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REPORT

Variation in depth of whitetip reef sharks: does provisioning ecotourism change their behaviour?

Richard Fitzpatrick · Kátya G. Abrantes · Jamie Seymour · Adam Barnett

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Abstract In the dive tourism industry, shark provisioning has become increasingly popular in many places around the world. It is therefore important to determine the impacts that provisioning may have on shark behaviour. In this study, eight adult whitetip reef sharks *Triaenodon obesus* were tagged with time-depth recorders at Osprey Reef in the Coral Sea, Australia. Tags collected time and depth data every 30 s. The absolute change in depth over 5-min blocks was considered as a proxy for vertical activity level. Daily variations in vertical activity levels were analysed to determine the effects of time of day on whitetip reef shark behaviour. This was done for days when dive boats were absent from the area, and for days when dive boats were present, conducting shark provisioning. Vertical activity levels varied between day and night, and with the presence of boats. In natural conditions (no boats present), sharks remained at more constant depths during the day, while at night animals continuously moved up and down the water column, showing that whitetip reef sharks are nocturnally active. When boats were present, however, there were also long periods of vertical activity during the day. If resting periods during the day are important for energy budgets, then shark provisioning may affect their health. So, if this behaviour alteration occurs frequently, e.g., daily, this has the potential to have significant negative effects on the animals' metabolic rates, net energy gain and overall health, reproduction and fitness.

Keywords *Triaenodon obesus* · Ecotourism · Shark feeds · Depth use · Disturbance · Behavioural response · Provisioning · Sharks

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R. Fitzpatrick · J. Seymour
School of Marine and Tropical Biology, James Cook University, Cairns, QLD 4878, Australia

R. Fitzpatrick · A. Barnett
Reef Channel, Townsville, QLD 4811, Australia

K. G. Abrantes
Coastal and Estuary Ecosystems, School of Marine and Tropical Biology, James Cook University, Townsville, QLD 4811, Australia

A. Barnett (✉)
Tasmanian Aquaculture and Fisheries Institute, Marine Research Laboratories, University of Tasmania, Private Bag 49, Hobart, TAS 7001, Australia
e-mail: Adam.Barnett@utas.edu.au

Introduction

Marine wildlife ecotourism has grown dramatically in recent decades (Dobson 2006). Although it has local economic benefits and encourages conservation by creating public awareness, ecotourism also has the potential to adversely affect a target species by altering an animal's natural behaviour (Laroche et al. 2007; Clua et al. 2010). Much of the research to date examining interactions of tourism with large bodied predators has concentrated on marine mammals. In particular, there is a substantial body of literature on the effects of tourism on cetaceans (Corkeron 2004; Lusseau 2004; Bejder et al. 2006; Williams et al. 2006). However, shark tourism has also seen increased interest recently, with a number of species specifically attracted to boats or divers with food (Brunnschweiler and Earle 2006; Dobson 2006; Laroche et al. 2007; Meyer et al. 2009; Clua et al. 2010). Many dive companies market trips specifically dedicated for this purpose. Given the growth of this industry, sharks have an important value to tourism (Topelko and Dearden 2005).

Shark tourism generates millions of dollars annually in a number of regions around the world (Topelko and Dearden 2005). In 2005, ~500 000 divers spent millions of dollars to get as close as possible to sharks of all temperament and size (Topelko and Dearden 2005). In the Coral Sea (Australia) alone, a total tourism value of ~AUD$14 M is generated from diving with reef sharks (Economists at Large and Associates 2009). However, with the continual growth of shark tourism, it is important to assess the impacts of increasing shark provisioning activities on their natural behaviour and to determine whether this type of tourism is detrimental to the sharks' health over time (Laroche et al. 2007; Clua et al. 2010). To date, most studies on shark ecotourism have concentrated on the socio-economic value or the effects that conditioning sharks to baits or stimulus may have on increasing the chance of shark attacks (Topelko and Dearden 2005; Dobson 2006; Meyer et al. 2009; Dicken and Hosking 2009; Brunnschweiler 2010). Despite it being a controversial issue, there is still very limited information on how provisioning sharks or tourism in general affects the natural behaviour and health of individual sharks. Of the limited information that is available on this topic, there is conflicting predictions, ranging from minimal long-term impacts (Laroche et al. 2007; Meyer et al. 2009) to significant alterations in natural behaviour that may have direct biological effects for the species and indirect ecological effects to the ecosystem (Gaspar et al. 2008; Semeniuk and Rothley 2008; Clua et al. 2010). Therefore, there is a clear need for further studies to address this highly relevant issue for additional species and locations.

The whitetip reef shark *Triaenodon obesus* is widely distributed in tropical and subtropical reefs of the Indo-Pacific (Randall 1977; Last and Stevens 2009). Due to their placid nature, they would probably be one of the most commonly encountered species by divers, and there is evidence of this species becoming habituated to divers over time (Nelson and Johnson 1980; Topelko and Dearden 2005) to the point of being hand fed (Randall 1977). Therefore, this species is ideal to initially test possible effects of dive tourism on shark behaviour.

Whitetip reef sharks commonly occur in depths of 8–40 m, but have been recorded as deep as 330 m (Randall 1977). However, most of this knowledge is based on direct observations or fishing records, and the depth used by whitetips is yet to be quantified with telemetry equipment. Qualitative work and anecdotal evidence of whitetip reef sharks in the wild have established a long standing paradigm that they are active during the night and rest during the day (Randall 1977; Nelson and Johnson 1980). A captive study using acceleration data loggers and respirometry to quantify activity patterns agreed with these observations, confirming that whitetips are nocturnally active (Whitney et al. 2007). However, empirical data on the activity pattern of whitetip reef sharks in their natural environment are still lacking.

Due to the ever growing popularity in marine wildlife ecotourism, it is imperative to understand the potential impacts of tourism activities on the target species. To do this, information on their natural behaviour is also needed. Therefore, the aim of this study was to test the long standing perception that whitetip reef sharks are nocturnally active in their natural environment and to identify the effects of dive tourism on their activity patterns.

Methods

Study area

Osprey Reef is an isolated seamount rising vertically from 2,400 m to less than 1 m in the Coral Sea (13°54.190′S, 146°38.985′E) off the north-east coast of Australia (Fig. 1). It is approximately 220 km due east from Cape Melville on the Queensland coast, and 125 km from the edge of the Great Barrier Reef. The Osprey Atoll is 25 km in length and 12 km wide, covering an area of about 195 km^2 (Fig. 1). The site used by local dive operators to attract sharks with bait is North Horn, which is located on the northern tip of the atoll (Fig. 1). The two sides of the reef that converge to form North Horn drop almost vertically to a depth of 1,500 m. North Horn itself is characterised by a vertical wall from the surface to a depth of 22 m. Below this point, the slope becomes more gradual, coral cover less complex and sand patches more common. Shark provisioning activities are conducted on top of a coral outcrop at 16 m called the 'Bull Pit' which rises from the base of the wall at 22 m. Sharks are abundant in the area with divers viewing an average of 10–20 grey reef sharks *Carcharhinus amblyrhynchos* and 5–10 whitetip reef sharks in a single non-baited scuba dive. In addition, silvertip sharks *Carcharhinus albimarginatus*, scalloped hammerhead *Sphyrna lewini* and great hammerhead *Sphyrna mokarran* sharks can also be present. During provisioning avtivities, significantly higher numbers (up to double) of grey reef sharks and whitetips are commonly observed.

Background: ecotourism conduct and methodology

During the period of research, four tourism operators visited Osprey Reef on a weekly basis. These vessels take guests to a number of dive sites around Osprey Reef over periods of 1–3 days. North Horn was the only site where shark provisioning was conducted during the research

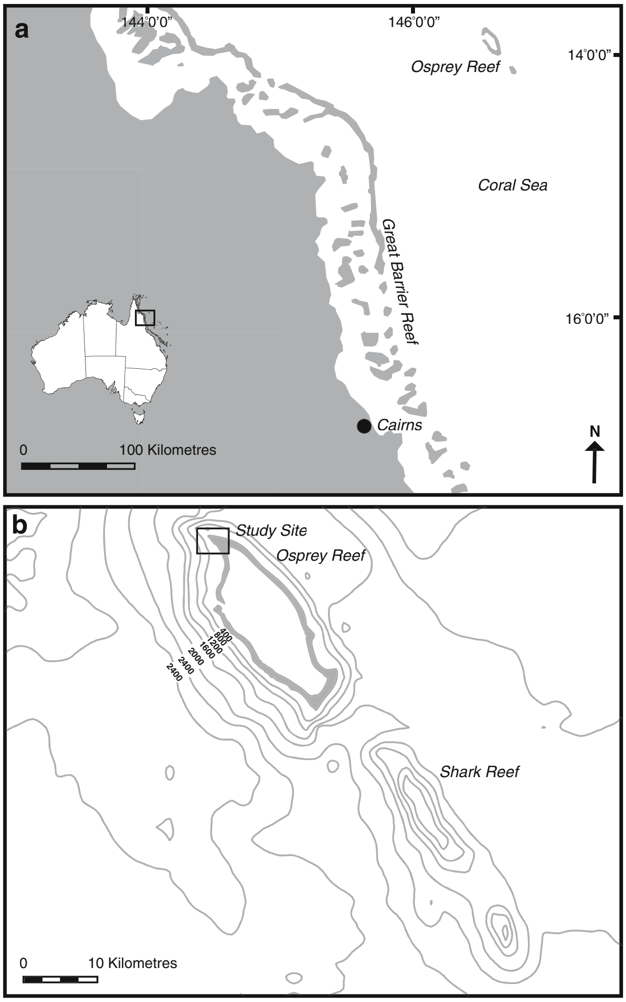

Fig. 1 Map showing the study site in the Coral Sea, Australia

period. All operators but one conducted one shark feed dive during their visits to Osprey, equating to one feed per week per operator. The fourth operator did not conduct shark feeds. Instead, they carried out shark attracts, where bait remained sealed in a crate for the entire experience. This technique allows the scent to reach the sharks but does not allow them to access the food.

The vessels moor at the site and dives are conducted directly from the vessel. Prior to shark feeds, guests (up to 26 divers) are positioned against the reef wall in depths between 10 and 16 m providing an unobstructed view of the top of the 'Bull Pit', located 12 metres away. During the feed, divers hang onto dead reef structure to stay in position. The bait is known as a 'chumsicle', a domestic garbage bin containing a frozen block of fish consisting of 1–4 frozen tuna heads and 4–10 frozen tuna frames, weighing 5–10 kg. Once guests are in position, the chumsicle is deployed from an inflatable tender vessel directly above the shark feeding area. A rope trailing from the bait is lowered to a dive staff member who runs it through a stainless steel pulley that is fixed on top of the 'Bull Pit' outcrop. This allows dive staff to safely drag the chumsicle down to approximately 2–3 m above the outcrop at the eye level of the guests. At the end of the day, the vessels move to a more protected area ~10 km further south of North Horn where they moor for the night.

Background: observations of shark behaviour

During a single feeding event, 20–40 grey reef sharks dominate the bait, but only a small proportion of these actually feed. A single grey reef shark usually consumes each tuna head/frame so the chumsicle is devoured in a matter of minutes by a small number of animals. The whitetip reef sharks observed during feeding events usually swim around on the periphery of the activity and receive little or no food due to the presence of larger grey reef sharks. The food they do receive is primarily small scraps.

Personal observations and tracking data show that individual whitetip reef sharks and grey reef sharks are strongly site attached to North Horn, being observed at the site, all year round over several years. This suggests that these sharks are associated with North Horn shark provisioning over extended time periods. In general, during non-provisioning dives at other Osprey reef dive sites, whitetips are usually observed resting during the day and are more active during night dives.

Tags, animal collection and tag attachment

Eight adult whitetip reef sharks (see Table 1 for details) were externally tagged with time-depth recorders (Star Oddie DST centi tags, 15 mm diameter × 46 mm length). Prior to the deployment, tags were attached with trace wire to a cable tie encased in a plastic tube. Animals were attracted to a closed crate containing fish frames, secured to a barren reef outcrop. When a whitetip reef shark started nudging the bait box, a diver gently grabbed the tip of the tail and quickly transferred the noose of a rope around the tail. The rope was then pulled tight around the caudal peduncle. Sharks normally struggle for up to a minute before they relax and hang upside down from the rope. The diver then slowly surfaced, and the shark brought aboard the boat for measurement, sexing and tag attachment.

Tags were placed around the base of the caudal peduncle using the plastic-covered cable tie, ensuring that this was not tight, i.e., there was always at least a 10 mm gap between the tie and the animal. The excess cable tie was then trimmed, and sharks released. The entire capture and tagging process takes approximately 5 min. Tags were recovered by repeating the capture process, but the tags were removed underwater by cutting the cable tie with scissors.

Table 1 Size and sex details of individual whitetip reef shark *Triaenodon obesus* tagged, including date tagged, number of full days (i.e. complete 24 h periods) in liberty, and number of days with boats present and with no boats present considered in the analyses

Shark ID	Total length (cm)	Sex	Date tagged	No. full days at liberty	No. days with no boat present	No. days with boat present
1M6837	133	F	14.12.04	2	1	1
1M6938	149	F	15.12.04	12	9	3
3M6948	144	F	13.12.04	2	1	1
7M6948	139	F	10.05.05	8	5	3
9M6944	124	M	10.05.05	8	5	3
14M6944	132	M	23.08.05	7	4	3
16M6942	129	M	10.08.05	5	4	2
23m6944	144	F	03.01.06	75	13	6

Data analysis

Tags were programmed to start collecting time, depth and temperature data 1 h after deployment. Since Osprey Reef has an almost vertical topography, depth data were used as a proxy for vertical activity level. Data were collected every 30 s. Depth data were corrected for tidal height.

To determine the effects of individual, time of day and boat presence on depth use by whitetip reef sharks, a Classification and Regression Tree (CART) was conducted using the Trees package on S-Plus 2000® (MathSoft, Cambridge, MA, USA). The size of the tree (or number of leaves) was selected by tenfold cross-validation, and the 1-SE tree was considered the final tree model. CARTS are a nonparametric method that provides statistically robust and ecologically meaningful interpretations of data (De'ath and Fabricius 2000). To avoid pseudoreplication and autocorrelation, for each individual shark depth, data were sub-sampled so that only data collected at 5-min intervals was used. Data were then grouped by hour for all days for each shark, and hour, along with boat presence and individual, was considered as a categorical variable in the CART. The number of days considered in this analysis for each individual is described in Table 1.

Changes in vertical activity levels with boat presence were also analysed. Here, change in depth was considered as a proxy for vertical activity levels. The absolute change in depth per 30 s was added in 5-min blocks for a random subset of data distributed among the eight individuals (Table 1). To investigate the diel pattern in vertical activity and the effects of boat presence, the absolute change in depth was assigned to hourly blocks over the 24 h of the day, and a CART was computed using individual, hour of day and boat presence as explanatory variables. Change in depth change data was firstly log transformed to reduce skewness.

A Fast Fourier Transform (FFT) was computed to identify any cyclical patterns in whitetip vertical activity in natural conditions (absence of boats) and in the presence of boats, and to identify the temporal periodicity in vertical activity. Input data were the absolute change in depth per 5-min blocks, which were calculated by adding up five consecutive absolute changes in depth per 30 s. Before analysis, data were smoothed with a Hamming window. A FFT separates time-series data into frequencies and identifies any sinusoid patterns, or periodicity, in the dataset. A power spectrum is then constructed and the dominant frequencies are represented by peaks in the spectrum (Chatfield 1996). Time series analysis was done using Statistica v.7.0. (Statsoft, USA).

Results

Sunrise time ranged from 05:50 h in summer to 06:40 h in winter, and sunset was between 18:10 h in winter and 18:55 h in summer. Depth used depended mainly on period of day, with sharks using shallower depths between 19:00 and 05:00 h (night-time) and deeper depths between 06:00 and 18:00 h (daytime; Figs. 2 and 3). For both day- and night-time periods, depth use depended on boat presence, with sharks using on average shallower depths when boats were present (Figs. 2 and 3). The CART model did not detect an effect of individual shark on depth use, as individuals were not responsible for any branch separation in the tree, meaning that there were no differences in depth use among individuals (Fig. 3).

In natural conditions (no boat present), whitetip reef sharks spent most of time at depths between 30 and 35 m during the day, while at night they used mostly shallower depths between 15 and 20 m (Figs. 2 and 3). There was an abrupt change in depth use at dawn (~05:00–6:00 h), when animals changed from using shallower depths to deeper depths (Fig. 2). Similarly, at the end of the day (~17:00–19:00 h), sharks abruptly changed from using mainly deeper depths to shallower depths at night.

The vertical activity levels of whitetip reef sharks also varied between day and night, and with the presence of boats (Figs. 4 and 5). Time of day explained most of the variability in depth change (Fig. 5), with vertical activity levels being

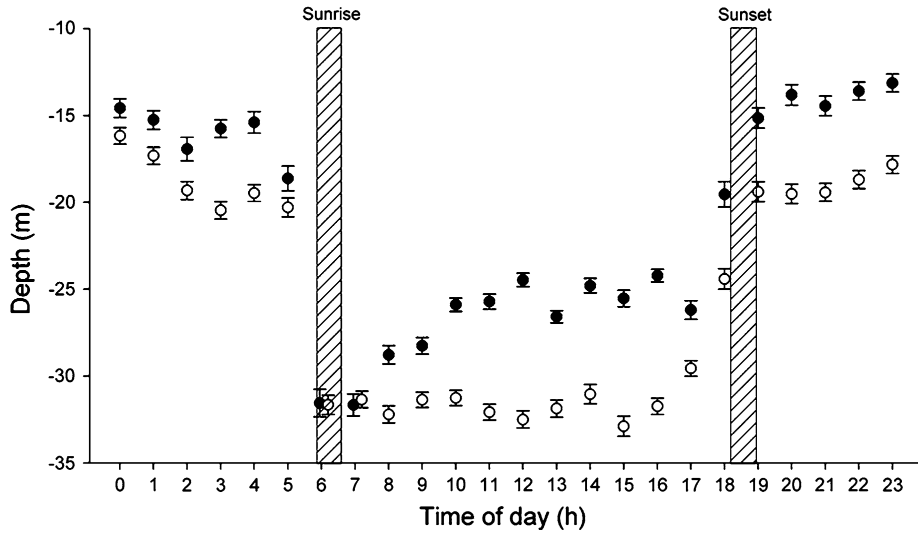

Fig. 2 Mean depth use (±95% CI) per hour for the whitetip reef sharks *Triaenodon obesus* in days when boats were absent (*white symbols*), representing the natural behaviour and in days when diving boats were present (*black symbols*). The data were offset when the two datasets had overlapping depth. *Shaded* areas represent sunset and sunrise hours during the study period

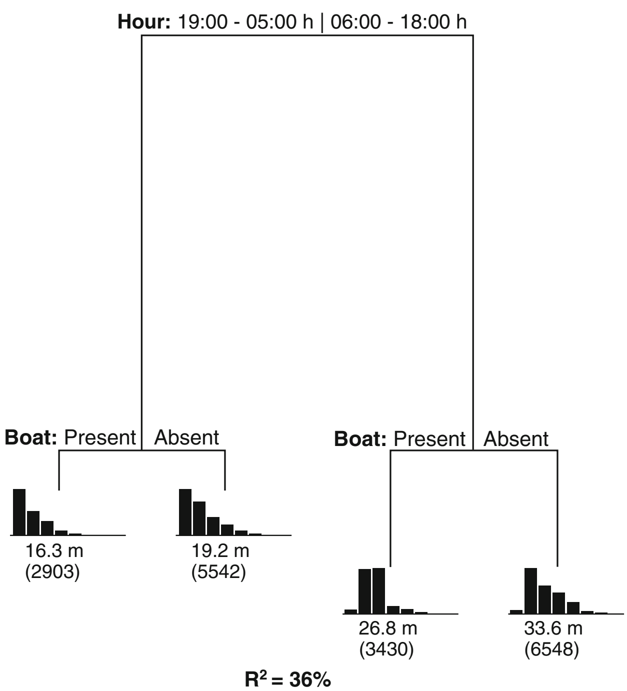

Fig. 3 Four-leaf classification and regression tree (*CART*) based on individual, hour of day and boat presence, explaining 36% of the variation in depth. Mean depth and sample size (in *brackets*) for each group is also indicated. Histograms of distribution of depth records are also shown below the terminal nodes (8 categories, from 0 to 100 m)

higher during night-time hours than during daytime hours (Figs. 4 and 5). During the day, vertical activity levels were higher when boats were present (Figs. 4 and 5).

In natural conditions (i.e. no boats present), sharks remained at more constant depths during the day (Figs. 4 and 5). There were some periods of vertical activity, but these were always short, generally lasting for less than 5 min (see Fig. 6). At night-time, however, sharks continuously moved up and down the water column (Figs. 4 and 6), and no long (>20 min) periods of vertical inactivity were detected for any individual. The decrease in vertical activity after dawn and increase at dusk was always very clear for all individuals and days (see Fig. 6 for an example). In days when boats were present, unlike in natural conditions, there were also long periods of vertical activity during the day, when sharks moved up and down the water column (see Fig. 6). In general, sharks showed greater depth variations at dawn and dusk (Fig. 4). However, depth variations were even greater at dawn on the days when boats were present (Figs. 4 and 6).

In the absence of boats, a circadian (24 h) periodicity in the vertical activity of whitetip reef sharks was observed in all individuals (see Fig. 7 for an example). Ultradian oscillations were also observed, although the periodicity was less regular and less pronounced than that of circadian oscillations, varying between 7 and 8 h. When boats were present, a much weaker ultradian (7–8 h), but not a consistent daily rhythm, was detected (Fig. 7), showing again that boat presence influences whitetip reef sharks' behaviour.

Discussion

Increased vertical movements at night, in contrast to small or no vertical movements during the day, suggest that whitetip reef sharks are nocturnally active and rest during the day. These results are in accordance with previous anecdotal observations of whitetip reef sharks in the wild (Randall 1977; Nelson and Johnson 1980), and with a more recent study in captivity (Whitney et al. 2007). Increased vertical activity at night is common in shark species (Standora and Nelson 1977; Klimley and Nelson 1984; Sims et al. 2001; Sundstrom et al. 2001; Heupel and

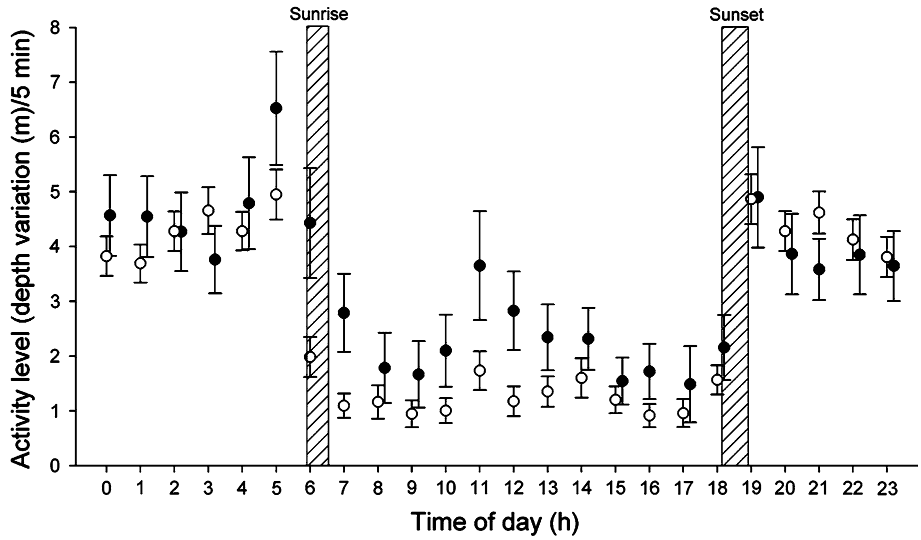

Fig. 4 Vertical activity level of the whitetip reef shark *Triaenodon obesus* measured as the absolute change in depth (measured in metres) over 5 min (mean ± 95% CI) over the 24 h period. *White symbols* boat absent; *black symbols* boat present. The data were offset when the two datasets had overlapping vertical activity level. *Shaded* areas represent sunset and sunrise hours during the study period

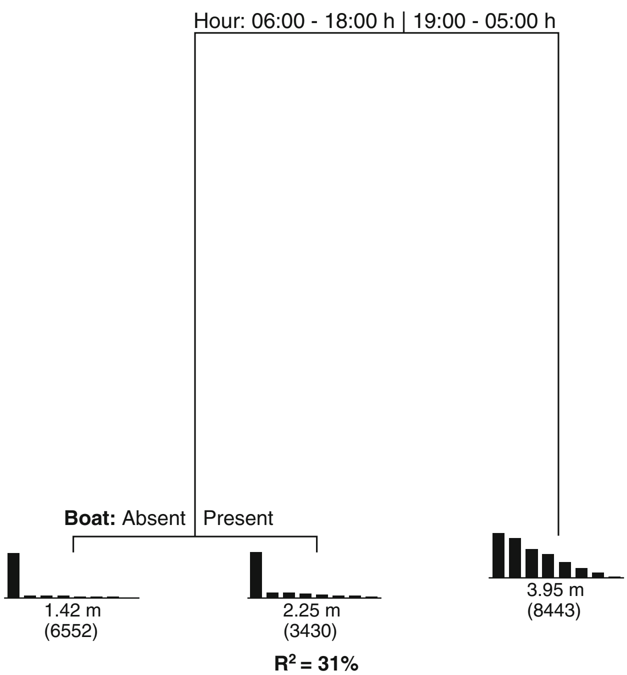

Fig. 5 Three-leaf classification and regression tree explaining whitetip reef shark *Triaenodon obesus* activity level (measured as depth change over 5 min blocks) based on individual, hour of day and boat presence. Data were log-transformed and histograms of distribution of log-transformed data are shown below the terminal nodes (ranging from 0 to 1). Mean depth (in metres) and sample size (in *brackets*) for each group is also indicated

Simpfendorfer 2005) and has often been linked to foraging behaviour (Klimley and Nelson 1984; Sims et al. 2001).

The continual vertical movement of whitetip reef sharks at night is likely to be related to the sharks moving up and down the reef wall searching for prey. It is generally assumed that whitetip reef sharks feed among the coral matrix on fish, octopus and crustaceans. However, supporting data comes from a small number of stomach samples (Randall 1977), and there is still no extensive study on the diet of this species. Nevertheless, whitetips have been observed hunting within the coral matrix (Randall 1977; Jimenez 1997), and the little information available on diet does support the theory that they are nocturnal feeders. For example, reef fish that are known to take shelter in the reef at night such as species from the families Scaridae and Acanthuridae have been found in stomach samples (Randall 1977).

Male dogfish *Scyliorhinus canicula* in Ireland rested in deeper, colder, water during the day before moving into warmer and shallow prey-rich water at night to forage, behaviour considered to be an energy conservation strategy to increase bioenergetic efficiency (Sims et al. 2006). Similar bioenergetic factors may also influence whitetip reef shark depth use. Alternatively, substrate structure such as coral cover and complexity may determine whitetip depth distribution (Nelson and Johnson 1980). The use of relatively shallow depths at night correlates with the greater habitat complexity at these depths, which is most likely related to greater availability of their main prey. The consistent deeper depths (30–35 m) used during the day is probably influenced by the availability of flat sandy areas for the sharks to rest. Due to the steep topography of North Horn, there are very little flat areas in shallower water (authors pers. obs).

Whitetip reef sharks have higher metabolic rates during the night, when they are more active, than during the day (Whitney et al. 2007). Although periods of resting and swimming were not quantitatively measured in the current study, if we speculate that the constant depth logged during the day is predominately associated with the resting periods consistently observed by the authors during dives, then the human induced vertical behavioural changes exhibited by

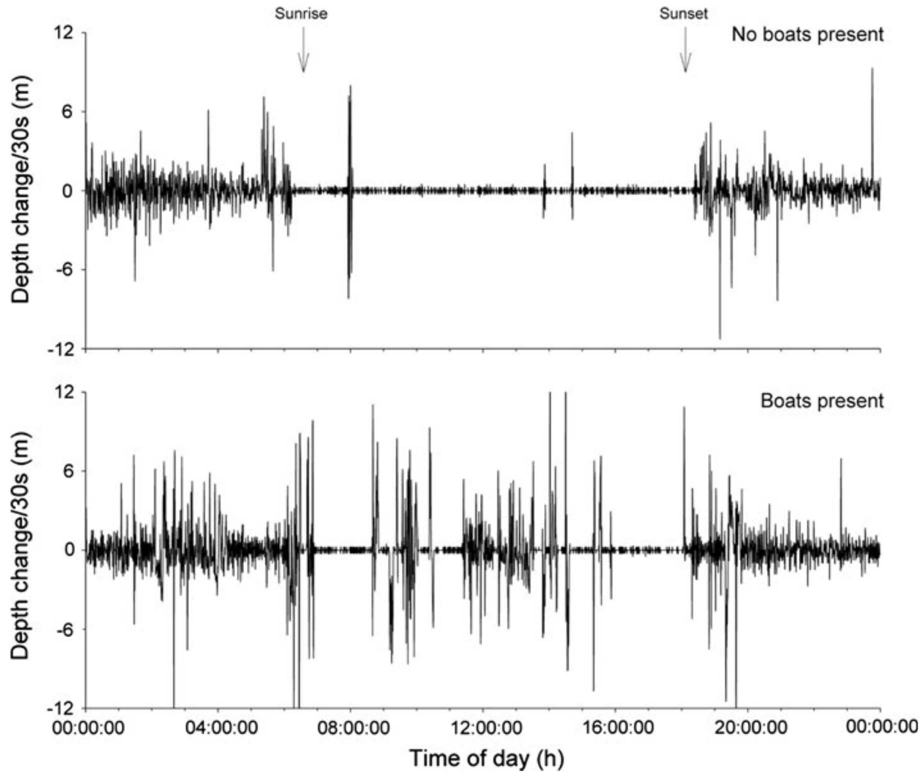

Fig. 6 Depth profile of an individual whitetip reef shark *Triaenodon obesus* (16M6942; raw data) in a day with no boats present (27th August 2005; *top*) and in a day when boats were present (23rd August 2005; *bottom*), illustrating a typical depth profile of a whitetip reef shark in the area. *Arrows* indicate sunrise and sunset times

sharks during tourism activities has the potential for repercussions to their fitness by altering diel activity patterns. Given that the high number of sharks present at feeding events insures that only a minimal number of individuals would actually receive a pay-off (i.e. consume food), if the alteration of behaviour occurs frequently, e.g., daily, this has the potential to have significant negative effects on the animals' metabolic rates, net energy gain and overall health, reproduction and fitness (Stephens and Krebs 1986; Lusseau 2004). For instance, tourism disrupted the resting behaviour of dolphins and caused them to avoid productive areas, which may have consequences to energy budgets (Lusseau 2004). Ecotourism activity has also been shown to interrupt feeding activity in a range of bird (Burger et al. 1997; Galicia and Baldassarre 1997; Ronconi and St Clair 2002) and mammal species (Stockwell 1991; White et al. 1999; Duchesne et al. 2000; Kerley et al. 2002; Williams et al. 2006). For example, the presence of boats interrupted and possibly limited killer whale feeding events, therefore affecting the whales' ability to meet energetic demands (Williams et al. 2006). However, nothing has been reported about the effects tourism may have on sharks' energetic budgets. In light of the findings in the current study and the ever increasing popularity of shark provisioning, this topic needs to be addressed in much more detail.

At present, there are approximately four shark provisioning events per week at Osprey Reef, so the effects on natural behaviour and energy budgets may be negligible. For example, Laroche et al. (2007) suggests that moderate levels of bait-associated ecotourism have only a minor impact on the behaviour of white sharks hunting around Seal Island in False Bay, South Africa. Likewise provisioning sharks in Hawaii for cage diving tourism is also believed to have no long-term effects on their behaviour (Meyer et al. 2009). In both these studies, the shark species attracted to the boats have seasonal cycles in abundance, indicating that ecotourism activities are not permanently conditioning sharks to ecotourism sites. In contrast, daily provisioning (2.5 h per day) of sicklefin lemon sharks *Negaprion acutidens* in French Polynesia has resulted in an increased number of resident sharks at feeding sites, which may have future population complications, such as reduced gene dispersal and inbreeding (Clua et al. 2010). Also, competition for limited food (not all sharks acquire food) during a feeding event appeared to fuel aggressive competitive intra-specific interactions, resulting in injuries to many individuals (Clua et al. 2010). Similarly, at Grand Cayman island in the Caribbean, the daily feeding of stingrays *Dasyatis americana* from early morning until mid-afternoon, when up to 2,500 tourists from 40 tour boats can be simultaneously interacting with stingrays, has changed their natural behaviour from nocturnal to diurnal foragers, reduced their area use (home ranges) and created a mating site. In addition to these behavioural changes, stingrays that reside at these feeding sites are more likely to

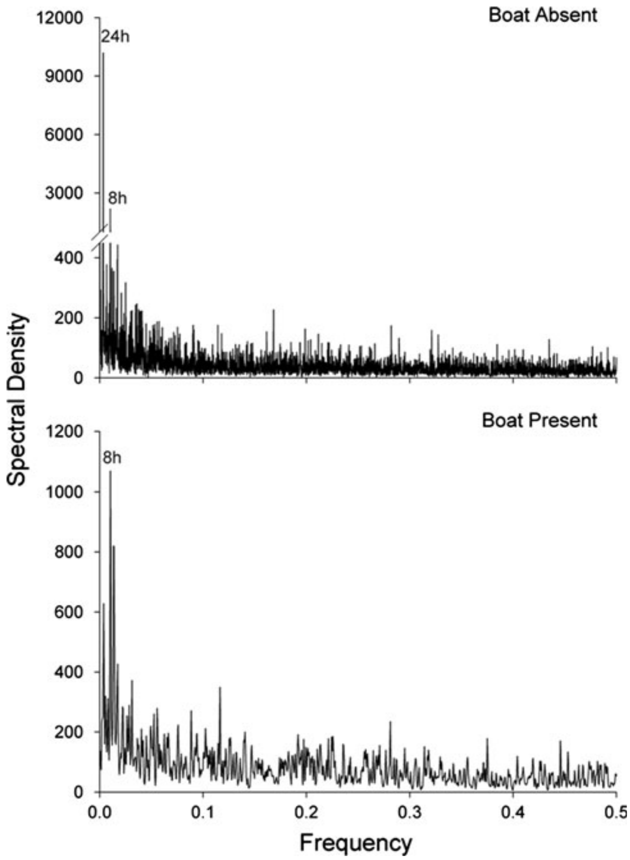

Fig. 7 Fourier transform of the time series of vertical activity (absolute change in depth (m) per 5 min) of shark 23M6944 when no boats were present (9th to the 21st January 2006; *top*) and when boats were present in North Horn (5th–8th January 2006; *bottom*). Periodicities of peaks are given over the peaks

be in lower body condition, injured, susceptible to ectodermal parasites and engaged in intense competition (Semeniuk and Rothley 2008). From the limited studies available on provisioning, both the species habitat (e.g. pelagic vs. reef) and the type and frequency of ecotourism activities may determine the degree of observed ecological impacts. However, many more species from different locations and habitats need to be studied to enable meaningful comparisons.

Further evidence of whitetip reef sharks being conditioned to the dive boats is that vertical activity is at its greatest at dawn on the days that boats were present. This peak coincides with the tour boats beginning their day, i.e., turning on engines and generators before motoring ~10 km to North Horn to dive with the sharks. Therefore, it appears that the peak in vertical activity at this time may be related to sharks anticipating the provisioning event that is associated with the sound of engines. Vessel engine noise also initially attracts sharks to cage diver operators in Hawaii (Meyer et al. 2009), and pink whiprays *Himantura fai* in French Polynesia display behaviour associated with anticipating feeding times 1–2 h prior to feeding (Gaspar et al. 2008).

It is not possible to conclusively determine whether the current level of tourism significantly affects whitetip reef sharks' health or long-term behaviour. Further research needs to be conducted at Osprey Reef and other shark provisioning localities to answer this question. Based on the behaviour effects evident in the current study, it is however likely that this effect will be significant if the number of boats or the periodicity of shark feeds at Osprey Reef increases and that the impact is considerable in other locations where shark feeds occur more regularly, e.g., daily or even multiple times a day.

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