

REVIEW

Sharks senses and shark repellents

Nathan S. HART and Shaun P. COLLIN

School of Animal Biology and the Oceans Institute, The University of Western Australia, Crawley, Perth, Australia

Abstract

Despite over 70 years of research on shark repellents, few practical and reliable solutions to prevent shark attacks on humans or reduce shark bycatch and depredation in commercial fisheries have been developed. In large part, this deficiency stems from a lack of fundamental knowledge of the sensory cues that drive predatory behavior in sharks. However, the widespread use of shark repellents is also hampered by the physical constraints and technical or logistical difficulties of deploying substances or devices in an open-water marine environment to prevent an unpredictable interaction with a complex animal. Here, we summarize the key attributes of the various sensory systems of sharks and highlight residual knowledge gaps that are relevant to the development of effective shark repellents. We also review the most recent advances in shark repellent technology within the broader historical context of research on shark repellents and shark sensory systems. We conclude with suggestions for future research that may enhance the efficacy of shark repellent devices, in particular, the continued need for basic research on shark sensory biology and the use of a multi-sensory approach when developing or deploying shark repellent technology.

Key words: sensory biology, sharks, shark depredation, shark repellents

INTRODUCTION

“Many shark experts believe that an important answer to the shark hazard will be a greater appreciation of the shark by man ... when more men learn to savour its flesh and more men are shod with its leather, the shark will be regarded as an asset and fished for more

extensively, and in doing so, as meshing has proved, the hazard will be greatly reduced. How fortunate that this solution can not only unveil an important untapped natural resource, but also reduce the numbers and therefore the dangers from sharks.”

(Gilbert & Gilbert 1973; pp. 78–79)

Perry and Claire Gilbert’s statement was made at a time when sharks were largely considered a nuisance by commercial fishermen and were not yet hunted on an industrial scale for their flesh, skin, cartilage, jaws, liver oil and fins. Moreover, the future ecological impacts of the massive quantities of shark bycatch that occur in present day commercial fisheries (approximately 32 million sharks annually [Worm *et al.* 2013]) were not appreciated. Rather, the focus of research on shark re-

Correspondence: Nathan S. Hart, School of Animal Biology (M317) and the Oceans Institute, The University of Western Australia, Crawley, Perth WA6009, Australia.
Email: nathan.hart@uwa.edu.au

pellents was the protection of human life. Today, sharks are increasingly seen as vulnerable to overexploitation due to their slow growth rate, late age of maturity, long gestation period and low reproductive output. Even one of the most prolific and resilient of shark species, the blue shark (*Prionace glauca* Linnaeus, 1758), which accounts for at least 15% (approximately 11 million sharks) of the present day total annual shark catch (approximately 63 million sharks) is already caught at a rate beyond its likely maximum sustainable yield (Clarke *et al.* 2006; Worm *et al.* 2013).

While the need for cheap and effective shark repellents for use by divers, swimmers, surfers and other water sports enthusiasts remains strong, the need to develop ways to reduce shark bycatch and depredation in commercial fisheries is now equally important. These two goals may require different configurations of the same technology, but both are based on the basic neurobiology of the shark's sensory systems and their influence on behavior. A spate of fatal shark bites in Australia during 2011–2012 has renewed interest in the development of shark repellents to protect human life, but other discoveries in recent years have generated new possibilities for bycatch reduction devices that protect the lives of sharks. Therefore, it is timely to review the progress that has been made within the broader context of research on shark repellents over the past 70 years (such that the wheel is not reinvented) and to identify future directions for the development of shark repellents and for filling the gaps in our understanding of the sensory abilities of sharks, on which the success of any new repellent technology depends.

AN OVERVIEW OF SHARK SENSORY ABILITIES

Sharks possess an impressive array of highly specialized sensory systems that have been shaped by over 400 million years of evolution. Each sensory modality allows the shark to detect and respond to a different set of biotic and/or abiotic stimuli within its immediate environment and over different spatial scales. The possession of multiple functionally distinct sensory systems not only provides redundancy when conditions are such that one or more senses are unusable (e.g. electroreception may be used instead of vision to find prey in turbid water or at night), but also increases the chances that a given stimulus or object will be detected and/or correctly identified (Stein *et al.* 2005).

A detailed knowledge of the sensory biology of sharks is essential for understanding the ways in which sharks interpret the world around them and, therefore, how their behavior can be manipulated. In this section, we provide a condensed overview of the various sensory systems of sharks with greatest emphasis placed on the capabilities and thresholds of each sensory modality, rather than dwelling on functional mechanisms, as detection abilities are most pertinent for the development of shark repellents.

Vision

As a group, sharks have well-developed eyes and display interspecific variations in eye structure that reflect adaptations for vision in different photic environments, ranging from the darkness of the deep sea to brightly lit surface waters (for recent reviews, see Hart *et al.* 2006; Lisney *et al.* 2012). Many sharks, especially those inhabiting shallow and brightly lit waters, have large eyes capable of providing a detailed image of their surroundings (Lisney & Collin 2007). Their visual acuity (spatial resolving power) is comparable to that of other marine vertebrates, such as teleost fishes (Collin & Pettigrew 1989; Fritsches *et al.* 2003) and marine mammals (Mass & Supin 2002; Hanke *et al.* 2009), and ranges from approximately 2 to 11 cycles per degree (Hueter 1990; Lisney & Collin 2008; Theiss *et al.* 2010). The lateral position of the eyes in the head affords a cyclopean visual field of 360° in the vertical plane and between 308 and 338° in the horizontal plane, with varying degrees of binocular overlap in the dorsal (4–9°), ventral (6–15°) and frontal visual axes (10–48°) (Harris 1965; McComb *et al.* 2009).

With the exception of some deep-water species that are thought to possess an all-rod retina (e.g. Bozzano *et al.* 2001), most sharks studied to date have a duplex retina containing both rod and cone photoreceptors and, therefore, are capable of using vision over a wide range of light intensities (Schaper 1899; Gruber *et al.* 1975; Litherland & Collin 2008; Schieber *et al.* 2012). As with other vertebrates (Walls 1963), the relative proportions of rod and cone photoreceptors in the retina of a given species of shark tends to reflect the relative intensity of light in its habitat, with the highly sensitive rod photoreceptors far more abundant in species that are predominantly active at night or in deep water compared to those that are shallow dwelling and more diurnal in habit (Hart *et al.* 2006).

The wavelength of peak sensitivity (λ_{\max}) of the visual pigment expressed in the rod photoreceptors rang-

es from 472 nm in the Portuguese dogfish (*Centroscymnus coelolepis* Barbosa du Bocage & de Brito Capello, 1864) (Denton & Shaw 1963) to 518 nm in the bull shark (*Carcharhinus leucas* Müller & Henle, 1839) (Hart *et al.* 2011). As with teleost fishes (Denton & Warren 1957; Munz 1958) and marine mammals (Lythgoe & Dartnall 1970; McFarland 1971), shark species that inhabit deeper water tend to have rod pigment λ_{\max} values that are shifted toward shorter wavelengths to match the restricted spectrum of light available at depth (Crescitelli *et al.* 1985; Crescitelli 1990).

In addition to a single spectral type of rod, only one spectral type of cone visual pigment has been measured in sharks: the λ_{\max} of the cone pigment ranges from 532 nm in the blacktip shark (*Carcharhinus limbatus* Müller & Henle, 1839) to 561 nm in the ornate wobbegong shark (*Orectolobus ornatus* De Vis, 1883) (Hart *et al.* 2011; Theiss *et al.* 2012b). Although visual pigments have been characterized in very few of the more than 500 described species of shark (Last & Stevens 2009), based on the diversity of the species studied it seems likely that cone monochromacy is widespread throughout the taxon. This is perhaps surprising given the presence of multiple spectral types of cone in the retinas of rays (Hart *et al.* 2004; Theiss *et al.* 2007; Van-Eyk *et al.* 2011) that inhabit similar photic environments and at least 1 species of chimaera (Davies *et al.* 2009).

While cone monochromacy on land is rare, it appears to be relatively common in the marine environment: whales, dolphins and seals also possess only a single medium-wavelength-sensitive cone pigment (Croganale *et al.* 1998; Peichl *et al.* 2001; Newman & Robinson 2005). The implication for both sharks and marine mammals is that, at best, they have only a rudimentary color vision system based on the comparison of signals from rods and cones (which differ slightly in spectral sensitivity) and, at worst, lack color vision altogether. Behavioral evidence for color vision in both sharks (Gruber 1975; Cohen 1980) and marine mammals is equivocal (Madsen 1976; Wartzok & McCormick 1978; Griebel & Schmid 1992, 2002). However, it seems likely that for both taxa, brightness contrast rather than color is likely to play a primary role in the detection and discrimination of ecologically relevant objects, such as predators, prey and conspecifics.

In addition to brightness contrast, the visual detection of motion is probably critical to many shark behaviors. Unfortunately, very little is known about motion vision in elasmobranchs. Sharks display compensatory eye movements during swimming that serve to stabilize the

image on the retina as the head oscillates from side-to-side, but this vestibulo-ocular reflex is driven by inertial motion detectors in the inner ear rather than visual input (Harris 1965; Paulin & Montgomery 1986). However, the accessory optic system of sharks, which also aids in gaze stabilization by generating eye movements that correct for self-motion, is driven by visual input (Masseck & Hoffmann 2008). Although only a single species of shark has been studied (the small-spotted catshark, *Scyliorhinus canicula* Linnaeus, 1758), it appears that the accessory optic system of sharks is atypical. In contrast to teleosts and tetrapods, the retinorecipient direction-selective neurons in the pretectum that detect large-field image motion caused by body rotations are broadly tuned in terms of preferred direction, are not inhibited by motion in the opposite (null) direction, and do not translate onto a vestibular or extra-ocular muscle reference frame (Masseck & Hoffmann 2008, 2009). The behavioral significance of this unusual arrangement is unclear.

There are, as yet, no direct studies on the ability of sharks to detect small object motion, which would be relevant to the detection of a prey item against the background (Eckert & Zeil 2001). However, the ability to detect temporal changes in image brightness alone is often used as a proxy for the ability to detect object motion (e.g. Fritsches *et al.* 2005), largely because visual motion cues are derived from spatiotemporally correlated variations in retinal image brightness (Reichardt 1961; Clifford & Ibbotson 2002). One measure of temporal resolution is the critical flicker fusion frequency (cFFF), which is the frequency at which a flickering light stimulus appears continuous to the observer. Photopic (i.e. light-adapted) cFFFs reported for various shark species range from 10 to 36 Hz (O'Gower & Mathewson 1967; McFarland 1990; McComb *et al.* 2010), which falls at the bottom end of the range measured in teleost fishes (McFarland & Loew 1983; Horodysky *et al.* 2008) but implies that they are likely to be able to detect reasonably fast object motion. Studies in a range of vertebrates have established that the frequency at which the visual system is most sensitive to changes in image brightness is typically around 15% of the photopic cFFF (McFarland & Loew 1983), which would suggest that, although capable of responding to higher rates, sharks are most sensitive to flicker in the 1–5 Hz range.

Hearing

The inner ears of shark are similar in morphology to those of other gnathostomes and comprise a membra-

nous labyrinth consisting of 3 orthogonally arranged, fluid-filled semicircular canals and 3 otolithic organs: the sacculus, utriculus and lagena (Retzius 1881; Maisey 2001). Sensory hair cells that respond to mechanical deflection with graded electrical potentials (Hudspeth & Corey 1977) are located on a ridge (crista ampullaris) in a swelling (ampulla) at the base of each semicircular canal and in a sensory epithelium (macula) on the wall of each otolithic organ (Tester *et al.* 1972). An additional sensory end organ, the macula neglecta, is located on the wall of the posterior canal duct (Corwin 1977). The hair bundles of sensory cells in the ampullae, macula neglecta and otolithic organs are embedded within a gelatinous mucopolysaccharide matrix or 'cupula'; in the case of the otolithic organs, the matrix also contains an aggregation of endogenous calcareous mineral granules (Carlström 1963; Tester *et al.* 1972) and/or exogenous sand particles (Lychakov *et al.* 2000; Mills *et al.* 2011) that form a denser otoconial mass.

Unlike many bony fishes, sharks do not possess swim bladders or other structures that can convert acoustic pressure into a displacement stimulus and are, therefore, thought to be able to respond only to the particle motion component of sound (acceleration, velocity or displacement) and not the pressure component, although this remains to be demonstrated conclusively (Nelson 1967; Gardiner *et al.* 2012). The sensory structures of the inner ear function as accelerometers that respond to both self-induced motion and displacements produced by external sources. As in other vertebrates, the semicircular canals are responsible for detecting rotational and translational movements of the head, and the otolithic organs detect linear acceleration caused by self-motion and the action of gravity. When a shark moves its head, the inertial lag of the endolymph filling the semicircular canals deflects the cupula of the crista ampullaris and, consequently, the hair bundles of the underlying sensory epithelium (Popper *et al.* 2003). Similarly, the inertial lag of the otoconial mass provides a stimulus for the macular hair cells under the effects of gravity or head movements. Thus, the inner ear is primarily and evolutionarily a motion detector, and is an essential part of the vestibular system that controls posture and balance (Ladich & Popper 2004).

Sound detection in elasmobranchs is thought to occur through two mechanisms, one mediated by the otolithic organs and the other involving the macula neglecta (Lowenstein & Roberts 1951; Fay *et al.* 1974; Corwin 1981). The first mechanism, the so-called otolithic channel, arises because of a difference in the density of the

otoconial mass compared to the rest of the shark's body. A shark exposed to a sound wave will move in concert with the surrounding water because its body has a similar density (and the shark is small relative to the wavelength of the sound wave) but the more dense otoconial mass will accelerate more slowly than the rest of the shark (Hanson *et al.* 1990; Hunt 1992; Bretschneider *et al.* 2001). This inertial lag will be transmitted to the macula via the otolithic membrane and cause the hair bundles to bend (Fay & Popper 1974). The second, and largely unproven, mechanism, the non-otolithic channel, relies on the conduction of particle motion into the posterior canal duct through a membrane-covered, fluid-filled opening (the fenestra ovalis) located at the base of a depression (the parietal fossa) in the dorsal chondrocranium (Daniel 1934; Lowenstein & Roberts 1951). Sound waves, particularly those coming from above and in front of the shark, would be transmitted to the endolymph within the posterior dorsal canal and cause local displacements of the cupula of the macula neglecta (Fay *et al.* 1974; Corwin 1977).

Hearing abilities are typically defined in terms of frequency range, threshold detection level (i.e. sensitivity) and directionality. Sharks are able to hear sounds up to approximately 1000 Hz and are most sensitive to frequencies below approximately 100 Hz (Nelson 1967; Popper & Fay 1977; Casper & Mann 2006, 2007a,b, 2009). In an open-water measurement of hearing thresholds in the Atlantic sharpnose shark (*Rhizoprionodon terraenovae* Richardson, 1836), the highest sensitivity to particle motion was recorded at 20 Hz, which was the lowest frequency tested (Casper & Mann 2009). As a group, sharks appear to be less sensitive to sound at all frequencies compared to teleosts fishes, either due to the lack of any pressure-to-displacement transduction mechanism (e.g. swim bladder and Weberian ossicles) or because their gelatinous otoconial masses are less dense than the solid otoliths of bony fishes and, therefore, less sensitive to linear motion and acceleration (Casper & Mann 2007a). Sharks are able to locate a sound source with considerable accuracy (Nelson 1967). However, while it is known that some sharks have omnidirectional hearing (Casper & Mann 2007b), the neural mechanisms by which sharks locate sound sources remain to be determined (Gardiner *et al.* 2012).

Lateral line

Like the inner ear, the lateral line is a mechanosensory structure capable of detecting particle motion and, therefore, may respond to mechanical disturbances pro-

duced by both auditory and non-auditory hydrodynamic stimuli (Parker 1904; Dijkgraaf 1963). In addition to low frequency sounds, the lateral line is used to detect the vibrations given off by prey, predators and conspecifics moving through the water, as well as the direction and velocity of water currents (Boord & Campbell 1977; Montgomery *et al.* 1995). Although the stimulus characteristics and frequency response of the lateral line system overlap with those of the auditory system, the lateral line is a short-distance sensory system that responds to low frequency water movements occurring within a few body lengths of the animal (Kalmijn 1989).

The end organs of the lateral line (neuromasts) closely resemble the vestibular and auditory receptors of the inner ear (Hama & Yamada 1977; Blaxter 1987). Each neuromast contains populations of sensory hair cells with differing directional sensitivities determined by the orientation of the stereocilia and kinocilia on their apical surface (Maruska 2001). The hair bundles are embedded within a gelatinous cupula that is displaced relative to the underlying sensory epithelium by movement of the surrounding fluid (viscous drag) and causes bending of the hair cells (Tester & Kendall 1968; Maruska 2001).

Neuromasts are located in sub-epidermal canals or superficially in grooves or pits between modified denticles (Johnson 1917; Tester & Nelson 1967; Peach & Marshall 2009; Theiss *et al.* 2012a). There are two types of canal system in sharks, one that has numerous pores connecting the canals to the surface of the skin via short tubules, and another that lacks pores and is sealed from the external environment (Maruska 2001; Theiss *et al.* 2012a). The non-pored canals do not respond to external hydrodynamic stimuli directly but instead respond to movement of fluid within the canals created by displacement of the skin (Maruska & Tricas 2004). Neuromasts in the non-pored canals are highly sensitive to low frequency (<10 Hz) displacements and are thought to function as tactile receptors during foraging and feeding behaviors because the non-pored canals are located close to the mouth (Maruska & Tricas 2004).

The pored canals of the shark lateral line system more closely resemble those of teleost fishes, and the neuromasts lining the canal lumen function as accelerometers that detect the pressure difference between adjacent pores (Denton & Gray 1983; Blaxter 1987). All canal neuromasts are low-frequency (1–200 Hz) receptors (Dijkgraaf 1963) and in elasmobranchs have greatest sensitivity in the range of 20–30 Hz (Maruska & Tricas 2004). Although there is as yet little direct evidence,

the pored canal system in sharks is likely to mediate similar behavioral functions (predator avoidance, prey detection and hydrodynamic imaging) to those in the closely related rays and also teleost fishes, especially in relation to prey detection (Montgomery *et al.* 1995; Jordan *et al.* 2009a).

Superficial neuromasts (pit organs) are distributed predominantly over the dorsolateral surfaces of the head and trunk with additional clusters around the spiracles, anterior to the gills and ventral to the mouth (Tester & Kendall 1967; Peach & Marshall 2009). The cupula of the pit organ neuromast is exposed to water flow in the external environment to a greater or lesser degree depending on interspecific variations in the shape of the pit within which it is located and the morphology and coverage provided by the modified denticles that surround them (Peach & Marshall 2000).

The role of pit organs in shark behavior is unclear, but they may subserve a similar function to the superficial neuromasts of teleosts fishes in detecting the velocity of water flowing over the body (Montgomery *et al.* 1997) and may be involved in orientation toward water currents (rheotaxis) (Peach 2001). Rheotaxis is thought to be used by many pelagic species of shark for locating and approaching prey and may be essential for orienting to food sources and following odor plumes (Peach 2003; Gardiner & Atema 2007).

Comparative studies of the lateral line system of sharks reveals marked interspecific variations in the distribution and morphology of both the canals (position, length, branching pattern and number of pores) and the pit organs (number and position) that reflect both phylogenetic inertia and ecological adaptation (Maruska 2001; Peach & Rouse 2004; Peach & Marshall 2009; Theiss *et al.* 2012a). Thus, it is likely that there are also interspecific differences in the sensitivity, directional resolution and behavioral functions of the lateral line, although much work remains to be done in this regard (Gardiner *et al.* 2012).

Chemoreception

Olfaction (smell), gustation (taste) and the common chemical sense collectively comprise the chemosensory system in sharks. Olfaction is associated with functions such as intraspecific social interactions, communication, reproduction and the detection of food. Gustation is primarily involved with feeding and incorporates the use of taste buds to orally process and evaluate the palatability of food through direct contact, eventually leading to a decision to either swallow or reject it.

Examples of stimuli thought to elicit a neurological response in the olfactory system of sharks include the odors of prey, conspecifics (e.g. reproductive partners), predators and specific habitats. The propagation of these chemoreceptive signals through the environment and the extent to which they are encountered by a given species of shark will depend upon the swimming mode/speed of the shark, water movements and odor concentration (Parker & Sheldon 1913; Parker 1914; Johnsen & Teeter 1985). The sensitivity of the shark olfactory system is impressive: using electro-olfactography (EOG), response thresholds have been found to lie in the sub-nanomolar range for both alanine (9.2×10^{-11} M) and cysteine (8.4×10^{-10} M) and in the micromolar range for proline and serine in the scalloped hammerhead shark (*Sphyrna lewini* Griffith & Smith, 1834) (Hodgson & Mathewson 1978; Zeiske *et al.* 1986; Tricas *et al.* 2009).

The detection of water-borne olfactory cues takes place in the paired olfactory cavities. The nares open onto an olfactory rosette consisting of numerous parallel stacks of lamellae that provide a large surface area of highly sensitive olfactory epithelium (Tester 1963). Interspecific differences in the placement, size and entrance shape of the nares, the orientation of the rosette within the olfactory cavity, and the number and shape of the lamellae, likely affect the hydrodynamics of water flow over the olfactory epithelium and, therefore, olfactory sensitivity (Tester 1963; Schluessel *et al.* 2008; Rygg *et al.* 2013). Benthopelagic sharks and rays possess significantly more olfactory lamellae and a larger sensory epithelial surface area than benthic species (Schluessel *et al.* 2008; Theiss *et al.* 2009). However, when species with a greater lamellar surface area were analyzed using EOG, there was no correlation with olfactory threshold, which was relatively similar across all species tested, suggesting that the density of olfactory receptor neurons may show interspecific variation (Meredith & Kajiura 2010). At present, there are no data on the number or density of olfactory receptors or the level of convergence of the olfactory signals at either the level of the olfactory bulb or the telencephalon in any species of cartilaginous fish.

The relative size of the olfactory bulbs is widely used as a neuroanatomical proxy for olfactory capability in vertebrates, including sharks (Lisney *et al.* 2007). The largest olfactory bulbs are found in pelagic coastal/oceanic sharks, particularly migratory species such as the great white shark and tiger shark (Yopak *et al.* 2014), which suggests that olfaction may also play a critical

role in short-distance and/or long-distance navigation. In contrast, the majority of reef-associated species possess the smallest olfactory bulbs, suggesting reliance on other senses such as vision or electroreception (Hart *et al.* 2006; Collin 2012; Kempster *et al.* 2012; Lisney *et al.* 2012; Yopak *et al.* 2014).

Interestingly, the olfactory bulbs of the lemon shark (*Negaprion brevirostris* Poey, 1868), the bonnethead shark (*Sphyrna tiburo* Linnaeus, 1758) and *R. terraenovae* are divided into two distinct hemibulbs or a series of connected swellings (Northcutt 1978). In a recent study by Meredith *et al.* (2013), the olfactory bulbs were shown to receive somatotopic input from the olfactory receptor neurons (both microvillous and crypt type), making elasmobranchs unique amongst vertebrates for whom the input to the olfactory bulb is typically chemotopic. The high sensitivity to amino acids observed in sharks appears to be mediated by the microvillous type of olfactory receptor neurons (as in teleosts [Sato & Suzuki 2001; Lipschitz & Michel 2002]), although the crypt type are also thought to be involved (Hansen *et al.* 2004; Vielma *et al.* 2008). However, despite the detection of bile salts being restricted to the ciliated olfactory receptor neurons in teleost fishes (which have not thus far been identified in elasmobranchs [Theisen *et al.* 1986; Eisthen 2004; Schluessel *et al.* 2008]), Meredith *et al.* (2012) confirm electrophysiological sensitivity to bile salts in *S. tiburo*, emphasizing that there may be a number of olfactory receptor types still to be characterized in sharks.

Like olfaction, taste plays an important role in feeding, but our understanding of the mechanism and function of taste in aquatic vertebrates is still rudimentary and even less is known in sharks (Atkinson & Collin 2010). In sharks, taste buds occur within papillae covering the oral and pharyngeal epithelium of the mouth, basihyal ('tongue') and gill arches, with a morphology that appears comparable to the taste buds of teleost fishes; that is, divided into Types I, II and III (Reutter *et al.* 1974). Papillae of various sizes project from the epithelium and are dispersed over the oropharyngeal cavity, gill bars and oral valves, which suggests that biting and manipulation of prey with the jaws is important for taste assessment. Taste buds in sharks appear more numerous in benthic species and are quite scarce in pelagic species. This suggests that taste bud distribution varies according to the feeding mechanism(s) adopted, that is, pelagic species feeding predominately on larger and more active organisms bite their prey (where the area around the jaws is more efficient for tasting) and benthic

species use suction to consume soft-bodied organisms (where tastebuds are found evenly distributed throughout the oral and pharyngeal cavities) (Atkinson & Collin 2010). Oral denticles lining the oral cavity in sharks are thought to provide a form of protection against abrasion during food consumption to increase friction and grip on prey items as they are manipulated within the mouth, and may control the density of taste buds (Atkinson & Collin 2012).

Elasmobranchs appear to have relatively low densities of taste buds relative to teleost fishes. In a study of 11 species of elasmobranchs, the lowest density recorded was 4 taste buds per cm² in the oral cavity of the spotted wobbegong shark (*Orectolobus maculatus* Bonaterre, 1788) and the greatest was 159 taste buds per cm² in the pharynx of the eastern fiddler ray (*Trygonorrhina fasciata* Müller & Henle, 1841), compared to 800+ taste buds per cm² in teleosts (C. Atkinson and S. P. Collin 2011, unpubl. data). Having more papillae, however, does not necessarily equate to a greater gustatory sensitivity as the percentage area of the oropharyngeal cavity covered by papillae was lowest (0.9%) in the sharptooth lemon shark (*Negaprion acutidens* Rüppell, 1837) and highest (2.9%) in the blue-spotted mask ray (*Neotrygon kuhlii* Müller & Henle, 1841) (C. Atkinson and S. P. Collin 2011, unpubl. data). Benthic sharks possess between 1350 and 2000 taste papillae; more pelagic species have between 9250 and 11 900 taste papillae (C. Atkinson and S. P. Collin 2011, unpubl. data).

Solitary chemosensory cells also populate the taste papillae of sharks. These receptors do not appear to aggregate in a bundle or bud, and it is unclear whether this type of gustatory organ is independently innervated (Fahrenholz 1915; Whitear & Moate 1994). The innervation of the axonless sensory cells of the taste buds in sharks is also not well understood (Finger 1997; Reutter *et al.* 2000; Finger 2007). When taste substances stimulate these cells in teleost fishes, information is transmitted to the central nervous system via the cranial nerves VII (facial nerve), IX (glossopharyngeal nerve) and X (vagal nerve) (Reutter *et al.* 2000). In teleosts, the facial nerve supplies the external taste buds on the barbels and lips, fins and body surface, and oral taste buds of the rostral palate, whereas the vagal nerve innervates most of the orobranchial taste buds; the glossopharyngeal nerve plays a minor role in gustatory supply to the oral cavity (Finger 1988; Laverack 1988; Reutter 1992; Kasumyan & Døving 2003). Further research is needed to investigate the gustatory input to the central nervous system via these three cranial nerves, especially in

light of the fact that no taste papillae have been identified over the external surface of the skin in sharks.

Electroreception

Sharks have specialized receptors that enable them to detect weak electrical potentials generated by other animals and inanimate objects (Murray 1962; Kalmijn 1982). Sharks use their electric sense primarily to locate and capture prey (Kalmijn 1971; Tricas 1982) and avoid predators (Peters & Evers 1985; Kempster *et al.* 2013b). They may also be able to detect the weak electrical fields induced in the surrounding water currents or their own bodies as they move through the Earth's magnetic field and use this information for orientation/navigation (Kalmijn 1978; Paulin 1995).

Shark electroreceptors (ampullae of Lorenzini) are of the ampullary type (Andres & von Düring 1988) and develop from lateral line placodes (Gillis *et al.* 2012). Each ampulla comprises an opening (pore) at the surface of the skin that is connected by a narrow (approximately 1 mm diameter) canal to a chamber (ampullary bulb) located deep within the dermis (Peabody 1897). In most species, the ampullary bulbs are grouped into three subdermal clusters and canals of varying lengths (ranging from <1 to >20 cm in marine species) radiate out from these clusters to pores distributed across the dorsal and ventral surface of the head (Fishelson & Baranes 1998; Tricas 2001). Interspecific variations in ampullae/pore abundance, pore location, canal length and orientation reflect ecological adaptations (e.g. habitat and feeding mode) and phylogeny (Raschi *et al.* 2001; Tricas 2001; Kempster *et al.* 2012). The morphology of the electro-sensory system is sexually dimorphic in some elasmobranchs, implying a differential usage of electroreception by the sexes in reproductive and/or other behaviors (Crooks & Waring 2013; Kempster *et al.* 2013a).

Each ampullary bulb comprises several bulbous pouches (alveoli) lined with a sensory epithelium consisting of receptor and support cells (Fishelson & Baranes 1998; Theiss *et al.* 2011). The lumen of the ampullary bulb and canal are filled with a conductive mucopolysaccharide hydrogel that provides an electrical connection with the external pore opening and subtly alters the electrical properties of the canal (Murray & Potts 1961; Doyle 1967; Brown *et al.* 2005). Tight junctions (*Zonulae occludens*) between the cells lining the lumen of the canal and ampullary bulb form a high-resistance barrier that ensures current flows only across the receptor cell membrane and does not leak out of the

canal (Clusin & Bennett 1977). The receptor cells amplify the potential difference between their apical surface inside the lumen and their basal surface outside the lumen (Lu & Fishman 1994). The clustering of the ampullary bulbs means that the receptor cells of different ampullae share an identical 'reference' potential on their basal surface to which the voltage developed along each canal is compared (Tricas 2001).

Ampullary receptor cells synapse with primary electrosensory afferents that travel to the brain via the anterior lateral line nerve (Bodznick & Northcutt 1980). Afferent nerve fibers exhibit a steady discharge of action potentials in the absence of electrical stimulation; the rate of discharge increases or decreases depending on whether the apical surface of the receptor is more negative or more positive than the basal surface, respectively (Murray 1962). Behaviorally, sharks are attracted most strongly to direct current (d.c.) electric fields, but the receptors themselves are low frequency, alternating current (a.c.) detectors that respond optimally to fluctuating fields between 0.1 and 10 Hz, with peak sensitivity at around 1 Hz (Peters & Evers 1985). To detect a steady d.c. voltage, the shark must be moving relative to the voltage source (Kalmijn 1978).

Sharks are capable of responding to voltage gradients $\leq 5 \text{ nV}\cdot\text{cm}^{-1}$ (Kalmijn 1982; Johnson *et al.* 1984; Kajiura & Holland 2002), which allows them to detect the localized biopotentials emitted by prey (1–500 mV) at distances of up to 0.5 m (Kalmijn 1972; Haine *et al.* 2001) and uniform inductive fields ($50\text{--}500 \text{ nV}\cdot\text{cm}^{-1}$) generated by ocean currents (Kalmijn 1971). The downside of such an exquisitely sensitive sensory system is that it is easily saturated by intense transient stimulation. In rays, which have a similar threshold sensitivity of $\leq 1 \text{ nV}\cdot\text{cm}^{-1}$ (Jordan *et al.* 2009b), the maximal firing rate of an electrosensory afferent nerve is reached when the voltage across the receptor's apical membrane is approximately 100 mV (Lu & Fishman 1994). Assuming a canal length of 10 cm, this voltage would be achieved in a uniform field with a voltage gradient of $10 \text{ mV}\cdot\text{cm}^{-1}$, provided the shark was oriented such that the long axis of the canal was parallel to the direction of the field gradient. Interestingly, Kalmijn (1971) notes that small spotted catsharks (*Scyliorhinus canicula*) exhibited strong escape responses when they encountered a d.c. voltage gradient of $1\text{--}10 \text{ mV}\cdot\text{cm}^{-1}$. These findings have obvious implications for the development of electrical shark repellent devices.

SHARK REPELLENTS AND THEIR EFFECTIVENESS

Shark attacks or shark depredation may be prevented either by making an object aversive (directly through its appearance or indirectly through something it discharges) or by altering its stimulus qualities to make it more difficult to detect (i.e. camouflage). Of the various attempts to develop shark repellents, by far the majority have relied on making an object aversive, perhaps because making an object 'invisible' to all of the sharks various senses at once is quite a challenge. The following section provides a summary of the major breakthroughs in shark repellent research over the last 70 years. Although excellent reviews of the earlier (pre-1980) work are already available (e.g. Nelson 1983), a synthesis is presented here along with the latest research, as many of the problems encountered in the past are entirely relevant to today's efforts to improve on existing repellent technologies and develop new devices.

Chemical repellents

The first concerted effort to identify an effective shark repellent began during WWII in an attempt to find a way to prevent sharks from attacking military personnel who found themselves adrift in the ocean. Preliminary experiments to identify substances that would disrupt shark feeding behavior were conducted in 1942 using smooth dogfish (*Mustelus canis* Mitchill, 1815) held in aquaria at the Woods Hole Oceanographic Institution (Burden 1945; Springer 1955). Numerous chemical agents were tried unsuccessfully, including known fish poisons such as rotenone, chlorine, metallic poisons, irritants, ink clouds, and other unspecified "chemical stenchers and poison gas generators" (Springer 1955). In many cases, the sharks readily ate bait containing toxins that subsequently killed them.

Feeding responses of *M. canis* were suppressed using maleic acid and malic acid. However, the best repellents were found to be rotten shark flesh, which had been allowed to stand for 4–6 days at 20° , and low concentrations of copper salts, notably copper sulfate (Springer 1955; Brown 1973). Further experimentation revealed that the primary repelling agent in rotting shark flesh was ammonium acetate. The finding that both acetate ions and copper salts were repellent led to the selection of copper acetate for further trials (Hodgson & Mathewson 1978). Subsequent open-water testing appeared to confirm the efficacy of copper acetate when it was shown to reduce the number of strikes on set baits pro-

tected by the repellent compared to control baits without the repellent (Burden 1945). However, under conditions described as a “feeding frenzy” triggered by discarding large amounts of waste fish from a shrimping boat, copper acetate was found to be considerably less effective in repelling sharks.

In 1943, the work on shark repellents was taken over by the US Naval Research Laboratory. It was found that a modified nigrosine-type dye (Calco WBSR) was highly effective in suppressing feeding behavior in a variety of feeding situations. Although the dye was originally intended to disguise a swimmer much like a cephalopod releases a cloud of ink to escape a predator, it was found to be effective during both day and night, suggesting a chemical, as well as visual, mode of action (Fogelberg 1944). On their own, both copper acetate and Calco WBSR were capable of deterring a variety of shark species, including blacknose sharks (*Carcharhinus acronotus* Poey, 1860), *C. limbatus*, and other carcharhinid and sphyrnid shark species. The combination of Calco WBSR dye (80%) with copper acetate (20%) was shown to have a synergistic effect in repelling sharks, even during mass feeding events, and was rapidly developed into a cake formulation bound together by water-soluble wax (the ‘Shark-Chaser’) that could be attached to a life jacket and exposed to the water by a floating survivor when required (Fogelberg 1944; Burden 1945).

In 1944, at the behest of the Royal Australian Air Force and the Royal Australian Navy, independent testing of copper acetate-based repellents was conducted in Shark Bay, Western Australia (Whitley & Payne 1947). Copper acetate, in combination with another basic dye (Methic Leather Black D.G.) that on its own was apparently only a weak deterrent, was shown to reduce shark catch on baited hooks by approximately 95% compared to controls lacking the deterrent. Although it was not possible to observe the species of shark that were repelled, especially as most of the catch was taken at night, the species caught on the control lines were predominantly tiger (*Galeocerdo cuvier* Péron & Lesueur, 1822), sandbar (*Carcharhinus plumbeus* Nardo, 1827), spinner (*Carcharhinus brevipinna* Müller & Henle, 1839) and nervous (*Carcharhinus cautus* Whitley, 1945) sharks.

After the war, further work on shark repellents was conducted as part of an extensive research program on basic and applied shark biology led by Perry Gilbert and funded largely by the US Office of Naval Research. Between 1958 and 1968 at the Lerner Marine Laboratory

at Bimini in the Bahamas, over 100 different chemical agents were tested on large sharks, including a variety of metallic salts, amino acids, nicotine, human sweat and urine (Hodgson & Mathewson 1978). In contrast to earlier results, copper acetate was shown to be ineffective as a feeding inhibitor or repellent for *C. plumbeus*, *G. cuvier*, *C. leucas*, *N. brevirostris*, dusky (*Carcharhinus obscurus* Lesueur, 1818), blacktip reef (*Carcharhinus melanopterus* Quoy & Gaimard, 1824) and nurse (*Ginglymostoma cirratum* Bonnaterre, 1788) sharks. The only compound shown to have a significant repellent effect on *N. brevirostris* was the nigrosine dye from the Shark Chaser (Gilbert 1970). Because of these conflicting and disappointing results, research on chemical shark repellents was largely abandoned.

However, interest in chemical shark repellents was renewed following the discovery of naturally occurring ichthyotoxins contained in a milky secretion released from paired glands located at the base of the dorsal and anal fin rays of soleoid fishes of the genus *Pardachirus* (Clark & Chao 1973; Clark & George 1979). The secretion from the Red Sea Moses sole (*Pardachirus marmoratus* Lacepède, 1802) was found to be highly toxic to small teleost fishes and could repel whitetip reef sharks (*Triaenodon obesus* Rüppell, 1837) and other predatory fishes for at least 17 h (Clark 1974; Clark 1983; Zlotkin & Gruber 1984). A protein with neurotoxic and haemolytic activity (pardaxin) was isolated from the secretion of *P. marmoratus* (Primor & Zlotkin 1975; Primor *et al.* 1978) and shown to cause mouth paralysis and acute irritation of the gills and pharyngeal cavity of the piked dogfish (*Squalus acanthias* Linnaeus, 1758) (Primor 1985). Three virtually identical isoforms of pardaxin-like protein were also isolated from the defence secretion of the congener peacock sole (*Pardachirus pavoninus* Lacepède, 1802) and were shown to trigger escape responses when injected into the mouths of *T. obesus* (Thompson *et al.* 1986).

In addition to pardaxin proteins, the secretions of both *P. marmoratus* and *P. pavoninus* were subsequently found to contain a number of ichthyotoxic steroidal aminoglycosides (saponins) called mosesins (M1–M5) and pavoninins (P1–P6), respectively (Tachibana *et al.* 1984; Tachibana *et al.* 1985; Tachibana & Gruber 1988). Both mosesins and pavoninins were shown to inhibit feeding behavior in *N. brevirostris* and/or rouse them from a state of tonic immobility when introduced into the buccal or olfactory cavities, indicating significant repellent activity. A similar steroidal saponin, holothurin, produced by the sea cucumber (*Actinopyga*

agassizi Selenka, 1867) as an anti-predator defence, is also known to be toxic and repellent to *N. brevirostris*, *G. cirratum* and *S. tiburo* (Sobotka 1965; Hodgson *et al.* 1967). Although promising as a shark repellent, the *Pardachirus* secretion is thermolabile and loses much of its ichthyotoxic activity when freeze-dried for long-term storage (Primor & Zlotkin 1975; Clark & George 1979). Moreover, while it is possible to synthesize pardaxin and pavoninins artificially (Shai *et al.* 1988; Williams *et al.* 2002), at the time of their discovery they could not be produced in sufficient quantities for widespread use (Sisneros & Nelson 2001).

However, subsequent studies on the chemical structure and pharmacological action of pardaxin and pavonin, in particular their ability to disrupt the integrity of lipid membranes (Primor 1983; Primor *et al.* 1984), led to the identification of some alternative repellent substances. Pardaxins and pavoninins exhibit strong surfactant activity (Thompson *et al.* 1986; Williams *et al.* 2002), which is a common feature of other toxic defensive skin secretions (Hashimoto 1979) and was thought to be responsible for both the toxic action and the repellent activity of pardaxin in particular (Zlotkin & Gruber 1984). To test this hypothesis, Zlotkin and Gruber (1984) screened a range of natural and commercially available surfactant chemicals for their ability to disrupt the feeding behavior of captive *N. brevirostris* or rouse them from a state of tonic immobility. They identified 2 anionic detergents as potent shark repellents: sodium dodecyl sulfate (SDS) and lithium dodecyl sulfate (LDS).

Further laboratory studies with horn sharks (*Heterodontus francisci* Girard, 1855), swell sharks (*Cephaloscyllium ventriosum* Garman, 1880) and leopard sharks (*Triakis semifasciata* Girard, 1855) confirmed that SDS was effective at triggering aversive reactions (Smith 1991; Sisneros & Nelson 2001). The effective concentration of SDS (at which half of the sharks demonstrated strong avoidance behaviors) was in the range of 83–175 ppm, although subtle reactions were evident at concentrations as low as 36 ppm. Importantly, the sharks did not habituate to the chemical when exposed to it repeatedly. In contrast, copper acetate at concentrations as high as 2240 ppm did not elicit any discernible responses (Smith 1991). Field trials with bait-attracted blue sharks *P. glauca* and white sharks (*Carcharodon carcharias* Linnaeus, 1758) also demonstrated that direct delivery of a 10% solution of SDS in seawater into the mouth of a feeding shark (compared to a seawater-only control) resulted in head shaking, mouth gaping and permanent departure from the test site (Nelson

& Strong 1996). While the promise of a reliable, readily available and comparatively cheap chemical repellent like SDS, which is also relatively non-toxic to humans, is appealing, the release of large amounts of any artificial chemicals into the marine environment is undesirable. Moreover, the concentration at which SDS is effective in repelling sharks is still considerably higher than that which is considered practical for creating a sustained, non-directional, surrounding-cloud type chemical repellent (10–100 ppb), based on the fact that even highly toxic or repellent chemicals will be diluted rapidly in open water (Baldrige 1990).

Recent attempts to identify more effective chemical shark repellents have focused on compounds (semiochemicals) that are of biological relevance to sharks rather than merely an irritant to their senses. Rasmussen and Schmidt (1992) hypothesized that juvenile *N. brevirostris* would inherently recognize chemicals (kairomones) given off by their natural predator, the American crocodile (*Crocodylus acutus* Cuvier, 1807). They demonstrated that water samples taken from holding tanks containing captive *C. acutus* could trigger the reversal of tonic immobility in *N. brevirostris*, whereas water samples taken from holding tanks of American alligator (*Alligator mississippiensis* Daudin, 1802), which are not a major predator of *N. brevirostris*, had no visible effect. A chemical analysis of *C. acutus* water extracts identified 2 candidate molecules that are probably excreted in crocodile faeces: 2-ethyl-3-methylsuccinimide (3-ethyl-4-methylpyrrolidine-2,5-dione) and 2-ethyl-3-methylmaleimide (3-ethyl-4-methyl-1H-pyrrole-2,5-dione). Even at very low concentrations (10^{-9} – 10^{-7} M; equivalent to 0.14 to 14 ppb given relative molar masses of 141.2 and 139.2, respectively) these compounds were able to reverse tonic immobility in *N. brevirostris* in 60–80% of trials (Rasmussen & Schmidt 1992). Although it is difficult to be certain that the state of tonic immobility was disturbed through an avoidance response rather than a feeding response to these compounds, the fact that sharks are able to detect the chemical signatures of potential predators indicates a promising avenue for the development of semiochemical-based shark repellents. For example, there are reports (Hainke 2010) of predation on bull sharks (*C. leucas*) by saltwater crocodiles (*Crocodylus porosus* Schneider, 1801), which share large areas of coastal and estuarine habitat in northern Australia. It may be possible to find similar semiochemicals that are effective in repelling *C. leucas*, a species responsible for both fatal and non-fatal bites on humans (Baldrige 1974).

Taking inspiration from the earlier work of Springer (1955), who show that rotting shark flesh is a potent repellent, Stroud *et al.* (2014) revisited the idea of ‘necromones’: semiochemicals given off by dead or decaying animals that function to alert other animals to the presence of potential predators (Yao *et al.* 2009). A commercially-available aerosolized preparation (Repel Sharks, LLC) of putrefied shark tissue extract was shown to be capable of dispersing competitively feeding aggregations of Caribbean reef sharks (*Carcharhinus perezi* Poey, 1876) and *C. acronotus* for approximately 10 min, even when delivered at relatively low concentrations. Some sharks (all *C. perezi*) returned after 10 min, but they appeared to be less interested in feeding. A chemical analysis of the shark extract revealed high concentrations of acetic acid in addition to a plethora of amino acids, short chain and fatty carboxylic acids, amines, and short chain lipid oxidation products (Stroud *et al.* 2014). Acetate ions have already been shown to repel sharks (see above), and it remains to be seen whether any of the other constituents are also repellent. A similar approach has been proposed for use in the Great Lakes to control invasive sea lampreys (*Petromyzon marinus* Linnaeus, 1758), which show avoidance behaviors when exposed to chemicals released by dead and decaying conspecifics (Imre *et al.* 2010; Pietrzakowski *et al.* 2013). The remaining challenges with all of these chemical repellents are to isolate compounds that are both non-toxic and effective at very low concentrations, such that rapid dispersion by water currents under real-life deployment conditions does not negate their repellent effect.

Electrical and magnetic repellents

A natural aversion by sharks to electrical fields was first recognized in 1935 when it was shown that blindfolded *S. canicula* demonstrated oriented escape reactions to a rusty steel wire brought close to the head. The galvanic currents generated at the surface of the wire were sufficiently large to be detected by the shark’s highly sensitive electroreceptive system (Kalmijn 1971). Although subsequent research demonstrated that sharks are also attracted to certain electrical fields (see above), it was quickly recognized that the use of electric stimuli that differ in frequency or strength from those characteristic of prey were clearly a potential mechanism by which sharks could be repelled.

Active electrical repellents

There have been various attempts to develop ‘active’ electrical shark repellent devices that utilize a power source to generate the electric field. One of the first successful devices, the original ‘Shark Shield’ developed by Electromagnetic Industries, was available in two configurations: one to be worn by scuba divers, and another for use to prevent sharks from damaging the cod-ends of shrimp-trawl nets (Nelson 1983). The device consisted of a rechargeable battery-powered capacitor-discharge unit connected to two or four woven-metal electrodes, which delivered a 120 V square wave pulse of 60 ms duration at a frequency of 1–2 Hz (Hurley *et al.* 1987). In aquarium tests, the Shark Shield was shown to be effective in repelling four different species of captive adult sharks known to be dangerous to humans, including *N. brevirostris* (Gilbert & Gilbert 1973). In field trials with tuna purse seine nets, the Shark Shield kept sharks at least 3 m from the electrodes (Nelson 1983). However, in many cases, the repellent effect of such electrical devices was highly species-specific. For example, Gilbert (1970) tested four different types of electrical repellent on captive sharks between 1958 and 1969, and showed that *G. cuvier* were attracted to electrical pulses that quickly repelled *N. brevirostris*. Similarly, studies aimed at preventing sharks from biting submarine telecommunications cables found that *N. brevirostris*, but not *G. cirratum*, were repelled by a moving dipole generating a d.c. current of 1.6 A (Hurley *et al.* 1987).

Research by the Kwazulu-Natal Sharks Board (South Africa) into the use of electrical fields to repel sharks led to the development of the SharkPOD (Protective Oceanic Device) for use by scuba divers. Similar to earlier devices, the SharkPOD consisted of an electrical waveform generator and two widely separated electrodes (one located on the scuba tank and the other located on the fin) that created an electrical field surrounding the diver (KZNSB 2011). Early testing showed that the SharkPOD was effective in eliciting avoidance behaviors from *C. leucas*, *C. carcharias*, *G. cuvier* and grey nurse sharks, *Carcharias taurus* (Taylor 1998), and significantly reduced the frequency with which *C. carcharias* attacked baits attached to an activated device compared to controls when the device was switched off (Smit & Peddemors 2003). Commercial distribution of the SharkPOD commenced in 1995/1996 and ceased in 2001, but the patented electrical waveform technology was subsequently licensed to an Australian company (SeaChange Technology, now SharkShield), which developed new versions of the electrical repellent de-

vice for use by divers, surfers and kayakers. The Freedom 7 and Scuba 7 devices are widely used by recreational, commercial and professional divers. A military version with reduced field strength is also available (Defense 2013). The Freedom 7 device produces exponentially decaying pulses lasting approximately 1.2 ms with peak amplitude of 105 V at a frequency of approximately 1.7 Hz (Huvneers *et al.* 2013). In field tests with wild *C. carcharias*, the device was shown to increase the time taken to consume static tuna baits located within 1–3 m of the electric field source (i.e. within the reported protective envelope), but overall did not reduce the number of baits attacked. In contrast, the device significantly and dramatically reduced the number of breaches and surface interactions against seal-shaped decoys towed along the surface of the water (Huvneers *et al.* 2013). Other devices with similar modes of operation are either in development or commercially available, including the Electronic Shark Defense System, although as yet no independent testing appears to have been conducted on this device.

Devices such as the Shark Shield were designed primarily for personal protection against sharks, but one of the challenges now is to explore ways of using electric repellents to reduce shark bycatch and depredation in fisheries, perhaps through miniaturization of electrical devices for deployment on nets or longline gear (Jordan *et al.* 2013), and for protection of humans over larger spatial scales such as beaches. Previous attempts to provide area-level protection, such as the anti-shark electrical cable that was deployed in the St. Lucia estuary (employing a pulsed d.c. field of 3–7 V·m⁻¹) and off Margate Beach in South Africa, proved effective at deterring a variety of shark species, including *C. leucas* (Smith 1974). However, these devices were either too costly to install and maintain or suffered from extensive damage when deployed over sections of exposed reef. Consequently, they were not widely adopted (Gilbert 1970; Cliff & Dudley 1992). Nevertheless, research into shark repellent cables is ongoing and may prove to be a credible option for protecting beachgoers, especially if the total cost of operation and maintenance can be reduced by modifications to waveform design and/or delivery (Cliff & Dudley 1992; KZNSB 2011).

Passive electrical repellents: Electropositive metals

Another approach to the design of electrical deterrents is the use of strongly electropositive metals (EPMs), which react vigorously with water when im-

mersed and generate electrical potentials that are thought to overstimulate the sharks' highly sensitive electroreceptors (Rice 2008; Stoner & Kaimmer 2008). Primarily intended as a mechanism to reduce shark bycatch and catch depredation in longline fisheries, without affecting the catch of non-electrosensitive target teleost fishes, EPMs can be formed into shapes that are easily attached to a fishing line or hook. Initial laboratory tests with captive sharks showed that several EPMs (including magnesium and rare-earth lanthanide elements such as cerium, lanthanum, neodymium and praseodymium) were effective in rousing *N. brevirostris* and *G. cirratum* from a state of tonic immobility (Rice 2008) and in repelling *S. acanthias* and *C. plumbeus* from tethered baits (Stoner & Kaimmer 2008; Brill *et al.* 2009). However, subsequent testing showed no repellent effect of EPMs on *S. tiburo* or *N. brevirostris* (McCutcheon & Kajiura 2013), and that aversive behavior shown by *S. acanthias* and *M. canis* was highly dependent on the duration of food deprivation prior to testing and/or the presence of conspecifics. Hungry sharks ignored the EPM to take the bait, especially when feeding in groups (Tallack & Mandelman 2009; Jordan *et al.* 2011).

The results of field trials using fishing gear fitted with EPMs were also mixed, with some studies showing a reduction in the catch rate of/depredation by *S. acanthias*, *C. plumbeus*, *S. lewini* and Galapagos sharks (*Carcharhinus galapagensis* Snodgrass & Heller, 1905) (Kaimmer & Stoner 2008; Wang *et al.* 2008; Brill *et al.* 2009; Hutchinson *et al.* 2012; O'Connell *et al.* 2014b). Other studies showed no effect on the catch rate of/depredation by *S. acanthias*, *C. plumbeus*, *C. galapagensis*, *G. cuvier*, *P. glauca*, shortfin mako (*Isurus oxyrinchus* Rafinesque, 1810) and pelagic thresher sharks (*Alopias pelagicus* Nakamura, 1935) (Tallack & Mandelman 2009; Robbins *et al.* 2011; Hutchinson *et al.* 2012; Godin *et al.* 2013). A number of factors may influence the efficacy of EPMs in repelling sharks, including the type of EPM used, the relative sensitivity of the electroreceptor system, shark density and competition, hunger level, and differences in feeding ecology (Godin *et al.* 2013). Other impediments to large-scale adoption of EPM technology by commercial fisheries include the relatively high cost of the rare-earth metals (although magnesium may represent a cheaper alternative), potential toxicity to other marine animals, and the fact that they dissolve rapidly in seawater and, therefore, must be replaced frequently (Brill *et al.* 2009; McCutcheon & Kajiura 2013; O'Connell *et al.* 2014b). The use of EPMs for personal shark deterrent devices is also hampered by the limited

effective range (<85 cm) of the electrical field they generate (McCutcheon & Kajjura 2013).

Passive electrical repellents: Permanent magnets

Possible alternatives to EPM repellents are permanent magnets, which are thought to act on the electro-sensory system indirectly through electromagnetic induction (O'Connell *et al.* 2014c), which is the same physical mechanism that is thought to allow sharks to detect the Earth's magnetic field (Kalmijn 1978; Kalmijn 1982). Both ceramic (barium-ferrite) and rare-earth type (neodymium-iron-boron) magnets have been investigated as possible shark repellents (O'Connell *et al.* 2014c). Ceramic magnets are comparatively cheap and do not degrade in seawater but are relatively weak (typical residual flux density 2000–5000 gauss (G), ASTM 2007) compared to rare-earth magnets. Therefore, larger ceramic magnets are required to provide a given magnetic field strength. Rare-earth magnets contain EPM elements that degrade in seawater and are more expensive than ceramic magnets but are considerably stronger (typically 8300–14 100 G, MMPA n.d.). Given that the Earth's magnetic field (approximately 0.5 G at the surface) is thought to be capable of inducing electrical potentials in ocean currents (50–500 nV·cm⁻¹) that would be readily detected by the shark's highly sensitive electroreceptors (detection threshold ≤5 nV·cm⁻¹; see above), strong permanent magnets are probably capable of inducing large potentials that would be quite unlike anything encountered by sharks in their natural habitat.

Sharks are clearly able to detect and respond to strong magnetic fields. Stroud *et al.* (2005) show that juvenile *N. brevirostris*, *C. limbatus* and *G. cirratum* could be aroused from a state of tonic immobility by magnetic fields of approximately 50 G, generated by moving a 10 000 G rare-earth magnet within 10–20 cm of their head. Rigg *et al.* (2009) demonstrate that free-swimming captive sharks, including *S. lewini*, grey reef sharks (*Carcharhinus amblyrhynchos*) and Australian blacktip sharks (*Carcharhinus tilsoni*), react to static magnetic fields greater than 25 G at distances of 0.26–0.58 m by swimming faster or turning away from the source. However, studies investigating the ability of magnets to protect baits from depredation have provided conflicting results. Captive *S. acanthias* and wild *C. galapagensis* displayed behaviors suggestive of irritation or aversion when encountering small rare-earth magnets attached to tethered baits, but the presence of the magnetic field (4–1475 G in the case of *C. galapagensis*) did not significantly reduce the overall likelihood of depredation com-

pared to controls (Stoner & Kaimmer 2008; Robbins *et al.* 2011). In contrast, O'Connell *et al.* (2010) show that *G. cirratum* avoided bait protected by a C8-grade barium-ferrite magnet (150 × 100 × 50 mm; residual flux density approximately 950 G) compared to baits paired with a non-magnetic clay brick control. Smith and O'Connell (2014) found that *S. canicula* actively avoided baits protected by an N52-grade neodymium rare-earth magnet (20 mm diameter × 30 mm height; residual flux density approximately 14 000 G) compared to baits associated with a lead weight control.

Mixed results were also obtained in a dual longline and hook-and-line study (O'Connell *et al.* 2011b). Shark catch rate on longline gear was not reduced by the presence of strong (14 800 G) neodymium magnets on the hook shaft but was significantly less than controls (bare hooks or hooks with a lead weight on the shaft) when using weaker (3850 G) C8 barium-ferrite magnets (O'Connell *et al.* 2011b). The repellent effect of the barium-ferrite magnets was also species-specific in that they significantly reduced the catch of *C. limbatus*, but not of *C. plumbeus*, *N. brevirostris* and other species. Using hook-and-line gear with either a magnet or lead weight control attached directly to the bait rather than the hook, strong neodymium magnets did result in a reduction in the catch of *M. canis* and *R. terraenovae*, but not *S. canis*. In a further example that the repellent efficiency of magnets and other deterrent technologies is highly species-specific, field trials with *C. carcharias* show that tethered baits protected by a strong ceramic magnet were actively avoided and eaten significantly less frequently than baits protected by a non-magnetic clay brick control (O'Connell *et al.* 2014a).

In an attempt to combine both EPM and magnetic repellent technologies, a so-called SMART (Selective Magnetic and Repellent-Treated) hook has been developed that generates a voltage of up to 1.3 V when immersed, as well as a magnetic flux of 80 G, and has been shown to reduce the catch rate of *S. acanthias* on longline fishing gear (O'Connell *et al.* 2014b). The fact that the relatively weaker magnetic fields generated by barium-ferrite magnets and the SMART hooks are more effective in reducing depredation across these studies, rather than stronger fields generated by neodymium magnets, highlights the need to establish a repellent 'strength' that is optimally effective rather than just opting for the maximum that can be generated.

The main impediments for incorporating magnetic repellents into fishing gear is the additional cost and weight of the material and the tendency for magnets to

attract one another (or other metal objects) and, therefore, cause entanglement (Rigg *et al.* 2009). Like EPMS, magnetic repellents only have a relatively short effective range because the field strength of a magnetic dipole falls off approximately as the inverse cube of the distance from the source. For example, *S. canicula* displayed avoidance behaviors only when they encounter flux densities of approximately 21–2152 G at a distance of approximately 2–20 cm from a powerful rare-earth magnet (Smith & O’Connell 2014), which highlights the potential importance of the proximity and location of magnets relative to the bait for preventing depredation (Robbins *et al.* 2011). Thus, a large number of magnets would be required to generate a magnetic repellent with extensive spatial coverage. However, it is possible that arrays of magnets could be deployed around gill nets to form a magnetic barrier that would deter sharks, while allowing target teleost species to reach the net (Jordan *et al.* 2013). In this respect, it is encouraging that native *N. brevirostris* have been shown to be reluctant to pass through openings surrounded by strong magnets, although they habituated to the magnets with repeated exposure, and so the repellent effect was short-lived (O’Connell *et al.* 2011a). Moreover, in a separate experiment using arrays of submerged vertical plastic pipes carrying either magnets or control bricks, the magnets appeared to enhance the ability of the apparent visual ‘barrier’ (represented by the pipes) to deter *C. carcharias* from passing through the array (O’Connell *et al.* 2014a). Such findings also show the potential for visual–magnetic barriers to be used to exclude sharks from designated areas, such as beach swimming zones. A trial currently underway near Cape Town, led by C. Matthee of Stellenbosch University, is investigating the use of such a structure (the ‘Sharksafe’ barrier), as an alternative to traditional shark nets. The Sharksafe barrier relies on the use of strong magnets as well as numerous rigid upright pipes that visually resemble stands of kelp, which *C. carcharias* are thought to avoid entering when in pursuit of prey (Maditla 2013).

Visual repellents

One of the most effective and technologically simple shark deterrents developed to date is the Shark Screen developed by US Naval Scientist C. Scott Johnson (Tester *et al.* 1968). Essentially a large impermeable bag with three inflatable collars around the opening at the top, it is designed such that a person adrift in the water can get into the bag, fill it with water and blow up the collars to keep it afloat. The bag does not provide

physical protection against a shark but instead completely conceals the occupant visually, contains body odors or effusions (e.g. blood and urine) that might attract sharks, isolates any bio-electrical emissions, and damps water displacements caused by body movements. Tests with captive and wild sharks, including *C. milberti*, *T. obesus* and *C. melanopterus*, revealed a general reluctance by the sharks to approach the bags. Even when motivated by the presence of food in the water nearby, the sharks largely ignored the bags while feeding (Tester *et al.* 1968).

The overall reflectivity of the bag had a significant influence on whether or not the sharks would approach it. White and silver bags with high reflectivity tended to attract sharks, whereas blue and black bags of low reflectivity were least attractive (Gilbert 1968; Tester *et al.* 1968; Gilbert 1970). Subsequent testing with other sea-survival equipment, including lifejackets and a cocoon-like infant flotation device (IFD) designed for commercial airlines, demonstrated a similar tendency for sharks such as *C. leucas*, *G. cuvier* and *C. milberti* to ignore objects with low reflectivity. In open water trials, *P. glauca* and *I. oxyrinchus* readily attacked child dummies dressed in standard bright yellow lifejackets but ignored dummies dressed in black lifejackets or housed within the black IFD (McFadden & Johnson 1978).

Sharks either have very poor color vision or are completely color blind (Hart *et al.* 2011 and see above); thus, the sharks were almost certainly not responding to the color (spectral reflectance) of the yellow life jackets but rather their overall reflectance, or, more specifically, their high visual contrast against the background. While devices such as the Shark Screen would no doubt be useful in a survival situation, they are not practical for use by people actively swimming in the water. Nevertheless, the same principles of visual camouflage may apply to swimming apparel such as wetsuits. With this in mind, reflectance spectra that provide minimal visual contrast against the water background for the shark visual system have been calculated (Hart *et al.* 2012, unpubl. data) and used to design ‘cryptic’ wetsuit patterns that may reduce the risk of shark bite (SAMS 2013). Field testing of the wetsuit prototypes is currently underway to determine whether a camouflaged design is less attractive to sharks than a standard black wetsuit.

Taking a different approach based on his experiences diving in the western Pacific, marine biologist Walter Starck developed a black-and-white banded wetsuit that was intended to mimic the banded poisonous sea snakes that many sharks appeared to avoid eating (Doak 1974;

Nelson 1983). While *T. obesus* appeared to be unaffected by the banded wetsuit, it was reported to have a repellent effect on *C. amblyrhynchos*, *C. galapagensis* and silvertip sharks (*Carcharhinus albimarginatus* Rüppell, 1837). Doubt was cast on the effectiveness of the banded suit based on testing performed in the Marshall Islands in the northern Pacific Ocean, but these negative results might have occurred because the test sites were not inhabited by sea snakes, and local shark populations may not have had the opportunity to learn to avoid them (Nelson 1983). This controversy also serves to highlight the difficulties in assessing repellence when complex multi-sensorial cues are available and the problems inherent in testing shark repellents when sharks must be induced (with food) to interact with them. The repellent effects of some devices may be subtle and provide a useful level of protection against unprovoked bites under normal conditions, but may be significantly reduced when sharks are provoked into feeding, especially when in groups (Gilbert 1962).

The use of visual ‘barriers’ has already been mentioned in reference to arrays of vertical pipes that resemble kelp stands into which white sharks are thought to be reluctant to swim, especially when combined with strong magnets (see above). Another attempt to generate a visual barrier that would repel sharks was the innovative use of a bubble curtain generated by air escaping from a submerged perforated hose. Initial trials in an aquarium with captive sharks appeared promising, with many large sharks reportedly refusing to swim through the bubbles (McCormick 1963). However, subsequent testing showed that only one of 12 adult captive tiger sharks was in any way repelled by a bubble curtain (Gilbert & Gilbert 1973). Similar species-specific responses to bubble curtains have been observed in teleost fishes (Sager *et al.* 1987). While the bubbles may or may not act as a visual repellent for different shark species, there is also the possibility that they can produce hydrodynamic cues that may affect shark behavior through stimulation of the auditory or lateral line systems. Modifications to the technology based on bubble size, air pressure and/or air flow rate may enhance the repellent effect of what would be a simple and environmentally-friendly deterrent device.

Many species of teleost fishes are known to avoid flashing lights. For example, xenon strobes operating at 2–10 Hz have been used successfully as ‘behavioral guidance’ tools to keep estuarine fishes away from power station cooling-water intake structures (Sager *et al.* 1987). These optimal flash frequencies are in close

agreement with the flicker rate of maximal contrast sensitivity in a range of fishes (5–13 Hz; McFarland & Loew 1983). A similar approach with flashing lights has been used to keep lions away from domestic livestock on farms surrounding national parks in Africa (Kermeliotis 2013), which further suggests that the very unnatural visual stimulation created by flashing lights may be repellent to a range of animals. No serious attempts appear to have been made to investigate the use of bright flashing lights to repel sharks. This work is currently underway in our laboratory.

Species-specific responses to lights may represent a way in which visual deterrents may be adapted to reduce fisheries bycatch of sharks and even increase the catch of target species (Jordan *et al.* 2013). Colored electric lights and chemiluminescent ‘cyalume’ sticks are used in tuna and swordfish longline fisheries as lures to attract target fish to a baited hook. Given some of the key differences in temporal resolution and spectral sensitivity between sharks and teleost fishes, it may be possible to design lures that emit light at a wavelength to which the target fish are more sensitive than are sharks, or at a frequency that is repellent to sharks but attractive to target fishes. For example, the retina of the yellowfin tuna (*Thunnus albacores* Bonnaterre, 1788) contains single cones, twin cones and rods that express visual pigments with λ_{\max} values at 426, 485 and 483 nm, respectively (Loew *et al.* 2002), whereas many pelagic sharks appear to have only a single type of cone containing a visual pigment with a λ_{\max} value between 532 and 554 nm, in addition to a rod pigment with a λ_{\max} value between 500 and 518 nm (Hart *et al.* 2011). Thus, the spectral sensitivity of the tuna is almost certainly greater at shorter (blue) wavelengths than the sharks’ sensitivity under both scotopic and photopic conditions, and the use of blue light-emitting lures instead of the popular yellow-green ones might help to reduce shark bycatch.

Auditory repellents

Sharks such as *G. cuvier*, *C. falciformis* and *C. leucas* are attracted to irregularly pulsed (amplitude modulated), mixed low frequency sounds, especially those in the 20–60 Hz range that resemble sounds emitted by injured or struggling fish (Nelson & Gruber 1963; Myrberg *et al.* 1972). In contrast, certain sounds can be repellent to sharks. Experiments with captive *N. brevirostris* and wild *C. falciformis* demonstrated their rapid withdrawal from a playback of the ‘scream’ of a natural shark predator, the killer whale (*Orcinus orca* Linnaeus, 1758) (Myrberg *et al.* 1978; Klimley & Myrberg 1979).

However, there appeared to be no unique quality to the killer whale scream: broad-band, low-frequency-biased 'pink noise' of a similar waveband (500–4000 Hz) to the scream was even more effective at repelling the sharks. Crucially, most sounds can elicit withdrawal if they start suddenly and/or rapidly increase in loudness, including medium-frequency pure tones and even low-frequency pulsed sounds that would otherwise attract sharks.

Infrasound (<20 Hz) has been used as a behavioral guidance tool for salmonids and eels to prevent them from entering hydropower facilities or cooling-water intakes, and may work to repel these fishes because infrasound stimulates the lateral line and mimics the hydrodynamic movements caused by larger, potentially predatory, fishes (Sand *et al.* 2000). It is unknown whether sharks are also repelled by infrasound, but its use as a repellent is limited by the great size and cost of the transducers required to generate low frequency particle motion that would travel any appreciable distance underwater (A. Popper, personal communication), and by the potential for disturbance of other marine animals.

Currently, only a single device (Sharkstopper[®]) is being marketed as an acoustic repellent for both personal protection (swimmers, scuba divers and water craft) and for prevention of shark depredation on fishing gear. Based on specifications obtained from patents (US7077153 and US6606963) filed by the inventor (Brian Wynne) and held by Sharkstopper LLC, the device emits pulsed sounds in the frequency range of 30–500 Hz or 200–1500 Hz, and is claimed to deter a variety of sharks including *S. acanthias* and *N. brevirostris* (Sharkstopper 2010). It is important to note that sharks quickly habituate to both attractive and repulsive sounds (Myrberg *et al.* 1969; Myrberg *et al.* 1978), which would mean that for any auditory-based shark repellent to remain effective it would have to be deployed only for short durations rather than being left on permanently.

FUTURE DIRECTIONS

“Practical problems are occasionally solved by freak discoveries, but the history of technology has shown repeatedly that advancements are most rapid and effective when a proper background in information and theory is available. When the need is complex, as, for instance, when an adequate system of protection against predatory sharks is desired, suitable answers are more likely to be found by theoretical advances than by trial and error ‘practical solutions’.”

(Aronson 1963; p. 165)

While our knowledge of the basic neurobiology and behavior of sharks is more extensive than it was when the first attempts to develop shark repellents were made, we are still some way away from a complete understanding of the sensory cues that drive their feeding behaviors. Many questions regarding the motivation behind a shark's decision to bite a human remain unanswered. For example, are the majority of shark bites a case of mistaken identity, where the shark has confused sensory cues emitted by a swimming human with those emitted by a more typical prey item such as a seal, or are sharks just not discerning diners and consider all animals in the ocean to be potential food? There may be no simple answers to such questions, but a more detailed understanding of the sensory biology and ecology of sharks will undoubtedly help us to better interpret and predict their behaviors when presented with a novel stimulus, whether that is a human scuba diver or a long line hook. Areas ripe for further investigation include the identification of visual cues (especially contrast and motion) used by sharks to detect and identify potential prey items, the identification of semiochemicals that have inherent biological meaning for sharks in terms of predator avoidance, and the integration of multi-sensory information in the brain that ultimately drives behavioral output.

Sharks are behaviorally complex animals and humans interact with sharks under a range of different scenarios. Thus, a single simple repellent device may not be achievable and combinations of repellents that manipulate a range of behaviors or sensory systems may prove to be more effective. For example, personal repellent devices might combine electrical fields and flashing lights, and area-based repellents might combine bubble curtains with controlled delivery of semiochemical odors. Combinations of visual and auditory stimuli have proved to be particularly effective as behavioral control measures in teleost fishes (Popper & Carlson 1998). It may also be worthwhile taking a 'push-pull' approach to deterring sharks; that is, deploying repellents in the immediate area of risk where the shark has strayed while simultaneously deploying attractant sounds or chemicals at a distant location to help draw the sharks away. Such an approach is well established in the control of insect pests (e.g. Cook *et al.* 2007). Of course, it is also crucial to consider any potential adverse effects that shark repellent technologies might have on other ocean inhabitants, an issue that places serious constraints on the use of chemical or acoustic repellents, for example.

In addition to a better understanding of shark neurobiology, many of the future challenges in developing shark repellents are technological or economic in nature. It is one thing to establish that sharks are deterred by a strong electrical or magnetic field, but quite another to adapt such technology to protect an ocean beach subject to the continual actions of tides and waves, or to reduce shark bycatch and depredation in commercial fisheries. In each case, the costs and practical difficulties of deploying repellents must be weighed against the need to protect the lives of humans or sharks. However, in a world that is increasingly aware of the plight of sharks, yet simultaneously exploiting them in increasing numbers, the need to develop cheap, harmless and effective shark repellents has never been more urgent.

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