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Original Article

Microprocessor-based prototype bycatch reduction device reduces bait consumption by spiny dogfish and sandbar shark

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Elasmobranchs contribute heavily to bycatch in longline fisheries globally, and an effective method of deterring them from baited fishing gear is needed. Electrosensory stimulus holds promise as a method of disrupting elasmobranch close-range feeding responses as their electric sense guides their final strike during prey capture. We used laboratory experiments to test the hypothesis that weak electric stimuli generated by a prototype electronic bycatch reduction device (BRD) could deter sandbar shark (*Carcharhinus plumbeus*) and spiny dogfish (*Squalus acanthias*) from eating bait. Voltage gradients $<1\,mV\,cm^{-1}$ at the location of bait were produced by an Arduino microcontroller powered by a 9 V battery and attached to carbon electrodes. Median bait consumption by groups of juvenile sandbar shark declined by 74% when bait was located 10 cm vs. 2 m from active electrodes. Spiny dogfish median bait consumption halved when bait was located 10 cm from active vs. inactive electrodes. Although laboratory studies often produce a larger effect for electrosensory shark deterrents than can be demonstrated during field trials, if the effects seen in our laboratory studies produced similar effects in the field, it could meet fishermen's requirements for a BRD.

Keywords: bycatch mitigation, conservation technology, elasmobranch, electrosensory, fisheries

Introduction

Sharks are heavily represented in fisheries bycatches worldwide (Bonfil, 1994; Stevens *et al.*, 2000; Ayers *et al.*, 2004; Horn, 2004), especially in longline fisheries (Oliver *et al.*, 2015). This can lead to negative outcomes for both shark populations and commercial fishermen—sharks are particularly susceptible to overfishing because of their relatively slow growth and reproductive rates (Walker, 1998; Schindler *et al.*, 2002), and shark bycatch can reduce fishing efficiency and damage fishing gear (Gilman *et al.*, 2008). Electrosensitive sharks and their chondrichthyan relatives detect extremely weak electric fields that can guide the final stages of their predatory strikes on prey (Kalmijn, 1982). An electronic shark bycatch reduction device (BRD) could potentially rely on voltage gradients that are within the range perceived by the elasmobranch electric sense but below the detection threshold of non-electrosensitive target species. Elasmobranch and teleost fishes possess a mechanosensory lateral line that is sensitive to voltage gradients $>10–100\,mV\,cm^{-1}$ (Murray, 1974) but unresponsive to voltage gradients of $5\,mV\,cm^{-1}$ (Bodznick and Northcutt, 1980). The threshold for a response to electric stimulus from teleost fishes' somatic nerve and muscle fibres is $20–80\,mV\,cm^{-1}$ (Lamarque, 1990), whereas elasmobranch fishes can detect voltage gradients as weak as $1\,nV\,cm^{-1}$ using their specialized electric sense (Kajiura, 2003; Jordan *et al.*, 2011). An electric stimulus below $5\,mV\,cm^{-1}$ should therefore be exclusively detectable by the specialized electrosensory systems of elasmobranch fishes, but imperceptible to non-electrosensitive fishes.

Shark electrosensory BRD research has, to date, generally employed magnets and electropositive metals (EPMs) to produce electrosensory stimuli, but with mixed results. An electromagnetic field is induced when a conductive body moves through a magnetic field, for example ocean currents moving through geomagnetic fields can induce electric fields as large as 2.5 μV cm^{-1} (Von Arx, 1962). EPMs undergo a hydrolytic reaction when immersed in seawater producing an electric field with a voltage gradient of 40 μV cm^{-1} at a site 10 cm from the ingot's surface (McCutcheon and Kajiura, 2013). When either magnets or EPMs were present near hooks, catch rates of some shark species declined by between 28% and 90% (Kaimmer and Stoner, 2008; Brill *et al.*, 2009; O'Connell *et al.*, 2011; Hutchinson *et al.*, 2012; O'Connell *et al.*, 2014). In other cases, no significant effects were found (Kaimmer and Stoner, 2008; Tallack and Mandelman, 2009; O'Connell *et al.*, 2011; Hutchinson *et al.*, 2012; Godin *et al.*, 2013; O'Connell *et al.*, 2014). One study even found a significant *increase* in the catch rate of blue shark (*Prionace glauca*) on hooks associated with magnets (Porsmoguer *et al.*, 2015). It is probably not possible to improve metal-based BRD effectiveness by optimizing their electric field because EPMs produce similar voltage gradients in seawater regardless of ingot alloy or shape (McCutcheon and Kajiura, 2013). EPMs are also impractical on several counts: they are expensive (Bell and An, 2008), corrode rapidly in seawater (Tallack and Mandelman, 2009) and produce a toxic, flammable precipitate (Sigma-Aldrich, 2010). High Gauss permanent magnets are alloys that include EPMs and thus face similar cost barriers as non-magnetized EPM, and they would likely be difficult to deploy during commercial fishing operations. Another challenge that these materials present is their visual impact on target species. Metal ingots near a hook increase gear visibility and can reduce catch rates of visual predators (e.g. swordfish [*Xiphias gladius*]; Godin *et al.*, 2013). Inconsistent performance of magnets and EPMs as elasmobranch BRDs, as well as their limited scope for improvement, high cost, low durability and potential to reduce catch rates of target catches make their commercial implementation unlikely.

An alternative mode of generating stimuli for an electrosensory BRD is a battery-powered microcontroller unit (MCU). This approach offers scope to optimize BRD electric output for a maximal deterrent effect, because a MCU can be programmed with variable voltage gradients and pulse frequencies, and connected to a customizable electrode configuration. The problem of dissolution of EPM-based electrosensory BRDs could be overcome with the use of a MCU housed in a non-metallic shell and connected to inert electrodes made from a material such as carbon or a conductive polymer. Longline fishermen commonly use chemical or battery powered LED lights to attract tunas (*Thunnus* sp.) and swordfish. A BRD based on a battery-powered MCU device could present LEDs together with a weak electric field for deterring sharks. Small MCUs are already mass manufactured and relatively inexpensive and, pending a resolution to the issue of battery cost and performance, could represent a low-cost BRD.

Our laboratory-based study assessed the ability of a prototype BRD to reduce bait consumption by sharks. A novel aspect of this methodology is the use of an open-source MCU development board, an Arduino Uno, for BRD prototyping. This tool was particularly appealing because it is designed for users with no special skillsets in electronics or programming. We programmed the Arduino, powered by a 9 V battery and attached to a custom-made electrode array, to produce pulsed electric fields with a voltage gradient of up to 386 μV cm^{-1} at sites 10 cm from the electrodes. Our aim was to contribute to the development of an electronic shark BRD by investigating whether electrosensory stimulus produced by a battery-powered MCU could reduce bait consumption by groups of juvenile sandbar shark (*Carcharhinus plumbeus*) or adult spiny dogfish (*Squalus acanthias*). Longline fishing pressure has resulted in strong declines in sandbar shark populations in the Northwest Atlantic (Sminkey and Musick, 1995) and harvest is now prohibited in the western Atlantic Ocean, although the species continues to occur as bycatch (Marshall *et al.*, 2015). A BRD that deterred sandbar shark could support the recovery of this species. Spiny dogfish occur in temperate coastal waters world-wide, and are typically unwanted by commercial fisheries due to their low economic value. For example, spiny dogfish make up about a third of New Zealand's total shark catches across all commercial fisheries (MPI, 2013), with the majority of that spiny dogfish catch discarded at sea (MPI, 2014).

Material and methods

Experimental animals and arenas

Sandbar shark experiments were conducted at the Virginia Institute of Marine Science (VIMS) Eastern Shore Laboratory with the approval of the College of William and Mary Institutional Animal Care & Use Committee (permit IACUC-2014-08-05-9728-rwbrill). Spiny dogfish experiments were conducted at the University of Otago (UoO) Portobello Marine Laboratory with the approval of the UoO Animal Ethics Committee (permits 31/13 and 104/15). Sandbar shark were caught in salt marsh areas near Wachapreague, Virginia, using recreational rod and reel fishing gear equipped with circle hooks. They ranged from 52 to 85 cm total length (TL), which indicates that they were juveniles less than five years of age (Grubbs *et al.*, 2005). Spiny dogfish were caught near the mouth of the Otago harbour, using bottom longlines equipped with de-barbed circle hooks. They ranged from 52 to 82 cm TL, indicating that they were at or near maturity (MFish, 2010). Both sandbar shark and spiny dogfish experiments were conducted in 3.6 m diameter, 0.6 m deep plastic pools (Intex Corp., 2017), located either indoors (sandbar shark) or outdoors (spiny dogfish). During the sandbar shark experiment, the average water temperature was 23.8°C (± 2.3 SD), with an average salinity of 33.4 ppt (± 0.8 SD) and an average conductivity of 49.9 mS cm^{-1} (± 3.2 SD). The reciprocal of this conductivity value gives the resistivity of seawater in the experimental arena, 20.4 Ω cm. During the spiny dogfish experiment, average water temperatures were 15.1°C (± 0.92°C SD), with an average salinity of 34.4 ppt (± 0.96 ppt SD) and an average conductivity of 53.5 mS cm^{-1} (± 0.19 mS cm^{-1} SD), which gives an estimated conductivity of 18.7 Ω cm.

Each experimental unit was a group of three individuals of the same species. Spiny dogfish are socially facilitated feeders and typically do not feed when isolated from their conspecifics (Jordan *et al.*, 2011) so it was necessary to study them in groups. Like spiny dogfish, juvenile sandbar shark feeding motivation appeared more vigorous in the presence of conspecifics.

Electric stimuli

Experimental stimuli were generated with a prototype BRD that was made up of an Arduino Uno MCU programmed to produce an electric field with variable frequency and amplitude characteristics attached to a custom-made electrode array (Figure 1) and powered by a 9 V battery. Stimulus development was ongoing during the sandbar shark experiment; a single electric stimulus was then selected for use in the subsequent spiny dogfish experiment. Detailed descriptions of all electric stimuli, along with the

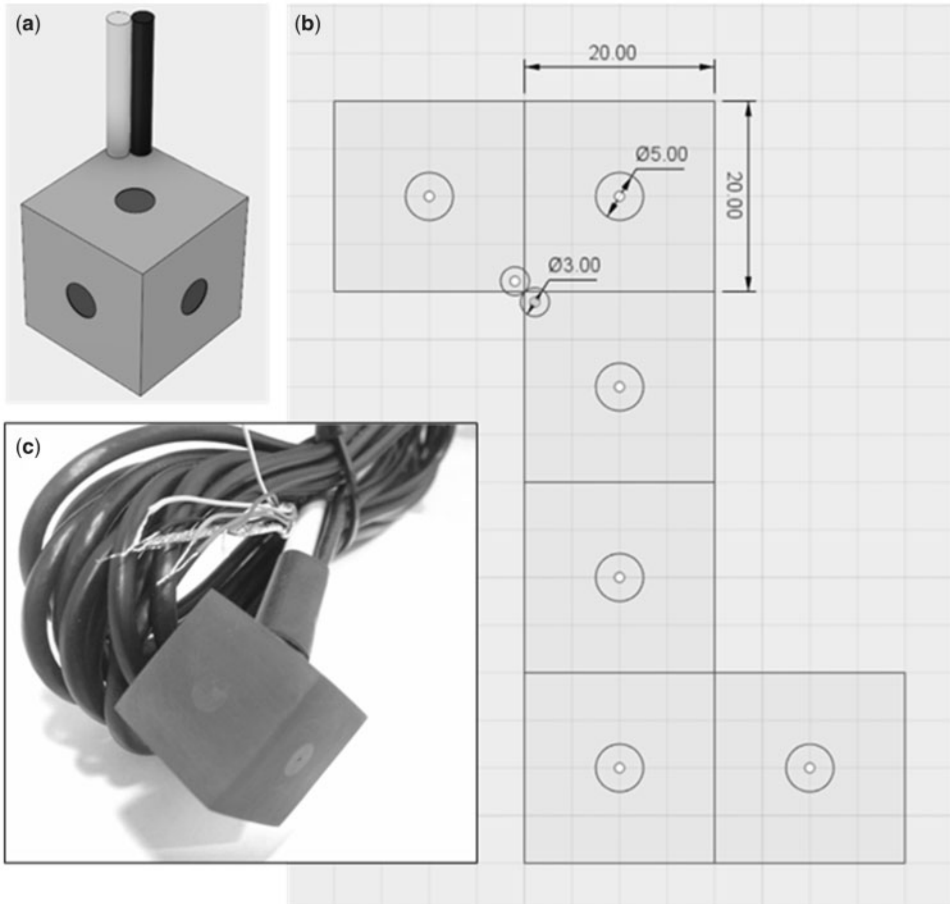

Figure 1. Model (a), plan (b), and photograph (c) of the die electrode array. One 5 mm diameter electrode is set into each of the die's six faces. The die is 20 mm^3 and the distance between each electrode is 18 mm. A cable and mounting rod (each 3 mm diameter) exit from one apex of the cube. Image credit (a) and (b): Chrissi Douglas-Hill.

relevant Arduino code, can be accessed in Supplementary Material. The different electric stimuli presented to animals during the sandbar shark experiment used 1.3–33 mA of current, employed frequencies between two and six Hertz, and were produced by two electrodes positioned 1.8 cm apart. This produced voltage gradients up 193 $\mu V\ cm^{-1}$ (3 s.f.) at a site 10 cm from the electrodes on the plane of the dipole axis, estimated using Kalmijn's (1982) formula ($\Delta V = (\rho * I * d / pi * r3^3)$) [Equation (1)] where $\rho = 20.4\ \Omega$ cm, $I = 33$ mA, $d = 1.8$ cm, and $r = 10$ cm. This formula models an electric field in half space, as when the electrodes are located on the tank floor, and has been validated with *in situ* measurements by Kajiura and Fitzgerald (2009). When electrodes were located in the water column instead of the tank floor, as in the sandbar shark experiment, the resulting voltage gradient was halved to give an estimate of the voltage gradient in whole space. Two other electrode arrays, used in a subset of trials and detailed in the Supplementary Material, produced voltage gradients up to 1 $mV\ cm^{-1}$.

All groups of sandbar shark experienced multiple electric stimuli produced by a cube-shaped electrode array that consisted of a 20 mm^3 plastic cube with a 5 mm diameter carbon electrode embedded in each of its six faces (Figure 1). Inside the electrode array, a copper wire was inserted into the base of every electrode and back-filled with conductive silver epoxy. A shielded cable, 3 m long, connected the electrode array to the MCU. Wires within the cable, each associated with individual electrodes, were plugged directly into pulse width modulation (PWM)-capable Arduino input/output (I/O) pins. In this way, it was possible to use as few or as many electrodes on a given electrode array as were required. The power source was a 9 V battery plugged directly into the Arduino "VIN" (voltage in) and ground pins.

Initially, all stimuli were direct current (DC), which was achieved by plugging one electrode directly into an Arduino ground pin, and the remaining electrode(s) into an I/O pin(s). Over time, electrodes developed pockmarks that were attributed to electrolysis; stimuli were therefore modified to use an alternating current (AC) that minimized electrode damage by swapping the "donor" electrode with each pulse of electricity. AC was achieved by unplugging the Arduino ground and plugging all electrodes into I/O pins. This took advantage of the I/O pins' low impendence state when designated as outputs, whereby each pin can act as a source or sink for up to 40 mA (Arduino, 2017). A Linrose bicolour LED in series was used during stimulus development to ascertain that the current was indeed AC; the LED lit up red when current was flowing in one direction, and green when the current flow was reversed. Fitzgerald (2002) demonstrated that sandbar sharks can detect AC stimulus, but we did not expect that sharks would be more or less averse to DC or AC stimulus.

Uncontrolled variation in stimulus amplitude occurred during some trials in the sandbar shark experiment. A 9 V nickel metal hydride (NiMH) battery was used to power the MCU, where one battery was selected haphazardly from a selection of eight apparently identical batteries. Although battery voltage was checked using a multimetre before each trial, one battery produced a voltage reading consistent with being "charged" but was later found to produce a maximum of only 4 mA while the other batteries produced a maximum of 33 mA. The issue initially went undetected because 4 mA was sufficient to turn on the Arduino's power light. Therefore, stimulus amplitude during most trials in the sandbar shark experiment cannot be defined beyond stating the range produced by different batteries. Subsequent to detecting this issue, all NiMH batteries were discarded and replaced with new lithium polymer (Li-Po) batteries. Current in the experimental circuit was then measured in series before each trial, with the electrode array submerged in seawater. A subset of sandbar shark groups ($n = 8$) underwent trials after this current supply issue was resolved, as did all spiny dogfish groups.

A pulsed, AC electric stimulus produced by two electrodes on the cube electrode array (Figure 1) was used throughout the spiny dogfish experiment (see: Supplementary Material). The duration of each pulse and inter-pulse interval was pseudo-randomly selected from between 80 and 250 ms, which corresponded to 2–6 Hz. Elasmobranch fishes are most sensitive to low frequency stimuli, and the frequency associated with peak electrosensory sensitivity varies among species (e.g. New, 1990; Tricas and New, 1998). The amplitude of each pulse was selected pseudo-randomly from between the PWM values of 85 and 255, where a value of "255" provided a 100% duty ratio (33 mA) and a value of "85" provided a 33% duty ratio (average current, 11 mA). This produced voltage gradients of 118–354 $\mu V\,cm^{-1}$ at a site 10 cm from the electrodes on the plane of the dipole axis, estimated using Equation (1), where $\rho = 18.7\,\Omega\,cm$, $I = 11–33\,mA$, $d = 1.8\,cm$, and $r = 10\,cm$. Random frequency and amplitude parameters mean that this stimulus made multiple gambles as to the specific voltage gradient that might have an optimal deterrent effect.

Experimental protocol

All animals were held in captivity for a minimum of two weeks before being used in an experiment, which was ample time for them to begin feeding consistently. Juvenile sandbar shark take four days at 23°C to empty their digestive tract (Medved *et al.*, 1988), so they were fed then fasted for four days before an experimental trial. Spiny dogfish take up to 4.7 days at 13°C to empty their digestive tract (Bangley and Rulifson, 2014), so this species was fed then fasted for five days before being used in a trial. Individuals were allocated to groups non-systematically. Dogfish groups were single sex, while sandbar shark groups were either single or mixed sex. This reflects the normal group composition of each species for their respective life history stages (Jensen, 1965; Compagno *et al.*, 2005). Each group was transferred from their holding tank to the experimental arena no less than 6 hours before a trial.

Trials were filmed using a GoPro Hero2 mounted either above the experimental arena for a bird's eye view (sandbar shark) or submerged and clipped to pool wall at the midpoint between the two bait stations for a lateral view of the stations (spiny dogfish). An olfactory stimulant was presented at the start of each trial. For sandbar shark, this was a menhaden (*Brevoortia tyrannus*) rinse and the bait was a ∼20 g piece of menhaden. For spiny dogfish, jack mackerel (*Trachurus declivis*) was used. At the start of each trial, we used a behavioural assay to determine whether groups of animals were motivated to feed. For sandbar shark, a "pass" involved at least one shark foraging in response to the olfactant within 2 min. "Foraging" was defined as an abrupt increase in swimming speed and turning frequency. In only one instance, a sandbar shark group failed the assay and was immediately fed to satiation and re-fasted, before undergoing a new trial four days later at which time it passed the feeding assay. For the spiny dogfish experiment, the feeding assay involved offering dogfish a pair of baits for 5 min at a time, three times in a row. A "pass" involved dogfish eating at least one of the pair of baits on at least two out of the three occasions. Out of 33 dogfish groups, three failed this assay and were released back to the wild without undergoing a trial.

For both sandbar shark and spiny dogfish, each trial involved repeatedly presenting a group with two baits for 5 min or until both baits were eaten, whichever occurred first. The two stations were then freshly baited and the procedure repeated *ad infinitum* until the animals reached satiation (sandbar shark) or three times only (spiny dogfish).

One bait was located on a station 10 cm from electrodes (the treatment), the other on a station two metres from electrodes (the paired control) (Figure 2). In the sandbar shark experiment, bait stations were located in the water column because experimental animals were typically observed to feed from the water column. For spiny dogfish, this method of bait presentation proved unsatisfactory, with pilot study animals searching vigorously for food on the tank floor immediately below the bait station. As a result, bait stations were presented on the tank floor during dogfish experiments, where animals readily located the baits.

For sandbar shark groups, satiation was defined as failing to eat either bait within 5 min in the presence of electric stimulus, then again failing to eat either bait after the stations were rebaited and presented in the absence of electric stimulus. The predetermined stopping point in the spiny dogfish experiment made satiation unlikely; an assumption supported by dogfish eating (on average) eight more pieces of fish offered after the trial had concluded.

Experimental design and data analysis

The sandbar shark experiment followed a repeated measures experimental design where each group of sharks was presented with a sequence of different electric stimuli (see: Supplementary Material), one at a time in a random order until they reached satiation ($n = 16$). Variation in the battery power supply, however, led to uncontrolled variation in stimulus amplitude during some sandbar shark trials. For this reason, the analysis of sandbar shark data simply assessed the percentage of baits eaten at the stations 10 cm and 2 m from the active electrodes. Groups of sandbar shark underwent up to four trials but contributed to the analysis only one data point per bait station. For example, one group of sandbar sharks was presented with electric stimuli five times over the course of two trials. They did not feed at the station 10 cm from electrodes (0% bait consumption), and they fed at the station 2 m from electrodes four times (80% bait consumption).

An independent control was used during the spiny dogfish experiment, where naïve groups of dogfish were randomly allocated

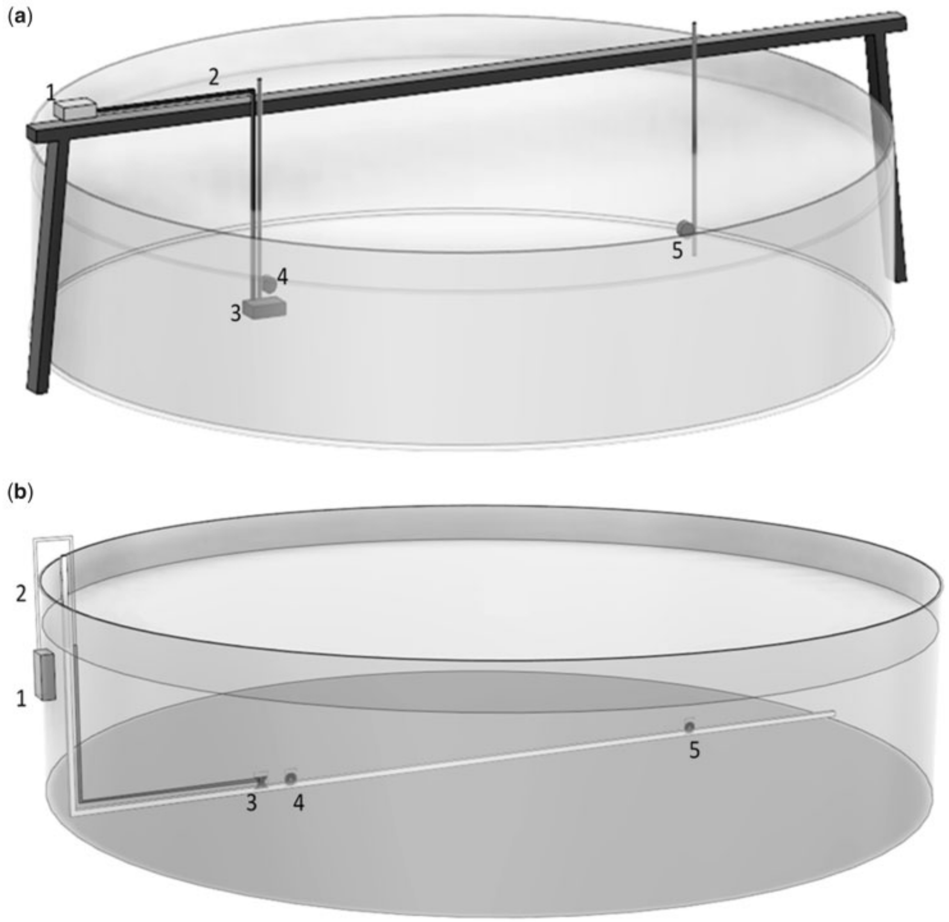

Figure 2. Schematic of sandbar shark (a) and spiny dogfish (b) experimental arena and apparatus, showing (1) stimulus generator, (2) cable connecting stimulus generator to electrodes, (3) electrode array, (4) bait located 10 cm from electrode array, and (5) bait located 2 m from electrodes. Image credit: Chrissi Douglas-Hill.

either a treatment ($n = 16$) or a control ($n = 14$). Electrodes were active throughout the treatment, or unplugged during the control. The paired control was retained to facilitate comparison between dogfish and sandbar shark results. The analysed metric was the percentage of baits eaten by each group from each bait station. Each group of dogfish underwent only one trial and the same electric stimulus was used throughout all trials.

Sandbar shark data were non-normal and data from the two bait stations were skewed in opposite directions. A paired one-sided sign test was used to test the hypothesis that the median percentage of baits eaten from the treatment station (located 10 cm from active electrodes) was less than that eaten from the paired control station (located 2 m from active electrodes).

Spiny dogfish data were also non-normal. A one-sided Mann Whitney U test was used to test the hypothesis that dogfish ate fewer baits at the station 10 cm from active electrodes compared with the same station during the control. A one-sided dependent samples sign test was used to compare the station 10 cm from active electrodes to the paired station 2 m from active electrodes. A two-sided Mann–Whitney *U* test was used to compare data from the station 2 m away from electrodes under treatment and control conditions. A two-sided sign test was used to compare data from the station 10 cm from inactive electrodes to the paired station 2 m away. The alpha level was set to 5% and the Bonferroni correction was applied so that a p-value ≤ 0.0125 indicated that the null hypothesis should be rejected. In each comparison, data shape and spread differed between datasets, so these tests should be interpreted as a comparison of distributions rather than medians.

Results

Most sandbar shark groups ate <20% of baits on the station located 10 cm from the active electrodes (Figure 3a). Most sandbar shark groups also ate 80% or more of the baits on the station located 2 m away from the electrodes (Figure 3b). Sandbar shark median bait consumption from the station located 2 m away from active electrodes was 87% (interquartile range [IQR] = 21%) (Figure 4). At the station immediately beside the electrodes, sharks ate only 13% of baits (IQR = 32%). This 74% decline in bait consumption between the two stations was highly significant ($S = 0$, $p < 0.001$). The sign test's S-statistic is a count of the positive differences between the data and the hypothesized median (R Development Core Team, 2014) and was zero because every group of sharks ate fewer baits at the station near electrodes than they did at the station far from electrodes.

During the spiny dogfish control, median bait consumption was 100% on both bait stations, although feeding behaviour appeared more consistent near electrodes than it was at the

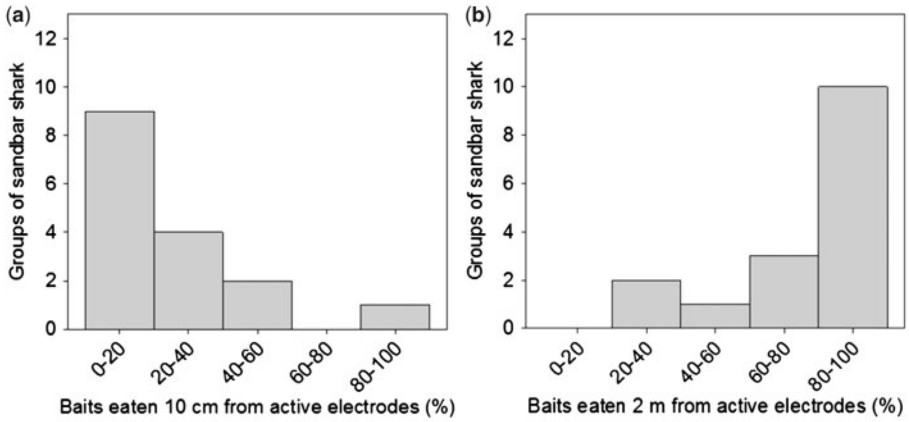

Figure 3. The frequency of sandbar shark bait consumption from stations near (a) and far (b) from electrodes producing weak electric stimuli ($n = 16$).

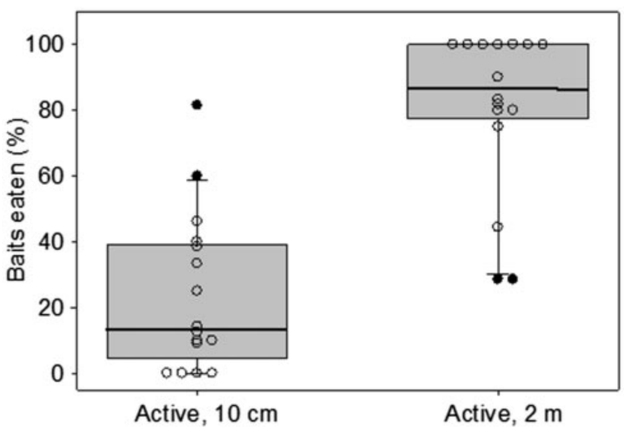

Figure 4. Sandbar shark bait consumption from stations near and far from electrodes producing weak electric stimuli. Circles represent the proportion of baits eaten by each group of sandbar sharks, horizontally offset for clarity ($n = 16$). Whiskers represent the nearest quartile plus or minus 1.5 times the interquartile range, but are only shown if this value differs from that quartile. Filled points represent value outside the 10–90th percentiles.

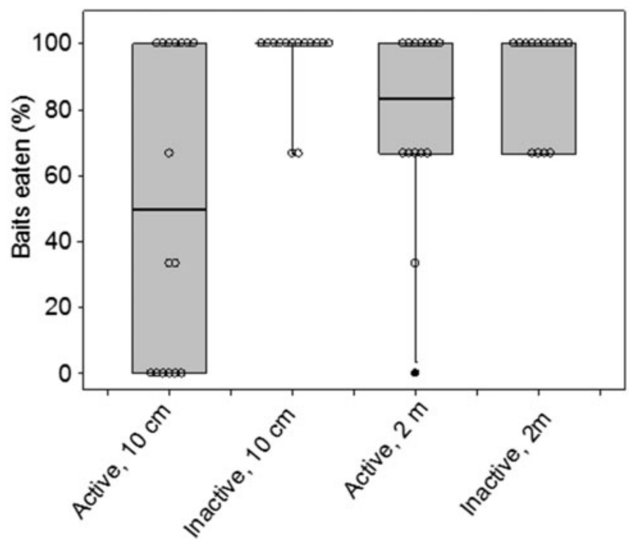

Figure 5. Bait consumption by groups of spiny dogfish at paired stations near and far from active ($n = 16$) or inactive electrodes ($n = 14$). Circles represent the proportion of baits eaten by each group of spiny dogfish, horizontally offset for clarity. Whiskers represent the nearest quartile plus or minus 1.5 times the interquartile range, but are only shown if this value differs from that quartile. Filled points represent value outside the 10–90th percentile range.

station 2 m away (IQR = 0% vs. 25%) (Figure 5). In the presence of the electric stimulus, median bait consumption on the station 10 cm from electrodes declined significantly ($U = 57$, $p = 0.004$) (Table 1), falling to 50% (Figure 5). This response was, however, highly variable as evidenced in the 100% IQR. On the station 2 m from electrodes, dogfish median bait consumption was not significantly different than the non-electric control ($U = 82$, $p = 0.2$). Likewise, median bait consumption in the presence of electric stimulus was not significantly different between the stations near and far from the electrodes when the Bonferroni correction was accounted for ($S = 0$, $p = 0.03$).

The effect of electric stimulus on spiny dogfish bait consumption at the station near to electrodes was bimodal, where almost half of the treatment groups of dogfish did not eat any of the baits, while five of the 16 treatment groups ate every bait offered (Figure 6a). In contrast, when bait was offered under control conditions (Figure 6b and d), groups of dogfish ate most or all of the baits presented to them.

Discussion

Electric stimuli strongly reduced sandbar shark and spiny dogfish bait consumption when bait was located near active electrodes. Juvenile sandbar sharks showed a 74% reduction in the median proportion of baits consumed from the station near active electrodes relative to a station 2 m away (Figure 4), while adult spiny dogfish showed a 50% reduction in bait consumption from the station near active electrodes, relative to the same station near inactive electrodes (Figure 5). The strong reduction in bait consumption near active electrodes indicates that this approach to shark bycatch reduction warrants further development. Field trials employing baited fishing gear are clearly required to determine if electronically generated electrosensory stimuli can effectively reduce bycatch of this species at similar rates to that observed in the laboratory. Caution should be applied when projecting possible

Table 1. Outcomes of sign and Mann–Whitney *U* tests comparing paired bait stations (10 cm and 2 m from electrodes) during spiny dogfish treatment (active electrodes producing weak electric stimulus, $n = 16$) and control conditions (inactive electrodes unplugged from power source, $n = 14$).

Bait station		Median bait consumption	Test statistic	*p*-Value (1 s.f.)
10 cm from active electrodes	10 cm from inactive electrodes	50% lower when electrodes active	$U = 57$	0.004*
10 cm from active electrodes	2 m from active electrodes	33% lower on station closest to electrodes	$S = 0$	0.03
10 cm from inactive electrodes	2 m from inactive electrodes	No change	$S = 3$	0.6
2 m from active electrodes	2 m from inactive electrodes	17% lower when electrodes active	$U = 82$	0.2

Comparisons that were significant at the 5% level after a Bonferroni correction are denoted with an asterisk.

field results from laboratory studies as electrosensory shark deterrents using captive sharks can produce larger effects than those attained using fishing gear in the field. For example, Stoner and Kaimmer (2008) found that an EPM near bait could reduce spiny dogfish bait consumption in the laboratory by up to 40%, but in their subsequent field trial, EPMs reduced spiny dogfish catch on fishing gear by only 19% (Kaimmer and Stoner, 2008).

Groups of spiny dogfish tended to eat either none of the baits offered near active electrodes or all of them, which produced an overall 50% reduction in bait consumption (Figure 6a). On the bait station far from active electrodes, spiny dogfish again ate either few baits or all baits, although many more groups ate all baits (Figure 6c). In contrast to the apparent bimodality evident when electrodes were active, in the absence of electric stimulus all groups of dogfish ate most or all baits (Figure 6b and d). These results offer insight into the highly variable results produced to-date by studies investigating electrosensory BRDs. For example, a pair of laboratory and field studies produced strong support for an electrosensory BRD aimed at spiny dogfish (Kaimmer and Stoner, 2008; Stoner and Kaimmer, 2008), but were followed by a study by Tallack and Mandelman (2009) which found that EPM ingots did not reliably deter spiny dogfish from bait in either the laboratory or the field. Further magnet and EPM field studies have since found deterrent effects on spiny dogfish (O'Connell *et al.*, 2014) as well as more non-significant outcomes for the same species (O'Connell *et al.*, 2011). Similarly, EPM-based deterrents have produced mixed results for sandbar sharks, with Brill *et al.* (2009) finding a strong deterrent effect in the field and Hutchinson *et al.* (2012) finding no effect on this species in the field. The inter-group variation in our spiny dogfish findings can be interpreted as support for the premise that differences among individual sharks' behaviour or the social dynamics within each group of sharks is a driver of the broader variation in shark responses to electrosensory BRDs seen across this area of research. In particular, preliminary observations during our experiments suggest that spiny dogfish bait consumption rates reflected the presence or absence of highly food-motivated or bold individuals in the group. If this was the case, the effect of an electrosensory BRD on spiny dogfish could be affected by the rate at which bold individuals were encountered. When the experimental unit is an individual shark rather than a group of sharks, the importance of individual variation to electrosensory deterrents' apparent efficacy is clear. Westlake *et al.* (2018) studied draughtboard shark (*Cephaloscyllium laticeps*) responses to rare earth magnets in proximity to bait and documented "substantial individual variation… both within and between treatments", as did Jordan *et al.* (2011) in their EPM deterrent-based laboratory study with smooth hound sharks (*Mustelus canis*).

An independent control was used in the spiny dogfish experiment, instead of the paired control in the sandbar shark experiment. The primary comparison in the spiny dogfish experiment was the difference in bait consumption at the station 10 cm from electrodes, when those electrodes were either active (treatment) or inactive (control). This focus was planned *a priori*, which is worth emphasizing because the spiny dogfish experimental design had the disadvantage of requiring multiple statistical tests to compare the four conditions. Multiple tests increase the risk of a type I error, although this was mitigated with the use of the Bonferroni correction. In contrast to the spiny dogfish experimental design, the primary comparison in the sandbar shark experiment was the difference between the bait stations near and far from the electrodes, which were always active. Sandbar sharks showed a strong, significant reduction in bait removal between these two stations. The same comparison for spiny dogfish shows that while dogfish ate 33% fewer baits on the station near active electrodes than they did on the station far from active electrodes, this difference was not significant (Table 1). The dataset from the bait station 10 cm from active electrodes had a lower quartile at zero and upper quartile at 100%, so the interquartile range encompassed the entire spread of possible outcomes (Figure 6). Therefore, despite the multiple comparisons, in the spiny dogfish experiment the risk of a type II error was high because the all-or-nothing response would be hard to detect unless there was an extreme and consistent difference, in either the spread of the data or the median (Hart, 2001), between the treatment and control. In this case, that is exactly what occurred, with the control data from the same station showing an extremely compressed distribution, with both the lower and upper quartiles at 100%. Future studies in this area might avoid this problem by offering baits until animals are sated, instead of offering a set number of baits. This would raise the issue of accurately distinguishing between satiation and deterrence, but it might also enable better detection of non-linear responses.

In a hypothetical situation where a bimodal reduction in spiny dogfish bait removal translated directly to the field, a BRD using electric stimuli might eliminate dogfish catches on half of the occasions that a spiny dogfish school is encountered while being ineffective the rest of the time. If this was the case, such a device may not meet fishing operators' performance requirements. In contrast to the spiny dogfish "all or nothing" bait consumption events pattern in the presence of electric stimulus, sandbar shark results included a gradient of responses. Sandbar shark bait consumption events at the station 10 cm from electrodes showed a positively skewed distribution with a steep drop off in frequency as bait consumption increased, and the reverse for the station 2 m from electrodes. If this outcome was replicated in the field, an electrosensory BRD would be a very promising method of reducing sandbar shark bycatch.

Direct comparison between spiny dogfish and sandbar shark experiments is difficult because different experimental parameters

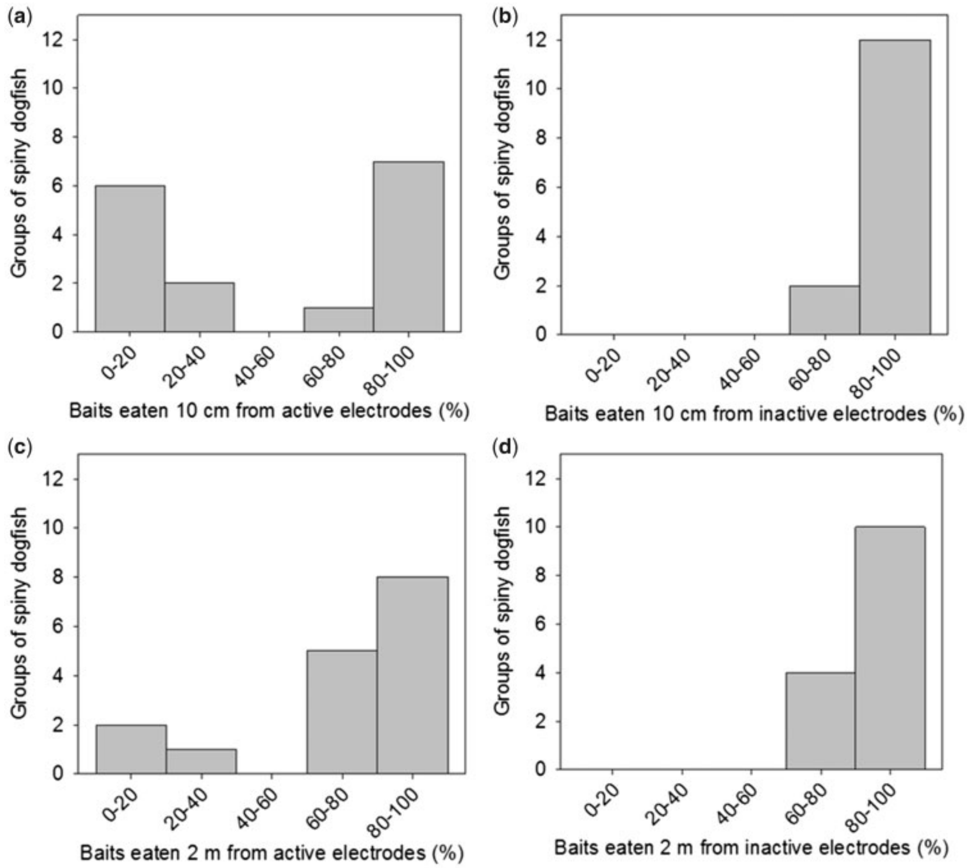

Figure 6. The frequency of spiny dogfish bait consumption from paired stations near and far from active ($n = 16$) or inactive electrodes ($n = 14$). The upper row represents bait stations located 10 cm from electrodes that are either active (a) or inactive (b). The lower row represents bait stations located 2 m from electrodes that are either active (c) or inactive (d).

were required to meet the two species' different behavioural and physiological requirements. Spiny dogfish required lower water temperatures than sandbar sharks, which in turn reduced water conductivity in the dogfish experiment. Sandbar sharks fed rapidly from bait stations located in the water column, while non-experimental spiny dogfish spent long periods of time searching the tank floor immediately below a midwater bait station, often failing to locate the bait despite foraging vigorously. Consequently, bait stations and electrodes were located on the tank floor during the dogfish experiment. This doubled the estimated experimental voltage gradients relative to those in the sandbar shark experiment [Equation (1)]. With these limitations in mind, sandbar sharks possess twice as many electroreceptors as spiny dogfish (Kajiura *et al.*, 2010), so they might reasonably be expected to be more responsive to electric stimuli.

Spiny dogfish bait consumption at the station 2 m from electrodes did not change significantly with the presence or absence of electric stimulus. Likewise, sandbar sharks ate most baits presented on the station 2 m from active electrodes. These findings indicate that an electrosensory shark BRD is only likely to be effective at close range, i.e. an electrosensory BRD would have to be present beside every bait. Longlines are constructed with a very long mainline that has many shorter branchlines clipped to it, each of which typically terminate in a single baited hook. For such an approach to be both economic and practical, the per-unit cost of the BRD would need to be very low. On the basis of consultation with 12 commercial fishermen who used either bottom longline gear to target ling (*Genypterus blacodes*) or surface longline gear to target tuna (*Thunnus* sp.) (Howard, 2018), a BRD mounted on every hook would need to be very small as well as neutrally buoyant in bottom longline fisheries where contact with the ground can result in sea lice damaging the catch. During personal communication, one skipper indicated that a "bead" type BRD that could be threaded onto the branchline and crimped at the desired distance from the hook would enable the BRD to be easily incorporated into existing gear when branchlines are made by the crew. Limiting electrolysis and galvanic corrosion is a critical part of maintaining a steel-hulled vessel, and this awareness is evident in the comments of a skipper who highlighted the risk for hook corrosion to be accelerated by the presence of a DC electric field.

A BRD small and inexpensive enough to be applied to every hook, which can number into the tens of thousands on large longlining operations, could be achievable using a MCU-based device. Electrosensory BRD research to-date has used magnets and EPMs to generate electric stimuli, but there are clear advantages in using a MCU-based stimulus generator instead of expensive EPMs that corrode rapidly in seawater. The components required to build an MCU-based BRD are already mass manufactured and thus relatively affordable. This is an area of rapid technological development so any discussion of specific components will probably become outmoded almost as soon as it is published. However, some examples of currently available components could be useful for researchers interested in extending this work. The Arduino Uno development board used in our study during prototyping has potential applications in a range of elasmobranch electrosensory behaviour research and is an affordable laboratory stimulus generator at only 22 USD (Arduino, 2018). This far exceeds the per-hook cost that is likely to be acceptable to a commercial fisherman, but a BRD would not require an entire development board. One example of the variety of small MCUs that might be used to control an electronic BRD is the Atmel range of ATtiny MCUs, which are $<13\,mm^3$ in size and presently cost ~0.24–0.69 USD per unit wholesale (Microchip Technology Inc, 2018a, b). ATtiny MCUs have an operating voltage of 1.8–5.5 V and, like the Arduino Uno, possess I/O pins capable of producing a sustained maximum output of 40 mA (e.g. Atmel, 2011; Arduino, 2017). This indicates that they could produce stimuli similar to that employed in the present study, where experimental circuits used a maximum of 33 mA. A newer example of a potentially suitable MCU is the Kinetis KL03, which is $<2.0\,mm^3$ in size, possesses I/O pins capable of producing up to 20 mA (NXP Semiconductors, 2017), and costs ~0.52 USD per unit (NXP Semiconductors, 2018). The lower recommended maximum output current probably limits the maximum voltage gradients a BRD using the Kinetis KL03 could produce. However, our study did not establish the optimal voltage gradient or gradient range for a deterrent effect. A circuit using less than the 33 mA maximum in the present study might still successfully deter sharks from bait.

Battery life, size and cost represent another unresolved issue in BRD development. Both the ATtiny range and the Kinetis KL03 consume very little power when inactive, using as little as 25 µA and 77 nA when in an idle or "deep sleep" state, respectively (Atmel, 2016; NXP Semiconductors, 2017). Low-power MCUs could maximize battery life by using sensors to determine immersion, movement or some other parameter to indicate either fishing activity or shark proximity. The MCU could sleep when not fishing or not in proximity to a shark, and wake when immersed or approached by a shark.

In conclusion, results from the sandbar shark experiment indicate support for the further development of an electrosensory BRD for this species or related carcharhinid species involved in global longline bycatch. The sandbar shark experiment did not succeed in identifying the optimal stimulus parameters for an electrosensory BRD for this species, but the strong and relatively consistent effect of pooled electric stimuli suggests that most electric fields in the range trialled were effective. Results from the spiny dogfish experiment found a significant reduction in bait consumption when an electric stimulus was present, but the bimodal nature of this effect suggested that the stimulus employed may not be effective enough for a commercially implemented BRD. The behavioural implications of different electric stimuli parameters are still poorly understood, and it is possible that further research into optimising these parameters could improve the deterrent effect of an electrosensory BRD on spiny dogfish.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

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