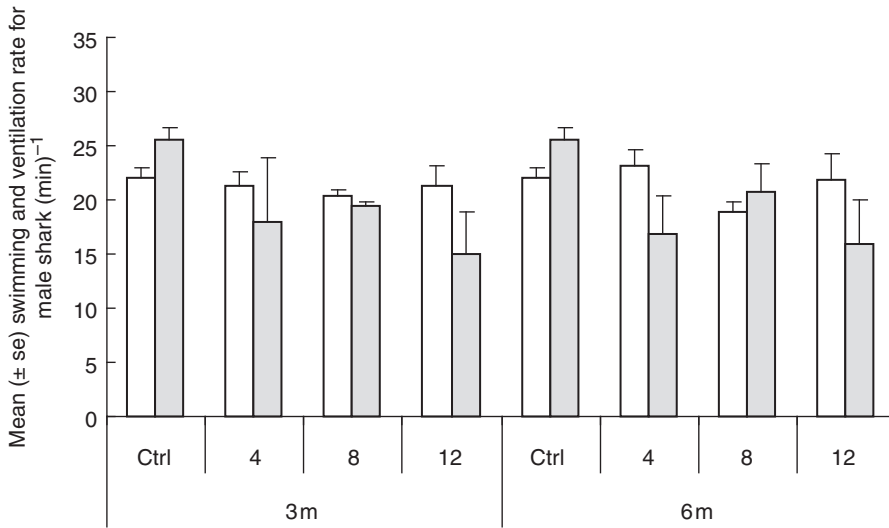

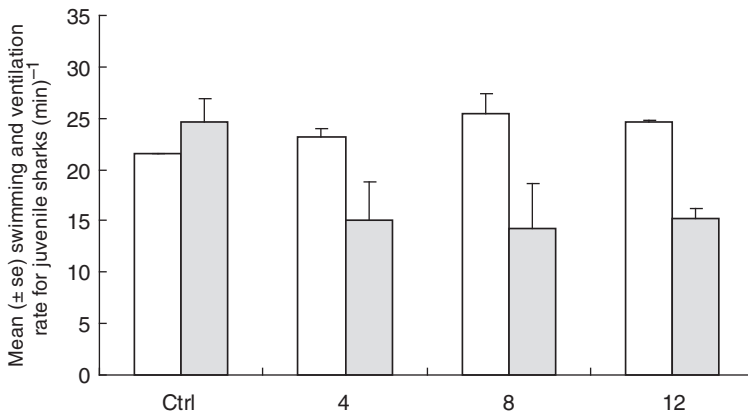Figure 6. Mean ($1 \pm SE$) swimming (white bar = number of tail flicks per minute) and ventilation (grey bar = ventilations per minute) rates for juvenile *C. taurus* in response to variations in diver group size (3 m and 6 m distance data pooled).

supplementary video clip 6, available online). The swimming rate of juvenile sharks, however, significantly increased when exposed to the presence of 12 divers (one-way ANOVA, $F_{1,2} = 180.585$, $P = 0.005$, Figure 6). This change in swimming rate was not mirrored by any significant change in ventilation rate (one-way ANOVA, $F_{1,2} = 15.7333$, $P = 0.058$, Figure 6).

Relationship of increased swimming and RAM ventilation

Assessment of video material from 37 different individual observations of *C. taurus* of all size ranges taken at Fish Rock and Magic Point suggest a critical point for changeover from 'active breathing' (buccal pumping or breathing via mouth and gill) to 'passive breathing' (RAM ventilation or increasing their swimming speed to force water over their gills) (Figure 7). On average, whenever the swimming rate increased to approximately 24 tail beats per minutes or more, the breathing rate changed from

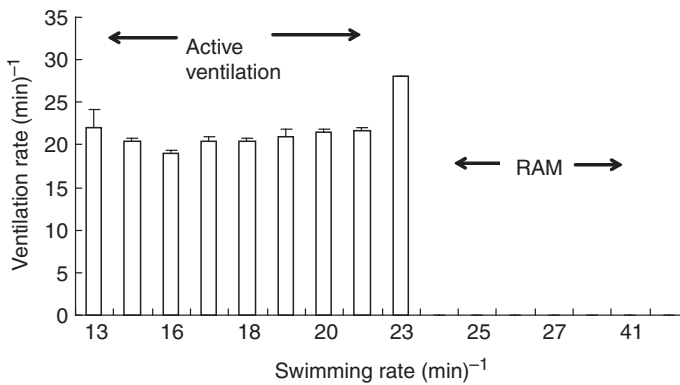Figure 7. Ranked ventilation rate (VPM) and swimming rate (number of tail flicks or FPM) of *C. taurus*, based on increasing levels of tail flicks ($n = 37$) during the 2008/09 study at Magic Point and Fish Rock.
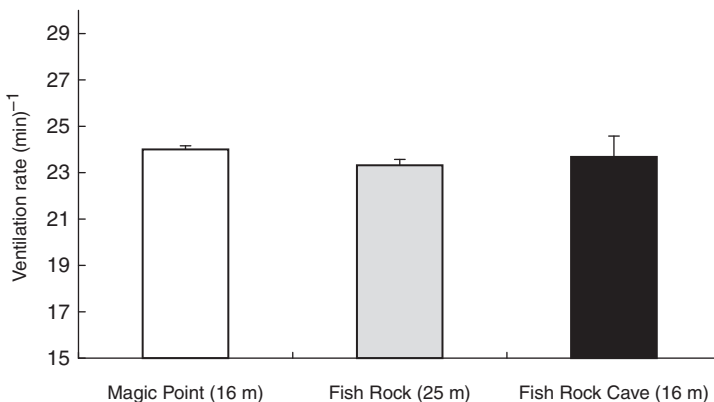

Figure 8. Mean ($1 \pm SE$) ventilation rate (number of ventilations per minute) for *C. taurus* for Magic Point (16 m), Fish Rock (25 m) and Fish Rock Cave (16 m) ($n = 30$ discrete observations per depth).

an average passive rate of 24 VPM (ventilations per minute) to RAM ventilation or 0 VPM (Figure 7).

Ventilation rates for sharks ($n = 30$) in the presence of two 'control' divers did not differ significantly between the three sites at variable depths studied, namely Magic Point Cave (16 m), South West Rocks Cave (16 m) and the deep end at South Rest Rocks (25 m) (one-way ANOVA, $F_{2,72} = 0.22$, $P = 0.807$, Figure 8).

Carcharias taurus agonistic displays

Only one case of 'tail popping' and one case of 'pectoral fin depression' were observed during these experiments (see supplementary video clip 7, available online).

Discussion

Carcharias taurus aggregation sites inevitably incorporate substantial reef structure including caves, overhangs and gutters. These sites may provide shelter from strong currents, as well as protection from other predatory sharks (Allen et al. 1999), particularly while the sharks are attempting to rest between nocturnal foraging activities. Such reef characteristics may therefore play a crucial role in the biology of this shark species. Unfortunately, the reefs that exhibit these characteristics are often also popular sites for human activities, including both fishing and recreational diving. Fishing has been identified as a primary source of ongoing mortality for Critically Endangered *C. taurus* on the east coast of Australia, leading to a reduced population viability at current levels of impact (Bradshaw et al. 2008). A second potential impact, the regular disturbance by SCUBA divers, has been highlighted as potentially affecting the reproduction, feeding and growth of *C. taurus*. Several countries have regulations for SCUBA diving with sharks (Dobson 2006), but the vast majority of these are either not enforced or voluntary in nature. Such a voluntary code of conduct is recommended for SCUBA divers visiting aggregation sites of *C. taurus* off Australia, while in New South Wales there is a legislated code for all ten of the recognised Critical Habitat Sites (DPI 2005). Few systematic studies of the impact of recreational SCUBA divers on *C. taurus* exist, with studies on the east coast either focussed on compliance by divers to the regulations (Smith et al. 2010) or on larger-scale movements of the sharks in relation to diving activities (Otway et al. 2009). This study determined the effects of recreational diver group size and their distance from *C. taurus* on the abundance and distribution of sharks within an aggregation site, while also investigating any physiological responses of the sharks to diver disturbance.

Shark numbers were significantly higher inside the cave at Magic Point than outside the cave for the non-diver control periods, thus confirming their diurnal preference for reef recesses under normal conditions (Otway et al. 2009; Barker et al. 2011). The seasonal variation in total shark abundance at Magic Point, with lowest abundance of *C. taurus* recorded during the winter months, potentially reflects the migration patterns of this species along the east coast of Australia (Otway et al. 2009). The inter-annual consistency in abundance at Magic Point corroborates the role of migratory movements in regulating shark abundance and distribution. Recapture of previously individually identified sharks at the same reef between nine and 14 months apart implies that philopatry may play an important role in

determining shark presence on reefs along the coast. Although philopatry may result in sharks being repeatedly exposed to our experiments, Otway et al. 2009 reports that *C. taurus* residency at aggregation sites averages 11 days, suggesting that independence of data was not compromised during these experiments. The number of sharks did fluctuate within the cave between treatments and experimental dives (Table 1). We were unable, however, to confirm individual identification of *C. taurus* using 'spot-matching' technology (van Tienhoven et al. 2007), with the video set up in the cave during the control period. This positioning reduced the opportunity for photo-identification with sharks not being parallel to the camera lens for successful photo-identifications (Speed et al. 2007). Speed et al. (2007) suggests spot recognition software programs that are specifically designed for *C. taurus* (van Tienhoven et al. 2007) will be compromised with sharks not lined up parallel to the camera lens. Although we could not accurately determine the level of independence of our data in this study, Barker and Williamson's (2010) photo-identification study at this location confirms that while juvenile sharks may frequently occupy this site there is a high turnover of adult male and female sharks, particularly during the time period for our current study.

The lack of significant change in shark abundance following increased diver presence is surprising considering that previous studies at this site have implied that increasing numbers of recreational divers will lead to decreasing numbers of *C. taurus* (Barker et al. 2011). However, the previous study relied on observations of natural diver behaviour, which included extremely close encounters with the sharks, whereas this study regulated diver approaches to a minimum of 3 m from the cave. This minimum distance may be outside the threatening space for grey nurse sharks, potentially corroborated by the relative lack of agonistic behaviours witnessed in this study when compared with their frequency when divers were within 2 m of this species (Smith et al. 2010).

Diver approach distance did affect shark distribution within the cave, particularly for groups of eight and twelve divers. These data support the findings of Smith et al. (2010) who reported that diver groups of six or more resulted in changed behaviour of *C. taurus* at Fish Rock. The change in shark distribution recorded between morning and afternoon observations suggests a response to morning diver exposure that lasts a few hours. However, Barker et al. (2011) report that behavioural changes are short-lived and that sharks return to more 'natural' activities within minutes of the divers leaving. Similarly, Otway et al. (2009) report minimal change in shark distribution in the presence of divers for 15 sites off NSW. These data, however, represent larger spatial areas as the acoustic range for tags and receivers used is several hundred metres. Notwithstanding the above, it appears that any impact is relatively short-term and unlikely to substantially affect the overall life history of *C. taurus* at current recreational diving levels. Should diver numbers increase to an almost continuous presence at an aggregation site, as seen at the Aliwal Shoal in South Africa, our data suggest consideration should be made to regulate diver group size.

The swimming and ventilation rate of *C. taurus* was significantly affected by the number of divers present. This is the first time that such a response to recreational divers in the wild has been documented for *C. taurus*. Adult male sharks did not respond to any diver treatments, possibly highlighting sexual discrepancy in response to perceived threat. Changes in both females and juvenile *C. taurus* were more apparent during the larger diver treatment group of 8 and 12 divers, with increasing

swimming and decreasing ventilation rates recorded for these treatments. Sharks also appeared to increase their swimming rates along the entrance of the cave when divers were at 3 m. Martin (2007, 12) describes this behaviour type as a 'rapid, or tight path swimming'. This type of apparent 'entrapment behaviour' by divers has been previously described (Pollard et al. 1996) and in our study led to a changed respiration technique from buccal pumping to more reliance on RAM ventilation.

Although agonistic behaviours were infrequently recorded, larger diver groups usually elicited these extreme reactions. One adult female shark exhibited 'tail popping' (Martin 2007), while a second female rapidly changed both swimming and ventilation rate in the presence of 12 divers. A juvenile shark showed 'pectoral fin depression' (Martin 2007) during an 8-diver group treatment. This display was also reported along with 'tail popping' in other portions of their Australian range (Smith et al. 2010) and internationally by North Carolina wreck divers (Martin 2007) and South African divers when close approaches are made (V.M. Peddemors, pers. obs.).

The apparent philopatry for specific sites such as caves and wrecks could lead to impacts being more significant for this cohort of animals (Bansemer and Bennett 2009; Barker and Williamson 2010). Juveniles and females in waters off eastern Australia are particularly important to protect because they are most sensitive to survival probability, hence the importance for development of appropriate diver protocols for this and other sites similar habitats worldwide (Otway et al. 2004).

Our gross data on swimming and ventilation rates confirms the change postulated by Hannon and Crook (2004) involving a shift from active to RAM ventilation as soon as *C. taurus* reach a specific swimming threshold. The difference between the previously reported threshold of 40 FPM for captive animals (Hannon and Crook 2004) and our threshold of >24 FPM's for wild sharks may relate to water circulation. Water circulation and oxygenation in the captive environment may exceed that in nature thereby allowing captive animals to rely on buccal pumping for longer periods of time. The acute threshold evident in *C. taurus* may be specific to elasmobranchs as the transition to RAM ventilation in fish is a graded rather than threshold process as swimming picks up from a resting state (Roberts 1975). The first indication that a critical swimming speed has been reached is signalled by the drop-out of single cycles. The drop-out continues until only occasional ventilator movement and 'coughs' are noticed (Roberts 1975). Fish must increase swimming velocities to overcome higher metabolic costs, while still ensuring complete blood oxygenation (Roberts 1975).

Comparable depth information on ventilation rates further illustrated that depth, in this case, had no bearing on ventilation frequency and that changes were in response to other environmental factors, most probably the presence of divers. Although it is currently unknown what calorific impact this changed swimming and respiratory behaviour may have on the energetic requirements of *C. taurus*, the relatively low number of diver visitations to aggregation sites along the east coast of Australia suggest impacts may be insubstantial. Should shark watching tourism increase at these aggregation sites as witnessed worldwide (Dobson 2006), however, more research into the physiology and bioenergetics of *C. taurus* and the effects of divers on these parameters should be initiated. Further work is also required to determine the magnitude and length of these impacts at other aggregation sites.

In conclusion, it is apparent that the impact of divers on *C. taurus* at their aggregation sites is likely to be relatively small at present diver numbers. While there are currently no reported fatalities from SCUBA diving activities on *C. taurus* in

Australia, there are concerns over the intensity of diver-related activities on potential nursery areas such as Magic Point (Barker et al. 2011). Further, these areas are close to major metropolitan centres where ongoing diver activities may be undertaken throughout the day. These combined pressures could increase the behavioural responses described here that impinge directly on *C. taurus*, particularly where the sharks are at the edge of their temperature tolerance (Bradshaw et al. 2008). This is unlikely to be an on-going issue if diver groups abide by the current code of conduct for diving in *C. taurus* critical habitats. The results for this study and that off Fish Rock (Smith et al. 2010) do, however, suggest that the number of divers should be restricted to less than six when within 3 m of the sharks. This may require a change to the current Code of Practice for SCUBA diving with *C. taurus*. Considering that dive groups regularly exceed that number at both Magic Point and Fish Rock (Barker et al. 2011 and Smith et al. 2010, respectively), this may require more active management of diver approaches to sharks by the dive leader. The positive educational experience attained by divers participating in shark dives highlights the value of live sharks and emphasises the urgency for management agencies to implement suitable sustainable management protocols to protect this threatened species from further anthropogenic impact.

Supplementary material

Supplementary video clips are available for this article and are accessible via the Supplementary Content tab of the article's online page at http://dx.doi.org/10.1080/10236244.2011.569991.

Clip 1. Video footage taken at Magic Point (cave) representing the swimming and respiratory behaviour during the absence of SCUBA diver groups (non-diver control).

Clip 2. Video footage taken at South West Rocks (Fish Rock) with *C. taurus* displaying normal swimming and respiratory behaviour.

Clip 3. Video footage taken at South West Rocks (Fish Rock) with *C. taurus* displaying active ventilation.

Clip 4. Video footage taken at South West Rocks (Fish Rock) with *C. taurus* displaying passive 'RAM' ventilation.

Clip 5. Video footage of a female *C. taurus* at Magic Point during the 12-diver group treatment at 3 m, with a lower ventilation rate when compared to the 'non-diver' control in clip 1.

Clip 6. Video footage of the 'recorder' diver positioned at 3 m, with a juvenile *C. taurus* displaying 'normal' swimming and 'respiratory' behaviour.

Clip 7. Video footage of an agonistic display with *C. taurus* in response to the 12-diver group treatment.

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