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ORIGINAL PAPER

Effects of auditory and visual stimuli on shark feeding behaviour: the disco effect

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Abstract Sensory systems play a central role in guiding animal behaviour. They can be manipulated to alter behavioural outcomes to limit negative interactions between humans and animals. Sharks are often seen as a threat to humans and there has been increasing interest in developing shark mitigation devices. Previous research has concentrated on stimulating the electrosensory and olfactory systems of sharks, whereas the influence of light and sound on their behaviour has received little attention. In this study, the effects of an intense strobe light and a loud, artificial sound composed of mixed frequencies and intensities on shark behaviour were assessed. We tested these stimuli individually and in combination on wild-caught captive Port Jackson (*Heterodontus portusjacksoni*) and epaulette (*Hemiscyllium ocellatum*) sharks in aquaria and on wild great white sharks (*Carcharodon carcharias*) in the field. When presented alone and in combination with sound, the lights reduced the number of times that the bait was taken by both *H. portusjacksoni* and *H. ocellatum* in captivity. The strobe light alone, however, did not affect the behaviour of white sharks, but when presented in combination with sound, white sharks spent significantly less time in proximity to the bait. As the lights and sound presented in this study did not show a pronounced deterrent effect on *C. carcharias*, we do not advise their use as a strategy for mitigating shark–human interactions. However, due to the potential effectiveness of strobe lights in deterring other species of sharks, there may be applications for this approach in the reduction of fisheries bycatch.

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Introduction

Animals use a range of sensory modalities to obtain information about their physical environment. The detection and accurate interpretation of this information likely contribute greatly to the success of an individual within its ecological niche (Collin 2012). Cartilaginous fishes (selachians, batoids, and chimaerids) possess a diverse range of highly developed sensory systems, including electroreception, olfaction, audition, vision, a lateral line, and possibly even magnetoreception (Hueter et al. 2004; Meyer et al. 2005; Wetherbee et al. 2012; Newton and Kajiura 2017). As in other vertebrate taxa, cartilaginous fishes exhibit great interspecific variation in the morphology and physiology of each of these sensory modalities (i.e., differences in afferent input and sensitivity thresholds), which reflect their phylogeny and sensory ecology (Hueter et al. 2004; Lisney et al. 2007; Lisney and Collin 2007; Litherland and Collin 2008;Yopak and Montgomery 2008; Yopak and Lisney 2012; Gardiner et al. 2012; Yopak et al. 2015). There is, for example, significant interspecific variation in the ratio of rod and cone retinal photoreceptors in the eyes of sharks (Hart et al. 2006; Litherland and Collin 2008), whereby deep-sea and nocturnal sharks possess a higher proportion of rod photoreceptors than diurnal sharks. Rods detect a single quantum of light and are used for low light (scotopic) vision, but process visual information at a slower speed compared to cone photoreceptors, which can function at much higher light levels and are used for bright light (photopic) vision (Stell 1972; Gruber and Cohen 1985; Litherland and Collin 2008; Schieber et al. 2012). Therefore, a higher proportion of rod photoreceptors in deep-sea sharks likely reflects their ecological niche. Similarly, there is a high degree of interspecific variation in the morphology of the inner ear (Corwin 1978, 1989; Evangelista et al. 2010; Mills et al. 2011) and behavioural and physiological studies have shown that different species possess significantly different acoustic thresholds, which may also confer functional differences in relation with a species' acoustic ecology (Kritzler and Wood 1961; Banner 1967; Kelly and Nelson 1975; Bullock and Corwin 1979; Corwin 1989; Kenyon et al. 1998; Casper et al. 2003; Casper and Mann 2006, 2007a, b). For example, the auditory sensitivity of the horn shark *Heterodontus francisci* ranges from 25 to 200 Hz (Kelly and Neslon 1975), whereas the yellow stingray *Urobatis jamaicensis* is potentially sensitive to sounds up to 1000 Hz (Casper and Mann 2006).

Existing knowledge of the sensory abilities of sharks may also inform initiatives to manipulate behavioural outcomes to develop management strategies (Madliger 2012). Several studies have tried to manipulate shark behaviour to reduce interactions with fishing gear (Brill et al. 2009; Robbins et al. 2011) or to prevent negative shark–human interactions (Hart and Collin 2015). These approaches typically alter the signals perceived by the shark by either masking or enhancing them. Most currently available shark mitigation devices function by overstimulating the electrosensory or chemosensory systems (Marcotte and Lowe 2008; Stoner and Kaimmer 2008; Brill et al. 2009; Huveneers et al. 2013a). For example, strong magnets have been found to reduce depredation and bycatch on fishing gear (Robbins et al. 2011) and rare-earth metals have been shown to have a deterrent effect on Galapagos (*Carcharhinus galapagensis*) (Robbins et al. 2011), sandbar (*Carcharhinus plumbeus*) (Brill et al. 2009), and scalloped hammerhead sharks (*Sphyrna lewini*) (Hutchinson et al. 2012). However, the metals were found not to be effective on all species (Godin et al. 2013; Hutchinson et al. 2012) and their effectiveness was reduced when animals were highly motivated to feed (Tallack and Mandelman 2009) or when there were high densities of sharks in the immediate area (Robbins et al. 2011). A commercially available electronic deterrent, the Shark Shield Freedom 7 (Shark Shield Pty Ltd), emits a pulsed, strong electric field that has been shown to deter white sharks (*C. carcharias*) from approaching static baits and seal-shaped decoys (Huveneers et al. 2013b; Kempster et al. 2016). However, the effective repellent range of the Shark Shield is approximately 130–200 cm, which means that the electric field emitted by the device attached to ankle of a diver may not be sufficient to protect the upper part of the body (Kempster et al. 2016). The device can also cause some discomfort for the wearer due to the high-voltage discharge emanating from the antenna. In addition, there is also evidence that sharks can habituate to the electronic pulse (Kempster et al. 2016) and there are lingering concerns over whether the electronic field attracts sharks from a distance (Bedore and Kajiura 2013). All these deterrent devices, therefore, all have a number of limitations.

The development of sensory-based deterrent devices is important, not only from a public safety perspective but also for shark conservation. Negative shark–human interactions have led to extreme measures of beach protection, such as culling and beach netting (Curtis et al. 2012; Neff and Yang 2013). These invasive methods negatively impact vulnerable shark populations, as well as other animals, through bycatch of non-target species (Wetherbee et al. 1994; Gribble et al. 1998; Reid et al. 2011) and indirectly through effects on trophic cascades (Ferretti et al. 2010; Barley et al. 2017). Studies have also shown population declines in certain shark species, like the blue (*Prionace glauca*) and shortfin mako (*Isurus oxyrinchus*) sharks, as a result of fisheries bycatch, which remains a major challenge to both conservationists and fishers (Lewison et al. 2004; Camhi et al. 2007; Gilman et al. 2007, 2008; Dulvy et al. 2008; Collin 2012). However, there has been little focus on changing shark behaviour in response to visual and acoustic deterrents, and even less on multisensory approaches.

For many sharks, vision plays a vital role in their ecology, particularly in detecting and identifying prey (Hobson 1963; Gilbert 1970; Strong 1996), intra- and interspecific communication like agonistic displays (Ritter et al. 2000; Martin 2007) and in navigating complex aquatic environments (Parker 1910; Fuss et al. 2014). The visual system of many shark species is relatively sensitive to brightness contrast and possesses several visual adaptations. Although there is documented interspecific variability in retinal topography (Hart et al. 2006; Litherland and Collin 2008), many sharks possess a retina dominated by rods (Litherland and Collin 2008; Schieber et al. 2012), which are more sensitive and operate at lower light levels than cones (Land and Nilsson 2012) and likely reduce visual resolution (Litherland and Collin 2008; Ryan et al. 2017). A reflective tapetum lucidum behind the retina also provides a second opportunity for photoreceptors to absorb light and increase sensitivity (Gilbert 1970). The high absolute sensitivity of the eyes to light may result in avoidance of bright flashing (strobe) lights. As a potential deterrent, strobe lights produce abrupt flashes, with alternating levels of light intensity over a short duration, which may limit retinal adaptation. Therefore, a strobe light may cause overstimulation of retinal photoreceptors (Chalupa and Werner 2004; Land and Nilsson 2012) or may represent a novel stimulus that is avoided by sharks (i.e., neophobia) (Mettke-Hofmann et al. 2002; Sneddon et al. 2003). Indeed, strobe lights have been found to deter a range of teleost fishes (Johnson et al. 2005a; Marchesan et al. 2005) and to reduce the entrapment of fish around dams and power plants (Anderson et al. 1998; Johnson et al. 2005a, b). Conversely, strobe lights may potentially have an attractant effect as seen in Antarctic krill (Wiebe et al. 2004) and some teleosts (Johnson et al. 2005b). No studies to date have examined the effect of strobe lights on shark behaviour.

Underwater sound is also an important sensory stimulus and represents a directional signal that is able to propagate over large distances. Sharks are known to be sensitive to low-frequency sounds up to 2000 Hz and have a peak sensitivity at around 100 Hz (Corwin 1989; Popper and Fay 1997; Myrberg 2001; Hueter et al. 2004; Gardiner et al. 2012). Low-frequency stimuli can propagate long distances underwater due to their long wavelengths and the high density of the water. Mixed low-frequency sounds (resembling a struggling fish) have been shown to attract sharks in the field (Nelson and Gruber 1963; Myrberg et al. 1969, 1972; Rizzari et al. 2014). In contrast, the sudden onset of an intense sound or transmission switch from an attractive sound can have a repellent effect on sharks (Banner 1972; Myrberg et al. 1978; Klimley and Myrberg 1979). As sharks do not possess a swim bladder or any other structure that can convert acoustic pressure into particle movement, they are thought to respond only to the particle motion component of a sound (Myrberg 2001). This suggests that sharks may be particularly sensitive to the near field (the sound field within approximately two wavelengths) of the sound source. Aside from the morphology of the inner ear, the distance at which sharks can detect a sound ultimately depends on the type of sound source, the intensity, and frequency spectrum of the sound and on the surrounding soundscape and habitat acoustics (Myrberg 2001).

Very few studies have used a multisensory approach to manipulate shark behaviour. In an experiment investigating the behaviour of three different species of sharks towards prey, Gardiner et al. (2012) demonstrated that sharks use their senses simultaneously, but switch the primary modality in a hierarchical way as they approach their prey. Even when blocking senses in different combinations, three species of sharks differing in sensory anatomy (*Carcharhinus limbatus*, *Sphyrna tiburo*, and *Ginglymostoma cirratum*) were still capable of successfully capturing prey using alternate sensory modalities (Gardiner et al. 2012). Therefore, the combination of different sensory stimuli may amplify avoidance behaviour in sharks by increasing the likelihood of detection through multiple mechanisms. A sound stimulus, for example, may be more effective over a greater distance, especially in turbid water, than a visual stimulus, even if the visual stimulus is a more potent deterrent at close range (Stein et al. 2008). Such a multisensory approach has proven to be an effective management strategy for a number of species of freshwater fishes. For example, increased avoidance behaviour is seen in freshwater and estuarine teleosts (i.e., *Brevoortia tyrannus*, *Leiostomus xanthurus*, *Morone americana, Alosa pseudoharengus, Osmerus mordax,* and *Dorosoma cepedianum*) in response to the combination of strobe lights and bubbles when compared to the response to each treatment presented in isolation (Patrick et al. 1985; McIninch and Hocutt 1987; Sager et al. 1987; Ploskey et al. 1995).

This study assessed the behavioural responses of three species of shark to strobe lights and an artificial sound, presented both separately and simultaneously. Experiments were performed in captivity on two benthic species, the Port Jackson shark, *Heterodontus portusjacksoni,* and the epaulette shark, *H. ocellatum*, and in the wild on the great white shark, *C. carcharias*, in Mossel Bay, South Africa. The captive species were selected due to their common availability, abundance, and manageable husbandry, while *C. carcharias* was chosen as one of the species responsible for most human fatalities globally (Baldridge 1996; West 2011). We hypothesised that: (1) intense strobe lights at different frequencies (5 and 10 Hz) will deter sharks from a bait source; (2) a loud artificial sound stimulus will deter sharks from a bait source; and (3) the combination of a sound stimulus and a strobe light will amplify the deterrent effect. We used a comparative approach to analyse the responses of each teste species to the sensory stimuli.

Methods

Animal ethics and acquisition

The sensory stimuli were tested on six wild-caught Port Jackson sharks, *H. portusjacksoni* (pre-caudal length (PCL) ranging from 20.5 to 44.0 cm, $n = 3$ females, $n = 3$ males) and five wild-caught epaulette sharks, *H. ocellatum* (PCL ranging from 41.0 to 49.0 cm, $n = 2$ females, $n = 3$ males) in an aquarium facility at The University of Western Australia (UWA) and within a wild population of white sharks, *C. carcharias*, in Mossel Bay, South Africa. The white shark population in Mossel Bay is dominated by individuals 275–325 cm in total length (Kock and Johnson 2006), with population sex ratio close to 1:1 (56% male:44% female, Gennari, unpubl data), but accurate values of sex and size of individual sharks are yet to be assessed. This study was carried out with the approval of the UWA Animal Ethics Committee (Application RA/3/100/1193) and in strict accordance with the guidelines of the Australian Code of Practice for the Care and Use of Animals for Scientific Purposes (8th Edition, 2013). The work was also approved by the South African Department of Environmental Affairs: Biodiversity and Coastal Research, Oceans and Coasts Branch (Permit RES2014/91).

Description of sensory stimuli

The sensory stimuli consisted of an artificial sound and/or a flashing 'strobe' light. The artificial sound was generated by an underwater speaker (Diluvio from Clark Synthesis, frequency response 20–17 kHz in the air, undetermined in water), which was connected to an amplifier (PBR300X4, Rockford Fosgate) and an MP3 player (Philips GoGEAR) powered by a 12 V battery. The artificial sound profile was constructed digitally with Adobe Audition CS5.5 and the digital audio workstation software Reaper v.4.62. Following the work of Myrberg et al. (1978), which showed that a sound with a rapidly changing amplitude and frequency elicited the withdrawal behaviour of free-swimming sharks, the sound was built by mixing ratios of different frequencies and intensities, from 20 to 20 kHz (Fig. 1). This stimulus was not created to represent a biologically relevant cue, but rather to present an unfamiliar, unnatural, and never encountered signal with an erratic signature (arrhythmic and mixed in frequencies). The relative amplitude ranged from − 1 to 1, with random silence intervals (Fig. 1). While the treatment sound contained audible frequencies (i.e., 20–2000 Hz), the control sound consisted of a sound inaudible to sharks, based on the current literature (Kritzler and Wood 1961; Banner 1967; Kelly and Nelson 1975; Bullock and Corwin 1979; Corwin 1989; Kenyon et al. 1998; Casper et al. 2003; Casper and Mann 2006, 2007a, b): 10 kHz tones, repeated every second at a maximum relative amplitude (Fig. 1).

The sound stimuli were quantified in the experimental aquarium (Fig. 1) as well as in open water (Fig. 6 in Online Resource) (Table 1). Although no audiograms are available for our targeted species, we assumed that hearing thresholds in *H. portusjacksoni* and *H. ocellatum* were similar to those measured in closely related species, the horn shark, *H. francisci*, and brownbanded bamboo shark, *Chiloscyllium punctatum* (Casper and Mann 2007a), respectively. Across these different shark species, particle acceleration thresholds at 100 Hz are approximately 1×10^{-3} m/s^2, which would be reached at a distance of approximately 10 m from the sound source for our artificial sound. The white shark audiogram is also unknown and no audiograms are available for any other members of the Lamnidae family. In an attempt to ensure that the sound stimuli were detectable by the white sharks, the sound playback was activated when the sharks had approached within 2 m of the source.

The strobe light was constructed from eight constant-current-controlled white light-emitting diodes (LEDs; Vero 13, Bridgelux), with four LEDs on two opposing sides (eight in total) of a rectangular aluminium tube (10 × 45 cm). The LEDs and all wiring were insulated and waterproofed by encasing the tube with clear epoxy resin. The intensity of the strobe was measured using a light meter (International light technologies, ILT1700) to be 1.22×10^3 W sr^{-1} cm^{-2}. Current to the LEDs was switched on and off at a rate of either 5 or 10 Hz (duty cycle of 5 and 10%) using a programmable microcontroller (Arduino Nano v3.0). Strobing speeds of 5 and 10 Hz were used as this rate is known to be much lower than the temporal resolution (critical flicker fusion frequency) measured in a range of sharks (McComb et al. 2010; Kalinoski et al. 2014; Ryan et al. 2017). At faster strobing speeds, our target species may not have been able to resolve the alternating strobe signal and perceive the light as continuous (McComb et al. 2010; Kalinoski et al. 2014; Ryan et al. 2017).

To ensure that the behavioural responses were a result of the light and sound stimuli and not a result of the electrical fields produced by the equipment, measurements of the electric fields of the strobe light, artificial sound and control sound stimuli were acquired (Online Resource). The control stimulus produced the greatest electric field, and thus effectively controlled for any behavioural effects due to electronic stimulation.

Experiment on captive benthic sharks

Experimental design

The behavioural responses to six different stimulus treatments were assessed for six *H. portusjacksoni* and five

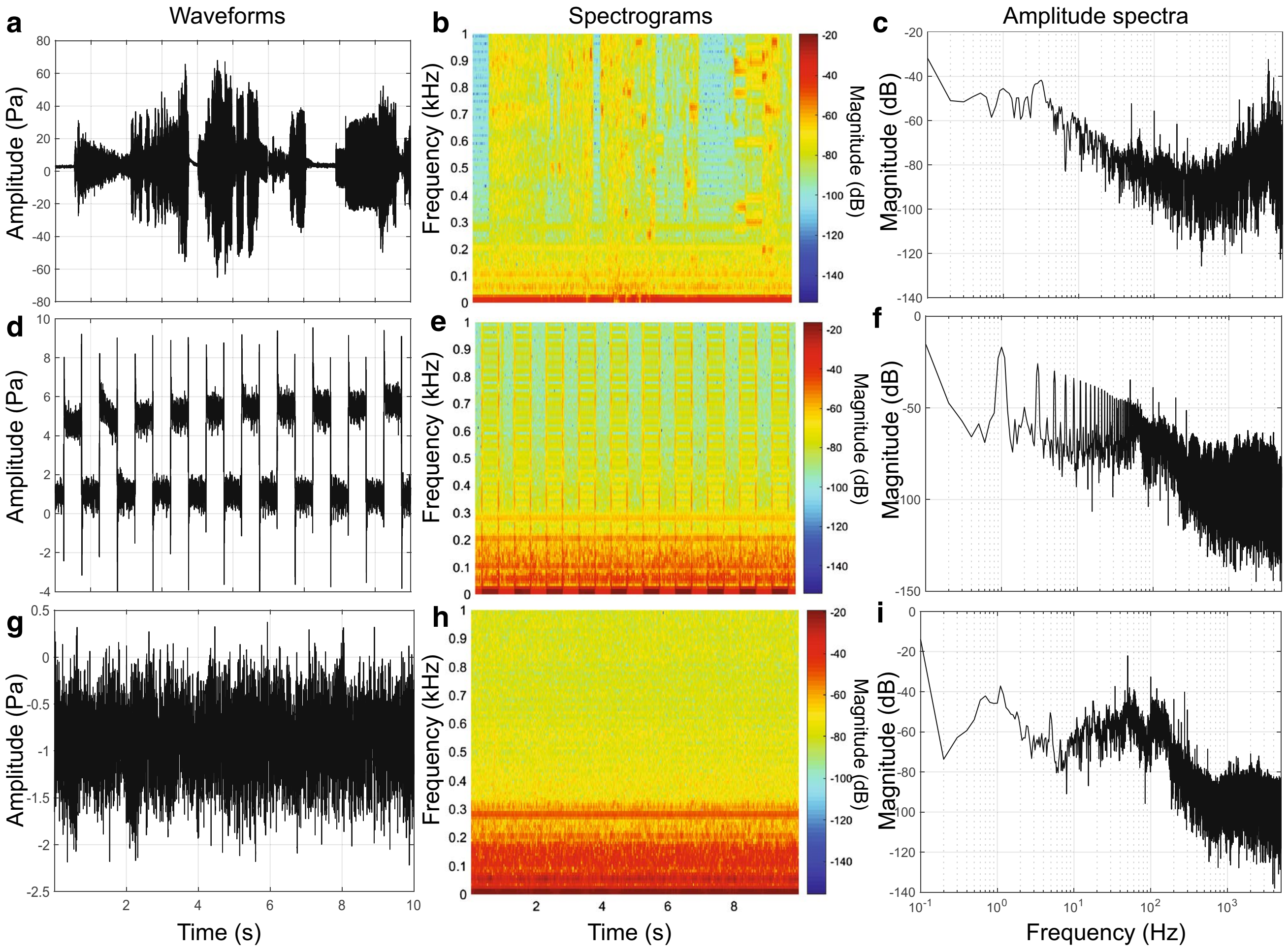

Fig. 1 Laboratory-based recordings in the experimental aquarium (from left to right: waveforms, spectrograms, and amplitude spectra) of a representative ten second extract of the artificial sound (**a**–**c**), the control sound (**d**–**f**), and the ambient background noise (**g**–**i**)

H. ocellatum. The six treatments consisted of: (1) a 5 Hz strobe light; (2) a 10 Hz strobe light; (3) the audible artificial sound; (4) a combination of the 10 Hz light and the artificial sound; (5) a sound control which consisted of a 10 kHz tone repeated every second (assumed to be inaudible for these species); and (6) a control without any stimuli. The effects of the light and sound treatments were assessed by comparing interactions to the control treatments. Only one combination treatment (10 Hz light and sound) was chosen due to the limited number of animals and the limited hours in the field, because the effect of the combination, rather than the differences in strobe frequencies (5 vs 10 Hz), was one of the main objectives of this study.

The experimental aquarium was a rectangular fibreglass tank filled with 2800 L of seawater. The tank floor was covered with a 5 cm layer of sand substrate. A PVC tube shelter was located at one end of the tank and a V-shaped polypropylene barrier positioned at the other end (Fig. 2a). The speaker was inserted into the vertex of the 'V' and the light was positioned horizontally, 20 cm in front of the speaker. A length of clear monofilament fishing line was suspended 10 cm in front of the strobe light device with a small sinker attached 15 cm above the bottom of the line; bait, used to attract sharks, was attached below the sinker. The barrier was used to funnel sharks towards the bait and prevent them from swimming into areas of the tank behind the speaker and lights. A rope, embedded in the sand and positioned at the opening of the V-shaped barrier, was used as a marker to delimit the entrance to the testing arena.

A Latin square experimental design restricted the randomisation of the order in which treatments were presented, thereby allowing to control for an individual's previous experience (Winer 1962). This testing pattern ensured that the treatments were repeated in a different order every day, such that each treatment was presented once at each of the possible time slots per day. Every individual was tested for each of the six treatments six times. For *H. portusjacksoni*, six trials (treatments) were

Table 1 Sound parameters for the artificial sound, the control sound (10,000 Hz tone) and the ambient background noise in the laboratory environment (aquaria), and in the field

	Lab			Field		
	Background noise	Digital sound	Audio control	Background noise	Digital sound	Audio control
Sound parameters						
RMS (Pa)	0.96	3.04	3.94	9.38	9.94	2.95
SPLpeak + (dB re luPa)	114.08	156.64	140.00	146.11	156.36	138.66
SPLpeak − (dB re luPa)	127.62	156.51	133.17	131.51	156.52	139.85
SPLpp (dB re luPa)	127.80	159.58	140.81	146.26	159.45	142.31
SPLrms (dB re luPa)	119.66	141.69	131.90	139.44	139.95	129.40
SNR (dB)	–	22.05	12.27	–	19.94	9.78
Particle acceleration						
X-axis acceleration (m/s^2)	0.0037	0.1261	0.0361	0.0094	0.1097	0.0331
Y-axis acceleration (m/s^2)	0.0050	0.1206	0.0483	0.0096	0.1348	0.0565
Z-axis acceleration (m/s^2)	0.0046	0.0992	0.0337	0.0086	0.0947	0.0638
Magnitude of acceleration (m/s^2)	5.9E − 05	0.0403	0.0048	2.5E−04	0.0392	0.0084

All measurements were made at a distance of 1 m from the speaker. Sampling rate: 100 kHz

RMS root mean square in Pa, *SPLpeak* + sound pressure level of the highest peak in dB re μPa, *SPLpeak* − sounds pressure level of the highest negative peak in dB re luPa, *SPLpp* sound pressure level of the peak to peak in dB re μPa, *SPLrms* sound pressure level of the root mean square value in dB re μPa, *SNR* signal-to-noise ratio in dB

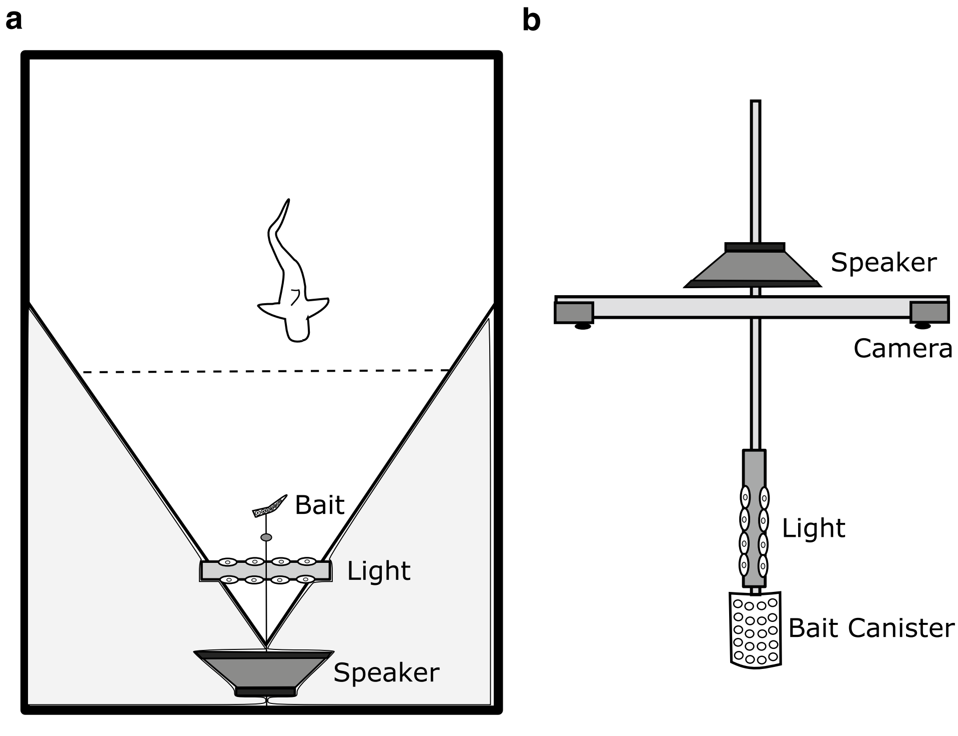

Fig. 2 **a** Plan view of the apparatus used for the aquarium-based experiments on benthic sharks. **b** Side view of the stereo camera rig used on white sharks in the field. The dotted line represents the marker rope

performed per day, for 6 days. Since *H. ocellatum* took much longer to approach the bait in comparison with *H. portusjacksoni*, only three trials (treatments) were performed per day, for a total of 12 days, although the order followed the same Latin square design. The treatment days were alternated with resting (fasting) days for both species, to ensure that the sharks were motivated to feed during the trials.

Procedure

Prior to each experiment, the sharks were held in a holding tank (identical to the experimental tank) for a minimum of 2 weeks. Tanks were on a 12:12 h light:dark cycle and ambient illumination was provided by filtered daylight and overhead fluorescent tubes. Water parameters were measured each day to ensure that both experimental and holding tanks were stable and identical (temperature = 24.8 ± 0.8 °C; salinity = 36.6 ± 1.7 ppt, pH 8.07 ± 0.5; mean and SD).

Each individual was moved to the experimental tank and allowed to acclimatise for 24 h prior to the start of the trials. In both the experimental and holding tanks, neither underwater artificial lights nor aeration was used, to prevent either overstimulation or habituation of their hearing and visual systems. For each trial, an approximately 2 × 1 cm piece of squid was attached to the fishing line and lowered into position, while the shark was not in the testing arena. When the shark entered the testing arena by crossing the marker rope, the trial commenced and the assigned treatment was initiated. Sharks were given 40 s to take the bait. If the shark entered and left the trial area three times without touching the bait, the trial was terminated. A GoPro camera positioned above the tank recorded all interactions. The observer was not visible and monitored the experiment from a computer positioned away from the experimental tank, linked to a live stream of the GoPro.

Data analysis

The video footage was reviewed to determine whether the bait was taken (binomial distribution) and to record the latency before taking the bait (Gaussian distribution). The effect of the sensory treatments was determined using a mixed model analysis performed in R (R Core Team 2015) using the package 'lme4' (Bates et al. 2013). The effect of the stimulus treatments was assessed by setting the treatment as a fixed factor and setting the random factors as the order of presentation, which was nested inside the number of times that the treatment had been experienced, and also the identification code for each individual shark. Akaike Information Criteria (AIC) were used to determine the most parsimonious model. Models with the lowest AIC score were considered to be the best fit. To determine differences between treatments, a multiple comparison for parametric models was performed using the R package 'multcomp' (Hothorn et al. 2008). Other factors such as individual, day, experience (with previous treatments), and order of presentation were also tested as fixed factors, but were found to be insignificant ($P = 0.36$) in explaining variation in the data.

Field experiment on white sharks

Experimental design

The laboratory experiments allowed us to validate a concept in benthic species like the Port Jackson and epaulette sharks in controlled conditions. Despite the difficulty of working in the wild, it is critical to test the deterrents on potentially dangerous shark species like the white shark, as they are most often implicated in negative human–shark interactions and, therefore, of utmost interest in the effectiveness of a shark deterrent. The behavioural responses to four different sensory stimulation treatments were assessed in *C. carcharias* using a stereo camera rig (Fig. 2b) deployed from a boat anchored at various locations within 2 km of Seal Island, Mossel Bay in South Africa, with water temperature averaging 17 °C. The four treatments were: (1) a 10 Hz strobe light; (2) the audible artificial sound; (3) a combination of the 10 Hz light and artificial sound; and (4) a control without any stimuli. Note that only 10 Hz strobe lights were tested in this experiment as no difference was observed in captivity between 5 and 10 Hz, to save valuable time in the field and decrease the amount of fixed variables in the analysis. Moreover, the 10 Hz stimulus was chosen, because the time interval between consecutive light flashes was shorter. The effects of the light and sound treatments were assessed by comparing interactions to the control treatment. A trial consisted of interactions (see below) occurring within the field of view of the cameras for a period of 3 min, while a single treatment was presented. Treatments were presented in an order randomly determined at the start of each day. A total of 52 trials were executed: 16 controls, 11 strobe lights 10 Hz, 13 artificial sounds, 12 strobe light, and sound combinations.

A custom-built, downward-facing stereo camera rig (Fig. 2b) was used to record interactions between sharks and a bait canister, adapted from a mid-water stereo camera system previously developed by Letessier et al. (2013), which has been described elsewhere (Kempster et al. 2016). The stereo rig was comprised of two GoPro Hero 3 video cameras, mounted (0.7 m apart) on a horizontal aluminium tube (Fig. 2b). A PVC canister containing 0.5 kg of crushed sardines was mounted in a central position, 1 m in front of the two cameras. A 2 kg weight was placed in the bait canister to keep the rig in a stable vertical orientation within the water column. The strobe light was mounted directly above the bait canister and the underwater speaker was positioned between the cameras, pointing down towards the bait canister.

Procedure

The stereo camera rig was positioned approximately 2 m off the stern of the boat with the cameras situated just below the surface of the water. The rig remained in the water for approximately 1 h, which will be referred to hereafter as a 'drop'. Between 2 and 4 drops were performed each day over a period of 5 days. The bait in the PVC canister was emptied and refilled with fresh bait prior to each drop. Individual sharks were initially identified from the boat and identification was later confirmed from video analysis, using their scars and markings, which allowed identification of the same sharks interacting in the experiment over 5 days (Domeier and Nasby-Lucas 2007; Anderson et al. 2011). Sharks were lured close to the rig using a tuna head attached to the end of a rope, secured to the boat. Once a shark had approached within approximately 2 m of the rig, as observed from the boat, the trial commenced and lasted for a period of 3 min. As the tuna head was positioned at the surface of the water and the video cameras 1.5 m below the surface, only sharks targeting the bait canister and entering the field of view were recorded. The trial was deemed invalid if more than one shark appeared in a 10 m diameter area from the boat.

Data analysis

Video footage of white sharks, *C. carcharias,* was reviewed to record that the total amount of time a shark was in the field of view (Gaussian distribution) and any interactions of the shark with the camera rig, bait canister, and sensory treatments (binomial distribution). Behaviours were classified and scored according to the level of interaction as: 1 = approach (individual enters and leaves the field of view without making contact with the rig); 2 = touch rig (individual touched any part of the rig); 3 = bump sensory stimulus device (individual touched the device with their head or mouth); 4 = bump bait (individual touched the bait canister with their head or mouth); 5 = taste bait (individual touched the bait canister with an open mouth); and 6 = bite bait (individual bit down on the bait canister).

To determine if the recorded shark behaviour was altered by any of the sensory treatments, a mixed model analysis was performed. The day, time of day, and previous experience (whether the animals had already experienced the treatment) had no effect as fixed factors, but they were included as random factors to account for their variance. The variables day and time of the day accounted for environmental conditions, such as differences in weather and ambient light. Individual was also treated as a random factor and the treatment was set as a fixed factor. To determine which treatments differed, a multiple comparison for parametric models was performed. To assess differences in behaviour exhibited by individuals of *C. carcharias*, we also performed mixed models, with individual as a fixed factor.

Results

Experiment on captive benthic sharks

Both *H. portusjacksoni* and *H. ocellatum* readily approached and took the bait in the control experiment trials. *Heterodontus portusjacksoni* took the bait in 86% of the control treatments and *H. ocellatum* took the bait in 100% of the control treatments. *Heterodontus portusjacksoni* exhibited a clear change in behaviour when presented with the strobe light treatments, often freezing at the onset of the strobe light. *Heterodontus portusjacksoni* took the bait in 42% of the 10 Hz strobe light trials, in 27% of the 5 Hz strobe light trials, and in 28% of the combined light and sound trials (Fig. 3). The results of the mixed model showed that the treatment had a significant effect on the percentage of sharks to take the bait [binomial (logit) mixed model, $n = 6$, $df = 5$, Chi squared = 91.24, $P < 0.001$] (Table 2). The 5, 10, and 10 Hz lights and sound combination were all significantly different to the controls. The sound treatment alone did not differ significantly from the controls. *Heterodontus portusjacksoni* took the bait in 92% of the audio trials, in 86% of the no-light/no-sound control trials, and in 94% of the inaudible sound control trials. In cases where the sharks took the bait, there was no difference in the latency in which the animals took the bait between all the different treatments (Table 2).

Hemiscyllium ocellatum also took the bait less during the light treatments (80% of the 5 Hz strobe light trials and 81% of the 10 Hz strobe light trials) and the light and sound combined treatment (74%) compared to the control trials (100%) (Fig. 4a) [binomial (logit) mixed model, Chi

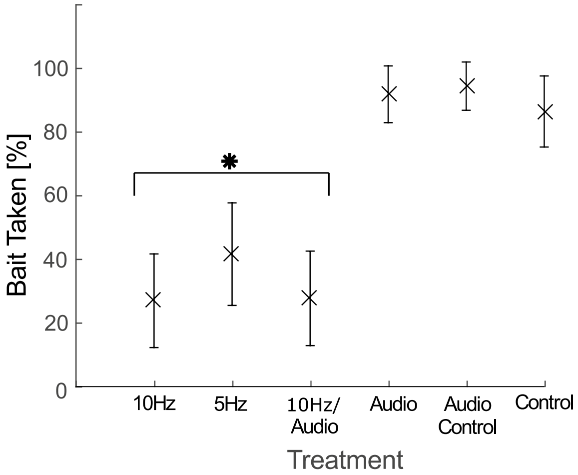

Fig. 3 Mean percentage of trials in which *Heterodontus portusjacksoni* took the bait for each of the stimulus treatments. Vertical bars represent 95% confidence intervals. $n = 6$ sharks, every individual was tested six times for each of the six treatments. The asterisk indicates a significant difference ($P < 0.05$) with the control treatment

Table 2 Results showing the levels of significance found from the mixed models for *Heterodontus portusjacksoni* ($n = 6$) based on 36 interactions for each individual

Response	Effect	*df*	Chi-sq	*P* value
Bait taken	+ Treatment	5	91.24	< 0.001*
Comparison	EST	SE	*Z*	*P* value
Control vs Hz light	2.87	0.61	4.68	< 0.001*
Control vs 10 Hz light	2.21	0.59	3.72	< 0.001*
Control vs audio	− 0.58	0.77	− 0.75	0.46
Control vs light and audio	− 2.83	0.61	− 4.61	< 0.001*
Control vs audio control	− 0.98	0.87	− 1.12	0.26
Response	Effect	*df*	Chi-sq	*P* value
Time to take bait	+ Treatment	5	52.75	0.49

Degrees of freedom (*df*), Chi-squared values (Chi-sq), and *P* values. The multiple comparison for the mixed models is also presented. Estimates of regression coefficients (EST), standard error (SE), *Z* value (*Z*), and *P* values are presented

* Indicates statistically significant results

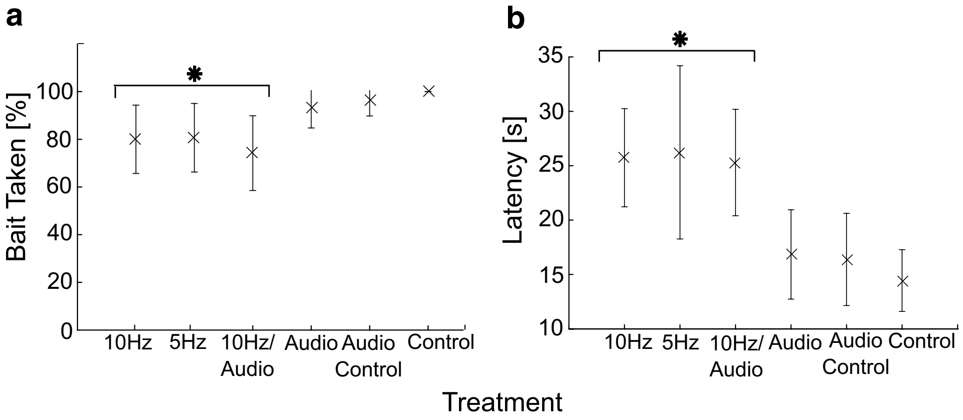

Fig. 4 Responses of *Hemiscyllium ocellatum* to the stimulus treatments: **a** mean percentage of trials in which the bait was taken for each of the stimulus treatments and **b** mean latency to take the bait (in seconds) for each of the stimulus treatments. Vertical bars represent 95% confidence intervals. $n = 5$ sharks, every individual was tested six times for each of the six treatments. The asterisks indicate a significant difference ($P < 0.05$) with the control treatment

squared$_5$ = 18.53, $P = 0.002$] (Table 3). Multiple comparisons revealed that the 5 Hz strobe light, 10 Hz strobe light, and the 10 Hz light and sound combination were all significantly different to the controls. *Hemiscyllium ocellatum* took longer to take the bait during the 5 Hz (26.0 s) strobe light, the 10 Hz (26.0 s) strobe light, and the combined light and sound trials (25 s) compared to the control trial (14 s) (Fig. 4b) (Gaussian mixed model (identity), $n = 5$, $df = 5$, Chi squared$_5$ = 28.55, $P < 0.001$). The sound treatment and both the inaudible sound control and no-light/no-sound controls were not significantly different in terms of the number of times that the bait was taken or the latency for the bait to be taken (Table 3).

Field experiments on white sharks

A total of 25 individual white sharks (*C. carcharias)* interacted with the rig a total of 242 times. Most interactions consisted of approaches (151 approaches). Sharks interacted with the bait on 72 occasions (bite bait = 17, bump bait = 31, and taste bait = 24) and interacted with the rig on 19 occasions (touch rig = 14 and bump sensory stimulus device = 5). The number of interactions for a single individual ranged from 1 to 39 events. There was no significant difference in the behavioural scores (i.e., interaction levels) between treatments (Table 4). No effect of the treatments was found when only interactions with the bait or the rig were considered (i.e., not considering approaches). We present the full data set (i.e., including approaches), as the deterrent effect of the sensory stimuli presented here should not only deter sharks upon a direct feeding incentive but also as they pass by in close proximity. There was no significant difference in the amount of time *C. carcharias* spent in the field of view (time on screen), regardless of treatment (Table 4, Fig. 5). As sound alone had no effect on the two species held in captivity in the lab as well as no effect on *C. carcharias* in the wild, we performed an alternative analysis by pooling the sound and control data, which we then

Table 3 Results showing the levels of significance found from the mixed models for *Hemiscyllium ocellatum*($n = 5$) based on 36 interactions for each individual

Response	Effect	*df*	Chi-sq	*P* value
Bait taken	+ Treatment	5	18.53	0.002*
Comparison	EST	SE	*Z*	*P* value
Control vs 5 Hz light	0.20	0.08	2.35	0.02*
Control vs 10 Hz light	0.19	0.08	2.23	0.03*
Control vs audio	0.03	0.01	0.30	077
Control vs light and audio	0.23	0.09	2.37	0.02*
Control vs audio control	0.03	0.10	0.38	0.71
Response	Effect	*df*	Chi-sq	*P* value
Time to take bait	+ Treatment	5	28.55	< 0.001*
Comparison	EST	SE	*Z*	*P* value
Control vs 5 Hz light	− 0.26	0.07	− 3.64	< 0.001*
Control vs 10 Hz light	− 0.23	0.07	− 3.22	0.001*
Control vs audio	− 0.06	0.07	− 0.84	0.40
Control vs light and audio	0.22	0.07	3.14	0.002*
Control vs audio control	0.03	0.07	0.41	0.68

Degrees of freedom (*df*), Chi-squared values (Chi-sq), and *P* values. The multiple comparison for the mixed models is also presented. Estimates of regression coefficients (EST), standard error (SE), *Z* value (*Z*) and *P* values are presented

* Indicates statistically significant results

Table 4 Results showing the levels of significance found from the mixed models for *Carcharodon carcharias*($n = 25$), based on 242 interactions

Response	Effect	*df*	Chi-sq	*P* value
Time on screen	+ Treatment	3	5.54	0.13
Time on screen	+ Treatment[a]	2	5.54	0.06
Comparison	EST	SE	*Z*	*P* value
Control vs light	0.07	0.04	1.74	0.09
Control vs light and audio	− 0.08	0.04	− 2.01	0.05*
Response	Effect	*df*	Chi-sq	*P* value
Behavioural scores	+ Treatment	3	224.7	0.63
Behavioural scores	+ Individual	24	45.01	0.005*

Degrees of freedom (*df*), Chi-squared values (Chi-sq), and *P* values. The multiple comparison for the mixed models is also presented. Estimates of regression coefficients (EST), standard error (SE), *Z* value (*Z*), and *P* values are presented

* Indicates statistically significant results

[a] Audio and control were pooled

analysed with a mixed model and multiple comparisons. The amount of time *C. carcharias* spent on screen was then significantly different between the light and sound combined treatment and the pooled sound and control data (Table 4) (multiple comparison, $n = 25$, $df = 2$, $z = -2.01$, $P = 0.05$). The pooling of the control and sound trials provided sufficient data to expose the small variation in the time that sharks spent on screen in the combined light and sound treatment. However, this difference only represents 0.8 s (Fig. 5). *Carcharodon carcharias* spent, on average, 3.0 s on screen during the combined light and sound treatment, compared to 3.8 s during the control. No further differences in *C. carcharias* behaviour were detected between treatments.

Different individuals of *C. carcharias* showed significantly different behaviours when interacting with the rigs (mixed model, $n = 25$, Chi squared$_{24} = 45.01$, $P = 0.005$) (Table 4). Four of the 25 individuals presented behaviours with significantly greater interactions with the rigs than the

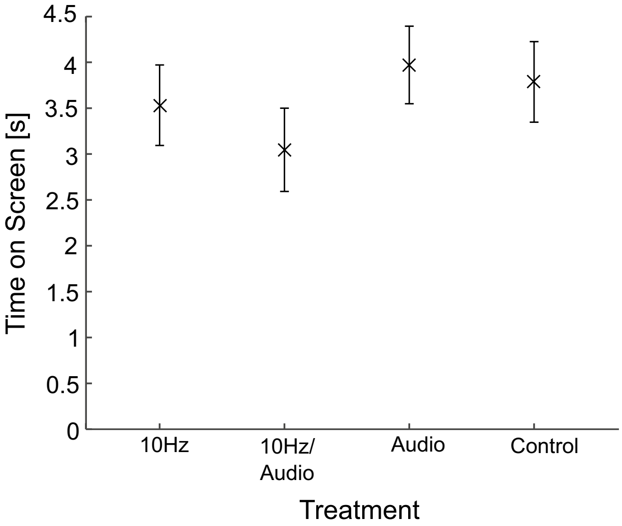

Fig. 5 Mean time *Carcharodon carcharias* spent in the field of view on the camera (time on screen) for each of the stimulus treatments. Vertical bars represent 95% confidence intervals. $n = 25$ sharks, 52 trials: 16 controls, 11 strobe lights 10 Hz, 13 Audio, 12 Strobe light 10 Hz/Audio

other sharks (based on higher classification scores). However, by removing these sharks from the analysis, there was still no significant effect of the sensory treatments on shark behaviour, even when behaviours 1–3 and 4–6 were pooled.

Discussion

We investigated the effect of strobe lights and an artificial sound on the motivation and latency of sharks to take or interact with bait. We presented strobe lights on their own, an artificial sound on its own, and strobe lights and sound in combination to benthic sharks in captivity (*H. portusjacksoni* and *H. ocellatum*) and white sharks in the wild (*C. carcharias*). We found that (1) intense strobe lights deterred some sharks from the bait/rig, but not all tested species were affected; (2) artificial sound stimuli did not significantly deter sharks from the bait or baited rig; and (3) the combination of strobe lights and artificial sound did not amplify the deterrent effects for benthic sharks in captivity, but may delay interactions with the baited rig for white sharks in the field.

Both *H. portusjacksoni* and *H. ocellatum* exhibited aversive behaviour during the strobe light treatments in captivity. For *H. portusjacksoni*, the strobe lights reduced the occurrence of the bait being taken by almost 50%. It was often observed that sharks stopped swimming as soon as the strobe lights were turned on and would resume swimming only when the lights were turned off again. Captive *H. ocellatum* also took the bait less often during the 5 Hz strobe light, 10 Hz strobe light, and combined light and sound trials; however, the bait was still taken in 74% of the strobe light trials. The strobe light treatment also delayed *H. ocellatum* from taking the bait, with sharks taking 11 s longer than in the control treatments to take the bait. Thus, the strobe lights indicate some potential as a deterrent, although the degree of the effect was not consistent across species.

The white shark, *C. carcharias,* is one of the main species of sharks responsible for human fatalities (Baldridge 1996; West 2011). However, in this study, none of the stimuli reduced the interactions between *C. carcharias* and the bait canister, as sharks still bit the bait in all treatments. *Carcharodon carcharias* spent less time around the light and sound combined treatment, although this (albeit significant) difference was only 0.8 s. The current design of the strobe lights, the sound stimulus, or the combination of the strobe light and sound stimuli would not be recommended as a form of shark deterrent for reducing the frequency or severity of human–shark interactions.

Species-specific effects of the strobe lights

The difference in the effect of the strobe light between species may be related to differences in their visual systems and/or trophic level. Rod photoreceptors within the retina are more sensitive to light than cones and readily saturate in bright light, whereas cones are not easily saturated (Campbell et al. 2005; Land and Nilsson 2012). It is assumed that species with more rods relative to cones are adapted for lower light conditions, such as in nocturnal or deep-sea species (Litherland and Collin 2008; Land and Nilsson 2012). *Heterodontus portusjacksoni,* which displayed the strongest responses to the strobe lights, is the only species of the three tested that potentially has a rod-only retina (Schieber et al. 2012). It is possible that the bright strobe lights may have saturated the rod photoreceptors, leaving *H. portusjacksoni* momentarily blinded. In contrast*, H. ocellatum* possesses both rods and cones and has a peak rod-to-cone ratio of 18:1 (Litherland and Collin 2008). This species was comparatively less affected by the strobe lights than *H. portusjacksoni*. Although both *H. portusjacksoni* and *H. ocellatum* are predominantly nocturnal (Last and Stevens 2009; Froese and Pauly 2013), *H. ocellatum* may be less sensitive to strobe lights, because they occupy tropical environments which are often brighter (McFarland 1990; Froese and Pauly 2013). The strobe lights may limit their vision by saturating a large number of rod photoreceptors, but still leave functionally significant numbers of cones, enabling this species to navigate and/or find the bait within the experimental tank.

Carcharodon carcharias showed no meaningful behavioural difference in response to the different sensory treatments. This species has a relatively low peak rod-to-cone ratio of 5:1 (Gruber and Cohen 1985) and is, therefore, likely to be less sensitive to bright flashing light than both *H. portusjacksoni* and *H. ocellatum*. Although the strobe light may have partially affected their rod-based vision, it possibly was not bright enough to cause any significant changes in the behaviour of *C. carcharias*. In designing light-based deterrents for personal use, there are practical limitations on the size of the light-emitting surface and also the size of the batteries that power them. These physical constraints in turn limit the maximum light intensity of the deterrent and may affect the efficacy of the deterrent. Although the strobe light used may have partially affected their rod-based vision, it was possibly not bright enough to cause any significant changes in the behaviour of *C. carcharias*. The experimental design for this study established a 2 m periphery from the rig for a trial to start. The strobe light intensity may have not been strong enough at this distance; reducing the distance or increasing the power of the light may be more effective at deterring *C. carcharias*. In addition, the difference of ambient lighting in the laboratory and in the field may have influenced the effect of the strobe lights. The strobe lights may have a greater effect in low light environments, such as in turbid water or at night (McIninch and Hocutt 1987; Sager et al. 1987). Similarly, different results may be expected without olfactory cues (i.e., bait) influencing the behaviour of individuals. However, a shark deterrent should be efficient under a variety of conditions and not strictly limited to one environmental situation.

The strobing frequency of the light may also influence the sharks' behavioural response. Animals with rod-dominated retinas typically have slower temporal resolution (Land and Nilsson 2012). *Heterodontus portusjacksoni*, which has a rod-only retina (Schieber et al. 2012), has a slower temporal resolution than *H. ocellatum* (critical flicker fusion frequency of 28 vs 40 Hz, respectively) (Ryan et al. 2017) and showed the strongest behavioural response to the strobe light. Thus, the frequency of the strobe light relative to the temporal sensitivity of the eye of this species may affect the strength of the behavioural response. Although temporal resolution has not been measured in *C. carcharias*, they are likely to have greater temporal resolution than both *H. portusjacksoni* and *H. ocellatum* as a result of their higher rod-to-cone ratio and their diurnal lifestyle (McComb et al. 2010; Land and Nilsson 2012; Kalinoski et al. 2014; Ryan et al. 2017), as well as their capacity to maintain elevated body and retinal temperature (Block and Carey 1985; Fritsches et al. 2005). Therefore, a faster strobe frequency (and possibly intensity) delivered during crepuscular times of the day may have a greater impact on the behaviour of *C. carcharias*. In addition, temporal resolution is known to be affected by the retinal temperature (Gacic et al. 2015), and although the frequency of the strobe lights was chosen to be in the correct range and resolvable for the species (McComb et al. 2010; Kalinoski et al. 2014; Ryan et al. 2017), the temperature may have influenced the effects of the lights on *C. carcharias*, even if as an endodermic species, their retinal temperature may be a few degrees higher than ambient (Block and Carey 1985). As we gain further knowledge on the temporal resolution of sharks, strobe lights may be better designed to specifically suit the visual system of white sharks.

The different responses exhibited that each of the three species of sharks to the strobe lights may also reflect their size, trophic level, and motivation to feed in terms of the perceived predatory threat that the strobe light posed. *Carcharodon carcharias* are large-bodied [animals found in Mossel Bay dominated by sharks 275–325 cm (Kock and Johnson 2006)], often considered to be a high trophic level species with few natural predators (Compagno 1990; Last and Stevens 2009; Froese and Pauly 2013), which has led them to be commonly referred to as an 'inquisitive' or 'curious' species (Peschak and Scholl 2006; Hammerschlag et al. 2012). Thus, they may even be attracted to, rather than deterred from, the novel stimuli. In contrast, the two benthic species tested were smaller (individuals tested ranged from 20 to 49 cm), lower trophic level species (Compagno 1990; Last and Stevens 2009; Froese and Pauly 2013), potentially making them more vulnerable to predators and thus more cautious around novel sensory stimuli. Research on a greater range of species performed in different light environments is required to better understand the reasons behind the species-specific differences in the effect of the strobe lights.

The findings of this investigation suggest that the deterrent effect of strobe lights is likely to be species-specific, and may not achieve a deterrent effect to sufficiently protect ocean users from negative interactions with sharks. However, the behavioural responses observed in the presence of strobe lights suggest that there may be potential applications for this technology to create species-specific bycatch mitigation devices. Lights are used in a number of fishing practices to either increase catch (Clarke and Pascoe 1985; Pascoe 1990; Wiebe et al. 2004) or reduce bycatch (Southwood et al. 2008; Wang et al. 2010), although how these light-dependent strategies may affect sharks is unknown. Further research on the response of a range of shark species to different strobe lights under a range of light conditions may provide further insights into this phenomenon.

Sound as a sensory disturbance

The artificial sound alone did not have any direct effect on the percentage of bait taken or the time spent in the arena, for any of the three species tested. This result may be explained by a number of factors. First, the speaker might have lacked the capacity to produce enough energy (particle motion) in the low frequencies that sharks are known to respond to (Corwin 1989; Popper and Fay 1997; Myrberg 2001; Hueter et al. 2004; Gardiner et al. 2012). Sounds with more low-frequency components (< 400 Hz), at higher intensities, might have induced a greater response. Underwater low-frequency transducers still represent a technological challenge: a transducer able to produce large particle motion levels at very low frequencies would be both very large and expensive. Currently, the sound levels (i.e., particle acceleration) required to elicit a behavioural response by sharks are unknown. Furthermore, different species might have different acoustic thresholds and sensitivities, causing them to respond differently towards auditory stimuli (Kritzler and Wood 1961; Banner 1972; Kelly and Nelson 1975; Bullock and Corwin 1979; Kenyon et al. 1998; Casper et al. 2003; Casper and Mann 2006, 2007a, b). For example, the nurse shark (*G. cirratum*) has a higher sensitivity (threshold at peak sensitivity 300 Hz is about 82 dB re 1 $\mu m/s^2$) than the yellow stingray (*U. jamaicensis*) (threshold at peak sensitivity 500 Hz is 92 dB re 1 $\mu m/s^2$) (Casper 2006). It is still unclear as to which ecological factors are driving these differences and how much sharks rely on their auditory modality. In addition, the acoustic field in laboratory settings (tanks and aquaria) is considerably different from the acoustic field that occurs in the animal's natural environment, and it is, therefore, very difficult to reproduce the same sound stimulus and properly compare the results of both captive and field experiments (Parvulescu 1967; Rogers et al. 2016). Finally, the particular sound played may not have been recognized as either an attractive or repulsive cue in the three species tested. More research focusing on auditory sensitivity and frequency discrimination of sharks in a range of species would allow a better understanding of the behaviour of these animals towards sounds and facilitate the design of auditory-based deterrents.

Multisensory stimulation and individual differences in white shark behaviour

The addition of the sound treatment may have enhanced the effect of the strobe light. In trials that combined the two treatments, *C. carcharias* spent less time in the field of view (0.8 s, 21% less than the control), although ultimately none of the light/sound treatments significantly deterred the sharks entirely from interacting with the bait. A combination of sensory stimuli might be the most effective strategy to control shark behaviour. In addition, a multisensory approach may be more effective in different species, as there are interspecific differences in the hierarchy of sensory cues used during predation (Gardiner et al. 2014).

Four individual *C. carcharias* displayed significantly different behaviours than the other 21 individuals. Although these observations are based on the individual responses to this particular experimental design and cannot be empirically extrapolated to all contexts, these results support the notion that there is intraspecific variation in behaviour between sharks (Wearmouth and Sims 2008; Jacoby et al. 2012; Huveneers et al. 2013a). Many diving operators and field researchers have noted that some *C. carcharias* individuals can be recognized by their actions and responses to stimuli (e.g., bait rope, shark cage, and outboard motor). Ontogenetic changes in the peripheral and central nervous systems in cartilaginous fishes (Lisney et al. 2007, 2017) suggest that the relative importance of different sensory systems can change as the animal ages (Jacoby et al. 2012) and between sexes (Wearmouth and Sims 2008; Kempster et al. 2014), which could further drive these behavioural differences. In the present study on *C. carcharias*, it is possible that four 'bolder' individuals were encountered (Sih et al. 2004; Byrnes and Brown 2016), or individuals of different ages/sex than the other sharks, which resulted in a higher degree of proactive action towards the bait despite the aversive sensory stimuli present. This highlights the importance of taking into account individual variations when testing shark mitigation devices.

Conclusion

Evidence from the present study does not support the use of strobe lights or loud underwater sounds as effective deterrents to prevent negative interactions between *C. carcharias* and humans. However, the strobe lights show potential application in reducing bycatch of certain shark species if fitted to the appropriate fishing gear. Although the sound alone in this study had no effect on the behaviour of *H. portusjacksoni*, *H. ocellatum,* and *C. carcharias*, we emphasise that more research is required on the auditory abilities of sharks to fully assess the effectiveness of acoustic deterrents across cartilaginous fishes.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical standards All applicable international, national, and/or institutional guidelines for the care and use of the animals were followed. This article does not contain any studies with human participants performed by any of the authors.

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