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Potential of electric fields to reduce bycatch of highly threatened sawfishes

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ABSTRACT: Sawfishes are among the most threatened families of marine fishes and are susceptible to incidental capture in net fisheries. Since bycatch reduction devices currently used in trawl fisheries are not effective at reducing sawfish catches, new methods to minimise sawfish bycatch are needed. Ideally, these should affect sawfish behaviour and prevent contact with the fishing gear. We tested the effects of electric fields on sawfish behaviour to assess the potential of electric pulses in mitigating sawfish bycatch. Experiments were conducted in a tank where 2 electrodes were suspended in the water column, connected to a pulse generator, and placed across the swimming path of sawfish. Two largetooth sawfish *Pristis pristis* were tested in control conditions, in the presence of a baseline pulse, and of 5 variations of that pulse where 1 parameter (polarity, voltage, frequency, pulse shape, pulse duration) was altered at a time. Conditional inference trees were used to identify the effects of various parameters (e.g. treatment, individual) on reaction type, reaction distance, twitching presence and duration, and inter-approach times. Sawfish reacted to electric fields, but reaction distances were small (typically <1.2 m), and no field tested consistently led to reactions conducive to escaping from moving nets. The following parameters induced the most response in both individuals: bipolar current, rectangular shaped, 5–10 Hz, ~1500 µs duration, and 100 V. We recommend further research focussing on moving nets, testing a V-shaped electric array preceding the net mouth by at least 5 m, and testing a setup similar to electrotrawling.

KEY WORDS: Bycatch reduction devices · Electric repellents · Sawfish · Prawn fisheries · *Pristis pristis* · Trawl fisheries

1. INTRODUCTION

The incidental capture of bycatch species is an important issue in fisheries worldwide (Hall & Mainprize 2005), with the impacts of fishing activities (including bycatch interactions) under increased scrutiny (Suuronen & Gilman 2020). Of all gear types, trawl fisheries produce the highest discard rates (Zeller et al. 2018, Gilman et al. 2020). This has led to the development of a range of gear innovations such as bycatch reduction devices (BRDs) and turtle excluder devices (TEDs), which are designed to reduce the catch of non-target species.

In Australia, the Northern Prawn Fishery (NPF) is the largest prawn trawl fishery (by area) and the most valuable Commonwealth-managed fishery (Patter-

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son et al. 2019). However, trawl effort occurs within the distribution of several threatened species, including sawfishes (Stevens et al. 2008). Although the introduction of TEDs and BRDs in 2000 successfully reduced the catch of many species, sawfishes (Pristidae) are still regularly caught (Brewer et al. 2006). For example, in 2019, the NPF recorded 607 sawfish interactions, of which 67 % were released alive (Laird 2020). Due to their life-history characteristics and morphology, sawfishes are highly susceptible to anthropogenic mortality, which has led to population declines (Simpfendorfer 2000, Stobutzki et al. 2002), and are now among the most threatened families of marine fishes globally (Dulvy et al. 2016).

Australia's northern coastline is one of the few remaining places in the world where viable sawfish populations occur. Current protected areas only cover a limited percentage of the sawfish species' distributions (Devitt et al. 2015). Four sawfish species are encountered in the NPF: narrow sawfish *Anoxypristis cuspidata*, largetooth sawfish *Pristis pristis*, green sawfish *P. zijsron*, and dwarf sawfish *P. clavata*. These species are listed on the Convention on International Trade in Endangered Species (CITES) Appendix I and the Convention of Migratory Species (CMS) Appendices I & II. These species are also listed on the IUCN Red List of Threatened Species as Critically Endangered (*P. pristis* and *P. zijsron*) or Endangered (*A. cuspidata* and *P. clavata*).

The threatened status of sawfishes, combined with their susceptibility to capture (Dulvy et al. 2016), limited refuge in protected areas (Devitt et al. 2015), the inefficiency of TEDs and BRDs in reducing sawfish bycatch (Brewer et al. 2006), and continuing captures despite temporal and spatial closures (Laird 2020), require the development of new approaches to minimise sawfish interactions with prawn trawls. The bycatch mitigation strategies currently used in the NPF typically allow unwanted species to escape after entering the nets. However, due to their long, toothed rostra and escape behaviour, sawfish are prone to entanglement in trawl nets (Brewer et al. 2006, Wakefield et al. 2017). A mechanism that repels sawfish before they enter the net would be necessary to reduce sawfish bycatch (Jordan et al. 2013). Such technology should repel sawfish at a distance far enough to allow them to effectively swim away from the trawl path.

The sensory capabilities of elasmobranchs have been used to develop repellent technologies, including electrical-based repellents (electric pulses, permanent magnets, electropositive rare earth metals) and semiochemicals (Hart & Collin 2015). These technologies use electrosensory or chemical stimuli to deter elasmobranchs, with the aim to reduce bycatch (e.g. Jordan et al. 2013) or minimise shark interactions with water users (e.g. O'Connell et al. 2014a, Huveneers et al. 2018). Electric pulses have the highest potential to reduce sawfish bycatch (Jordan et al. 2013); as with other elasmobranchs, sawfish have highly sensitive electroreceptors, the ampullae of Lorenzini, that allow them to detect and capture prey (Wueringer 2012, Wueringer et al. 2012). Other methods, such as strong magnets or rare earth metals, only affect some elasmobranchs and within very short distances (i.e. <0.5 m) (e.g. Rigg et al. 2009, Westlake et al. 2018), with several species unaffected (e.g. Tallack & Mandelman 2009, Grant et al. 2018). Necromones or semiochemical deterrents can also be effective at repelling sharks (Stroud et al. 2014, O'Connell et al. 2014b). However, these are only effective at the dispersal location and for a short period because dilution rapidly reduces concentration. The effect of such deterrents on other species, including targeted species, is unknown. In contrast, several elasmobranch species respond physiologically and behaviourally to weak, low-frequency electric fields as low as <1 nV cm^{-1} (e.g. Kajiura & Holland 2002, Jordan et al. 2011). Moreover, devices that produce electric fields have been successfully incorporated in prawn and flatfish trawlers (Soetaert et al. 2015, Verschueren et al. 2019), showing that such technology can be logistically used in commercial fishing vessels. For example, the use of electrotrawling in the brown shrimp *Crangon crangon* fishery in the North Sea resulted in an average bycatch reduction of 35 % and a significant decrease in seabed contact, without affecting prawn catches (Verschueren et al. 2019).

Field studies using personal shark-bite deterrents suggest that sharks can detect and react to electric pulses from distances up to 5–6 m (Huveneers et al. 2013, 2018). It is thus possible that sawfish can detect and react to electric fields at similar distances. Therefore, the aim of this study was to test the effect of electric fields on sawfish behaviour to determine the potential of electric pulses to mitigate sawfish bycatch. The specific objective was to assess if and, if so, how sawfish behaviourally respond to electric fields. To prevent capture, the ideal response would be for sawfish to be repelled by the electric field and swim away from the path of the approaching trawl. Since sawfish have burst speeds of up to 2.8 m s^{-1} (Simpfendorfer & Wiley 2006), and the 9.5–16.5 m wide nets of the NPF trawl at speeds of 1.6–1.8 m s^{-1} (Bishop & Sterling 2007), we estimate that, to successfully escape the moving nets, sawfish would need to respond to the electric field when within ~5.5 m from the electrodes. This value was calculated assuming that a sawfish was positioned halfway between the edges of a 16.5 m wide net and would respond to the electric field by swimming sideways parallel to the net. That sawfish would need to swim for 8.25 m (half the net width) to avoid capture, which, at the maximum burst speed recorded for sawfish (2.8 m s^{-1}; Simpfendorfer & Wiley 2006), would take 3 s. In those 3 s, a net travelling at 1.8 m s^{-1} would have moved 5.4 m, meaning sawfish would need to respond and swim away from the path of the net when within at least ~5.5 m. If sawfish respond by swimming away from an approaching net at an angle, then the reaction distance needed would be smaller, e.g. at 45°, it would need to respond within 4.2 m. Note, however, that the calculations of reaction distance reflect escaping a single net, while most of the NPF fleet currently uses quad gear (i.e. 4 nets), so a sawfish could escape one net and swim into the path of another. Nevertheless, promising results could lead to this technology being incorporated into prawn trawl gear to reduce sawfish bycatch.

2. MATERIALS AND METHODS

2.1. Animal capture and housing

Two *Pristis pristis* (sawfish 1: 1.02 m total length [TL]; sawfish 2: 1.65 m TL, both males) were caught from the Norman River (17° 30′ S, 140° 51′ E), North Queensland, Australia, in April 2019 using light-weight multistrand set nets (mesh size 20–50 mm). Nets were continually monitored to quickly remove sawfish upon capture. Captured sawfish were transported to the Biopixel/James Cook University (JCU) Aquarium facilities in Cairns (North Queensland, Australia) in 1200 l round tanks. Air was pumped through a carbon block air stone and dissolved oxygen content was monitored. On arrival, sawfish were kept in 3 m diameter holding tanks for 4 wk to acclimate to aquarium water conditions. Sawfish were then moved into the 4.6 × 6.0 m experimental tank where they were acclimated for a further 4–5 d prior to the commencement of the experiments. The experimental and holding tanks are part of a closed system, with seawater sourced from a local estuary (Trinity Inlet, Cairns). Water salinity, temperature, and pH were monitored daily. Ammonia, nitrite, nitrate, carbonate hardness (KH), calcium, and phosphate were monitored weekly.

Sawfish were fed dead fish (mostly mullet [Mugilidae] and pilchards [Clupeidae]), squid (Loliginidae), and prawns (Penaeidae) twice a day. Uneaten food was collected at the end of the day. Sawfish were kept in separate tanks, with one animal in the larger experimental tank, and the other in a smaller (3 m diameter) holding tank. Sawfish body condition, feeding behaviour, swimming behaviour, and body attitude were assessed daily to monitor health and wellbeing.

2.2. Experimental arrangement

Experiments took place in a 4.6 × 6.0 m fibreglass tank with a water depth of 64 cm and a ~2 cm layer of sand with some rocks on the tank floor. The electrode arrangement was based on the Ocean Guardian Freedom7, a commercially available portable personal device that emits an electromagnetic field to discourage sharks from approaching divers, spear fishers, and other recreational water users (Huveneers et al. 2013, Kempster et al. 2016). It therefore consisted of 2 galvanised steel electrodes (each 40 cm long) placed in line and 112 cm apart (Fig. 1). The electrode setup was hung horizontally halfway through the water column (Fig. 1). To keep in place, the electrodes were tied to a wooden beam with fishing line. The beam was held ~12 cm above the water surface by 2 round floats (25 cm diameter) tied at its ends (Fig. 1). The electrodes were then connected, via 12–15 m long power leads, to an adjustable laboratory pulse generator (LPG1; EPLG).

The pulse generator produces electrical pulse stimuli and allows the user to independently adjust pulse parameters including polarity, voltage, frequency, pulse duration, and pulse shape. When connected to the electrodes, it generates an electric dipole that produces an electric field in the surrounding water. The pulse generator can reach a maximum output of 150 V, 280 A, and 42 kW, and is equipped with a feedback system to ensure that the output matches the set values. An oscilloscope (Agilent Technologies, DSO1072B) was used to measure the characteristics of each pulse to verify the pulses generated by the pulse generator and to ensure the desired pulse was present on the electrodes.

Although our electrodes were made of galvanised steel while the Ocean Guardian Freedom7 uses stainless steel, the use of a different type of steel does not affect how the electrical current passes through the electrodes and into the seawater, meaning electric field characteristics should not differ. To confirm this, an Ocean Guardian Freedom7 was tested under similar conditions to our experimental arrangement (i.e.

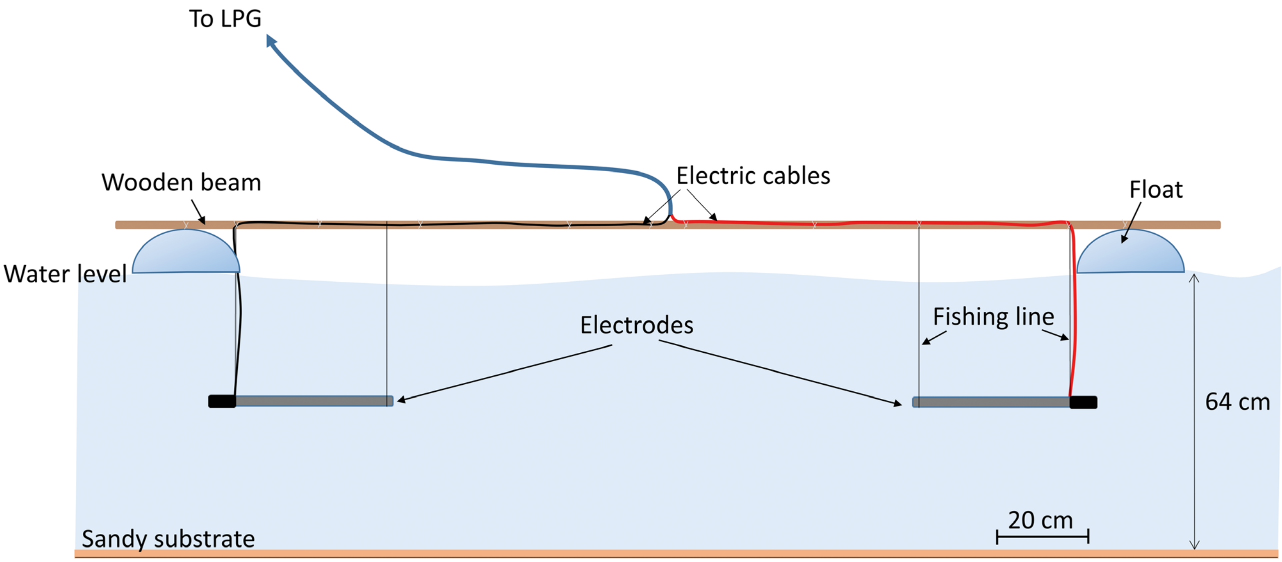


Fig. 1. Electrode arrangement, showing 2 galvanised steel electrodes (40 cm long, 1.5 cm diameter) attached to a 2.4 m wooden beam by fishing line and kept above the water by 2 floats (25 cm diameter). Electrodes are at 112 cm distance from each other, and each is connected to a 14 gauge power lead (20–23 m long) that connects to the laboratory pulse generator (LPG)

Table 1. Pulse parameters used for each treatment and of the 2 devices upon which the experimental electrode arrangement was based: Ocean Guardian Freedom7 and Rpela (source: Chateauminois et al. 2019). For each of the 6 electrified treatments, the parameter that differs from the Baseline pulse is in **bold**. N: number of experiments run for sawfish 1 and 2; AC: alternating current; BC: bipolar current; DC: direct current

	Polarity	Shape	Frequency (Hz)	Duration (µs)	Peak voltage (V)	N (1/2)
Treatment						
Control	No current	–	–	–	–	(3/3)
Baseline	BC	Rectangular	5	1500	100	(2/2)
AC	**AC**	Rectangular	5	1500	100	(2/2)
Exponential	BC	**Exponential**	5	1500	100	(2/2)
10 Hz	BC	Rectangular	**10**	1500	100	(2/2)
500 µs	BC	Rectangular	5	**500**	100	(2/2)
50 V	BC	Rectangular	5	1500	**50**	(3/2)
Other devices						
Freedom7	BC	Exponential	1.5	1000	115	
Rpela	DC	Close to rectangular	14.7	200	200	

attached to the wooden beam with fishing line and placed at the same location and depth as the experimental electrodes), and oscilloscope measurements confirmed that the waveforms of our experimental setup and that of the Ocean Guardian Freedom7 were the same (Table 1).

For the trials, the wooden beam was placed perpendicular to and against one side of the tank, in the swimming path of the sawfish (Fig. 2a; Fig. S1 in the Supplement at www.int-res.com/articles/suppl/n046p121_supp/). Although placement in the middle of the tank would minimise the effect of the tank boundaries on the electric field, this arrangement was chosen as it allowed quick removal of the electrodes from the water when needed. The positioning of the electrodes near the non-conductive tank edge resulted in an electric field stronger at the edge side than it would be if the electrodes were placed in the middle of the tank (see Fig. S1). Regarding electric field propagation, higher voltages lead to larger electric field sizes, while changing pulse width or frequency has no effect on the field strength or shape. These concepts are described in more detail by Soetaert et al. (2019). The electric field strengths for a similar setup (Ocean Guardian Scuba7) placed in mid-water, close to the surface, and close to the seabed can be seen in Figs. 4 & 5 of Thiele et al. (2020).

Initial observations showed that sawfish swimming between the electrodes could display signs of distress combined with an inability to move out of the electric field. In such situations, the experiment was interrupted, and the electrodes promptly removed from the water (Fig. 2b).

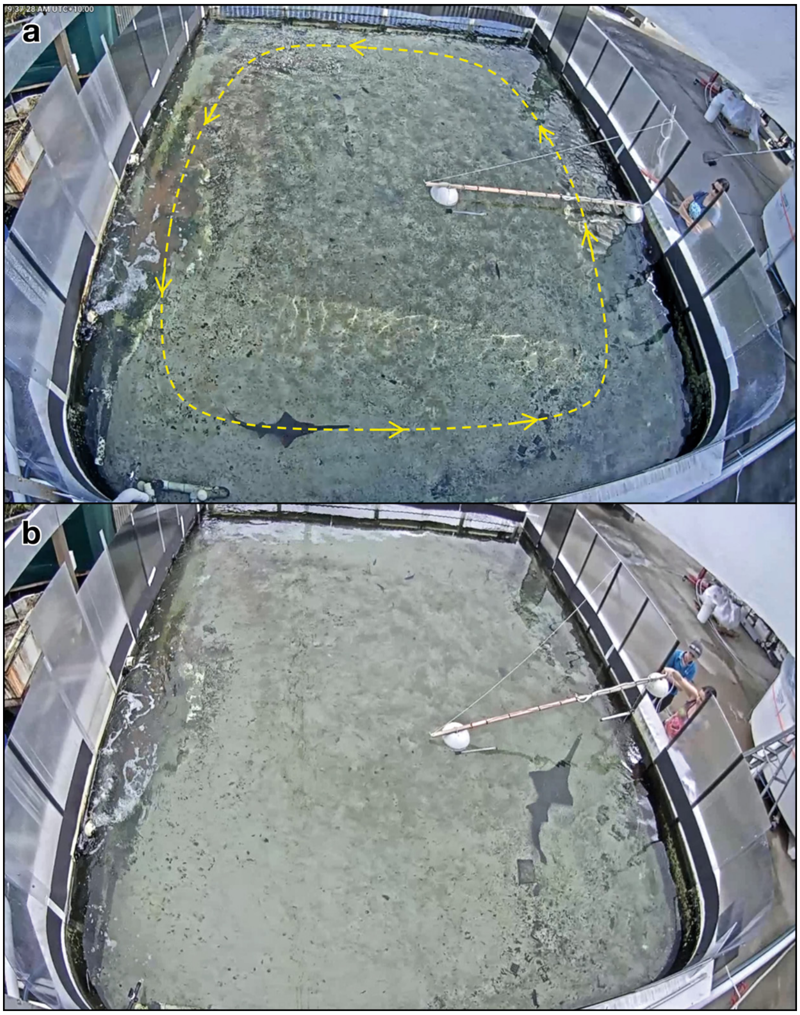


Fig. 2. Overview from the overhead video camera. (a) Positioning of the electrodes and the observer, and the swimming path typically taken by the sawfish just before the beginning of each experiment (yellow dashed line). (b) Operator removing one of the electrodes from the water after the sawfish showed signs of distress during the Exponential treatment (see Table 1 for treatment details)

2.3. Treatments

The first step of this study involved determining if a strong electric field induces a fleeing response in sawfish. Therefore, pilot trials were conducted (separately from the data shown) over 2 days (13–14 May 2019), to select a waveform that provoked a fleeing response. The initial selection of the waveform parameters was guided by the field characteristics of the Ocean Guardian Freedom7 (ocean-guardian.com.au/collections/dive-series/products/freedom7) and Rpela (rpela.com) recreational shark repellents (see Table 1 for pulse characteristics). In those trials, pulses of different polarity (alternating current [AC] or bipolar current [BC]), shape (rectangular or exponential), voltage (25–150 V), frequency (1–20 Hz), and duration (200–2000 µs) were tested, resulting in the selection of a waveform that seemed to best deter sawfish (hereafter referred to as 'Baseline', Table 1). Note that frequency in the present study refers to the number of uninterrupted pulses per second, because this has more relevance for the reaction of the sawfish. Therefore, for AC, where a positive and negative pulse are emitted as one uninterrupted stimulus (see Fig. S2f), this corresponds to the standard definition of frequency, i.e. to the number of unique pulse cycles per second. For BC, this corresponds to the so-called 'apparent frequency', i.e. to the number of stimuli per second (see Fig. S2a–e), as defined by Soetaert et al. (2019), which is twice as high as the standard frequency. Indeed, bipolar (pulsed) current is characterised by a temporal break between each positive and negative pulse, and as a result the animals experience 2 separate stimuli per unique pulse cycle.

Sawfish behaviour was tested in presence of the Baseline pulse stimulus and 5 variations of that pulse (Table 1; Fig. S2), where only one parameter was altered to assess the effect of that change. The extremes used for each parameter were based on observations during the pilot trials. For example, low frequencies of 1–2 Hz led to almost no response, while at 5–10 Hz, sawfish were still able to escape the electric field despite twitching, and at a higher frequency of 20 Hz strong involuntary muscle contractions of the fins and body were observed, which led to immobilisation. Therefore, 5 and 10 Hz were used as extremes (Table 1). In general, the voltage measured by the oscilloscope at the electrodes (in-water) was within 5 V of the value set at the pulse generator (Fig. S2). Sawfish behaviour was also tested in control conditions, i.e. with the pulse generator inactive and electrodes in the water, to account for the behavioural response of sawfish to the physical presence of the device.

Experiments were run over 5 d for sawfish 1 (spread between 3 and 13 June 2019), and over 7 d for sawfish 2 (spread between 21 and 29 May 2019), following acclimatisation to the experimental tank of 4–5 d. Up to 3 electrified treatment sessions were run per day. In total, each individual was subjected to 2–3 trials for each treatment type. Treatments were done in a random order and typically took less than 10 min. To prevent sawfish associating the experimental arrangement with strong electric fields, the equipment was placed in the water without electric fields activated for ca. 30 min before and after each experiment. The equipment was also left in the water for extended periods after trials, and sometimes between trials. As with the electrified experiments (see below), an observer or other aquarium personnel regularly positioned themselves at the observation site to limit the effect of the presence of the observer on sawfish behaviour.

For the electrified treatments, electrodes were only turned on after sawfish established a circular swimming pattern to increase the likelihood of sawfish approaching the electrode arrangement several times throughout the trial (e.g. trials were not initiated when sawfish were resting on the substrate). We initially aimed to obtain data from at least 5 approaches per trial, i.e. to describe sawfish behaviour when attempting to swim through the electric field 5 times. However, sawfish did not always approach the electrode arrangement 5 times during the trials. In those cases, the experiments were left to run for 10–12 min.

2.4. Data collection and analysis

During the experiments, an observer was positioned at ~0.5 m from the edge of the tank (see Fig. 2). For consistency, the same observer recorded all behaviours and measurement estimates, but these were regularly confirmed by a second observer. During the trials, the pulse generator was turned on only when the sawfish was swimming >3 m away from the electrode arrangement to avoid startling the animal. The observer recorded the time of approach, the angle of approach, reaction distance, and type of reaction. Reaction distance was estimated as the distance at which a sawfish showed a reaction to the experimental arrangement (e.g. by rapidly moving its head side to side, twitching its whole body, or changing speed or direction). Distances between the sawfish and the electrodes were estimated using the 60 cm skirting panels placed around the experimental tank.

Experiments were also recorded with a video camera placed above the tank, and video footage was used to code sawfish behavioural responses using the open source event-logging software 'Behavioural Observation Research Interactive Software' (BORIS v.7.7.3) (Friard & Gamba 2016). For these analyses, a range of behaviours were defined and encoded as point events (for short behaviours) or state events (for longer behaviours for which time is recorded) (Table 2). Due to the non-central positioning of the overhead camera (see Fig. 2) and the variability in swimming depth, distances were more accurate when directly estimated by an observer rather than through video footage. Therefore, data on reaction distances were taken from direct observations. Data were tabulated into ethogram tables, which were used to produce timelines of the observed behaviours and to quantitatively analyse the data to describe the responses of sawfish to the different treatments.

Upon swimming towards the electrodes, 4 different reactions were observed: (1) Turning back: the sawfish turned back after sensing the electric pulses (see Videos S1 and S2 at www.int-res.com/articles/suppl/n046p121_supp/); (2) Swimming parallel: the sawfish changed swimming direction and continued on a path parallel to the electrodes, along the wooden pole (see Video S5); (3) Swimming between: the sawfish continued its path and swam between the electrodes (see Videos S4 and S5); and (4) Freezing: the sawfish moved its head side to side with the rostrum at 30–45°, while seemingly losing the ability to swim away from the electric field (see Video S6) (Table 2; Fig. S1). The first behaviour (turning back) would be the most desirable for the development of a sawfish repelling device, as it would mean that the animal would actively turn back and swim away from a net, displaying an effective escape behaviour. The second behaviour (swimming parallel) can also be considered a positive outcome, as it means the sawfish can sense the electric field, actively responds to it, and swims away from the direction of the trawl. The last 2 behaviours (swimming between and freezing) are not desirable, as both would lead to the sawfish being entangled in the mesh. Indeed, when entering trawling nets, sawfish teeth typically get entangled in the forward sections of the nets (Wakefield et al. 2014, Campbell et al. 2020), and when freezing, sawfish become stationary and start twitching, quickly moving their heads side to side with the rostrum up, which would lead to teeth being entangled on contact with the net, even if the animal does not enter the net.

Conditional inference trees (Hothorn et al. 2006) were used to identify the effects of individual, treatment, treatment day, session number, trial number,

Table 2. Ethogram showing the behaviours recorded for the quantitative analysis of sawfish reaction to the various electric fields. Behaviour types: point events, for short behaviours; state events, for longer behaviours for which time is recorded

Category	Behaviour	Behaviour type	Description
Activity	Swimming	State	Sawfish is swimming throughout the tank
	Resting	State	Sawfish is resting on the substrate
Approach	Approach	Point	Sawfish swims towards the experimental arrangement
Direction of approach	Direction of approach	Point	Direction of the swim in relation to the electrode arrangement. Classified as 'towards the area between the electrodes', or 'towards the electrode placed in the middle of the tank'; see Fig. S1
Reaction distance	Reaction distance	Point	Distance from the electrodes at which the individual showed a reaction. Reaction could be e.g. head twitching or changing swimming speed and/or direction
Reaction type (see Fig. S1)	Turning back	Point	Sawfish turned around ~180° after sensing the electric field, and typically swam away at higher speed; see Videos S1 & S2
	Swim parallel to electrodes	Point	Sawfish changed direction to swimming parallel to the electrode arrangement, towards the middle of the tank, after sensing the electric field; see Video S3
	Swim between electrodes	Point	Sawfish swam between the electrodes, through the middle of the electric field; see Videos S4 & S5
	Freeze	Point	Sawfish tensed its muscles, including fins and body, quickly moving the head side to side in a stationary position, while seemingly losing the ability to swim away from the electric field; see Video S6
Twitching	Twitching	Point	Presence/absence of twitching (yes/no)
	Twitching duration	State	Duration of twitching behaviour

approach number, and time of the day on (1) reaction distance, (2) reaction type, (3) twitching presence, (4) twitching duration, and (5) inter-approach times (see Table 3 for details). Trees were constructed using the function 'ctree()' in the R package 'party' (Hothorn et al. 2010, 2015). Conditional inference trees use significance test procedures to recursively split the dataset into 2 relatively homogeneous and mutually exclusive groups based on only 1 explanatory variable (Hothorn et al. 2006), therefore identifying the predictor variable(s) that best explain(s) the variability in the dependent variable. This non-parametric method can be applied to a range of data (e.g. nominal, ordinal, categorical, unbalanced) and leads to easy-to-interpret graphical results in the form of a tree, with the root node at the top, representing the overall dataset, from which branches and leaves emerge, representing the final groups and the explanatory variables responsible for group formation.

The use of conditional inference trees allowed for the use of each individual repeatedly by including independent variables related to time as continuous predictors (Table 3). Although repeatedly testing on the same individual leads to some shortcomings, it has the advantage of allowing for the testing of conditioning, learning, or habituation, where it is possible to determine if the sawfish becomes accustomed to the electric fields and changes its behavioural response through time.

3. RESULTS

For both sawfish, the typical behaviour (with electrodes out of the water) was to swim in a circular pattern along the edge of the tank, sometimes stopping by the water outlet with the rostrum breaking the water surface. Resting on the substrate was also commonly observed. Water conditions were similar for the 2 sawfish, with water temperatures (measured between 08:00 and 09:00 h) ranging between 24.5 and 26.0°C (mean ± SD = 25.0 ± 0.5°C), and salinities between 31.2 and 32.5 ppt (31.9 ± 0.5 ppt). Based on the measured salinity and temperature values, the estimated seawater conductivity was 47.6–49.4 mS cm^{-1} (average 48.3 mS cm^{-1}) (Lide 2002).

We recorded 201 approaches to the electrodes, including 166 (82.5%) towards the area between the

Table 3. Parameters used in the quantitative analyses of sawfish behaviour in response to the different electric fields. TL: total length

	Description	Predictor type
Independent variables		
Individual	One individual sawfish. Tests were done on 2 individuals: sawfish 1 (1.02 m TL) and sawfish 2 (1.65 m TL)	Categorical
Treatment	One of the 7 treatments (including a Control treatment) used to investigate sawfish reaction to the electric fields. See Table 1 for pulse characteristics of each treatment	Categorical
Treatment day	Treatment days ranged from Day 1, when the sawfish was first subjected to a treatment,to the last day on which trials were conducted (Day 5 for sawfish 1 and Day 7 for sawfish 2). Only days that involved experimental trials were included in this count	Discrete
Trial number	Trial number, for each sawfish. Sixteen trials (experiments) were run for sawfish 1, and 15 for sawfish 2 (including Control treatments)	Discrete
Session number	If the experiment was the first, second or third electrified session of the day (Sessions 1–3)	Discrete
Approach number	Approach number, within an experiment. During each experiment, sawfish approached the experimental arrangement a number of times	Discrete
Time of day	Time of the day when experiment was run: morning (09:00– 11:30 h), mid-day (11:30–13:00 h), afternoon (13:00–15:00 h)	Categorical
Response variables		
Reaction distance	Distance from the electrodes at which sawfish showed some reaction to the experimental arrangement (e.g. twitching, rapid change in speed and/or direction, etc.). Note that this variable was also considered as an explanatory variable for the analysis of twitching presence and twitching time	Continuous variable
Reaction type	Reaction of the sawfish to the experimental arrangement. Reaction was separated into 4 categories: turning back, swimming parallel, swimming between, and freezing	Categorical
Twitching	Presence of twitching behaviour (yes/no)	Categorical
Twitching duration	Duration of twitching behaviour, in seconds	Continuous variable
Inter-approach time	Period of time between 2 consecutive approaches to the electrode setup,in seconds	Continuous variable

electrodes (see Video S7), and 35 towards the inside electrode, i.e. towards the electrode placed in the middle of the tank (Fig. S1; Video S8). All electric pulses affected sawfish behaviour, but only when sawfish were close to the electrode setup, typically within 1.2 m. A clear visible effect of the electric pulses on sawfish was 'twitching', where the sawfish moved its head and saw side to side simultaneously to the frequency of the electric pulse. Occasionally, more intensive twitching, which included muscle spasms over the body and fins, would make the sawfish unable to swim out of the electric field, in a behaviour classified as 'freezing'. Reactions also included a rapid change in swimming direction and speed.

3.1. Reaction distance

Sawfish did not display aversive behaviour when the pulse generator was first activated. However, for 1 of the 2 AC treatments (electrified Trial 13, second session of the day), sawfish 1 avoided the electrode area during the whole 11 min experiment, remaining >2 m away.

In general, reaction distances were small, typically <120 cm. For the conditional inference tree analysis, only reaction distances from approaches made towards the area between the electrodes (Fig. S1) were considered (n = 126), as it was often difficult to estimate reaction distance when sawfish approached from the side of the tank opposite to the observer. The tree resulted in 4 terminal nodes and shows that treatment had the most significant effect on reaction distance (Fig. 3), with distance being larger for the Baseline and 10 Hz treatments (mean ± SD for both treatments and both sawfish: 84 ± 36 cm) than for the remaining treatments (48 ± 42 cm; Fig. 3). Further splits indicate that time also had a significant effect on reaction distance, demonstrating learning. For the Baseline/10 Hz treatments, a secondary split indicates that reaction distance was significantly smaller ($p < 0.01$) for the first experiments of the day (60 ± 30 cm) than for experiments run on the second or third sessions of the day (102 ± 30 cm) (Fig. 3). For the remaining electrified treatments (50 V, 500 µs, AC, and Exponential pulse treatments), the effect of time was related to trial number, with reaction distances smaller for the first 10 electrified trials for each sawfish (36 ± 30 cm) than for the last trials (72 ± 42 cm) ($p = 0.01$) (Fig. 3).

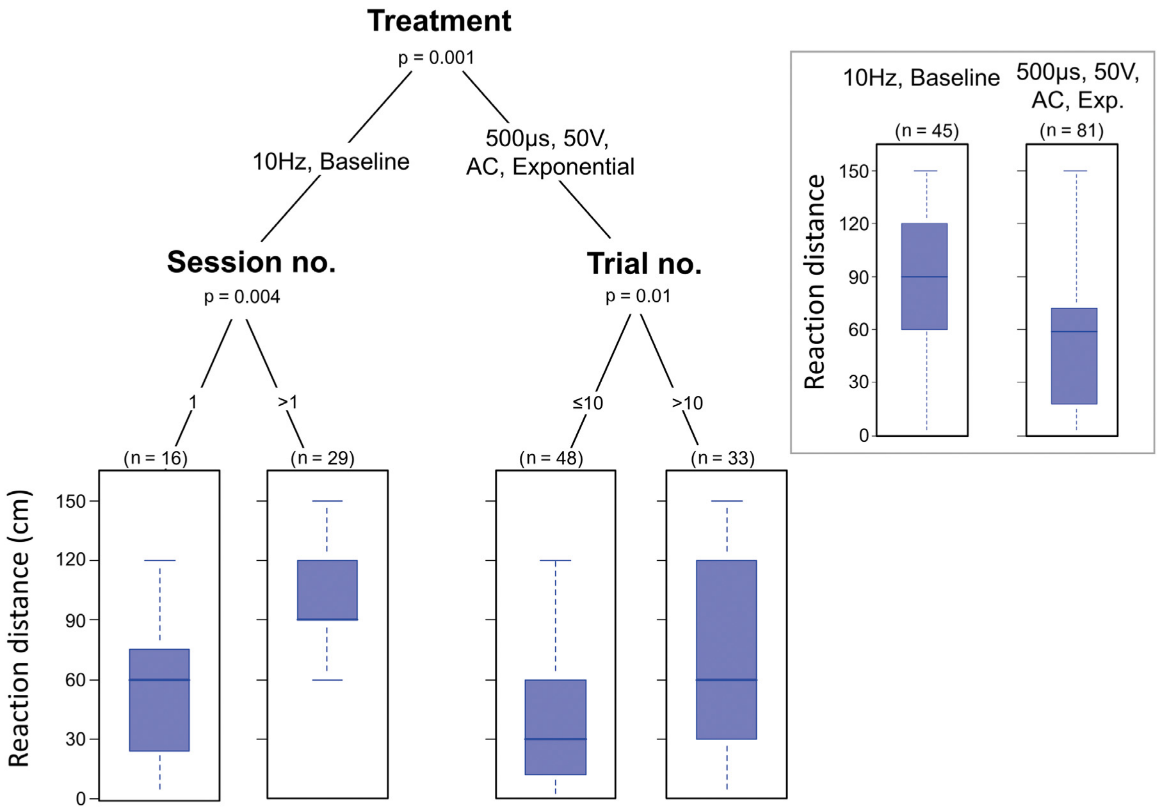


Fig. 3. Conditional inference tree model for the contribution of various factors on sawfish reaction distance. Inset on the right shows the distribution of reaction distances for the first split of the tree. Box and whisker plots show the distribution of reaction distance values for all samples included in each terminal node, where boxes show the upper and lower quantiles, lines within boxes are the medians, and whiskers are the minimum and maximum values. Only data from approaches towards the area between the electrodes were included in the model

3.2. Reaction type

In the Control treatments, the behaviour most commonly recorded was swimming between the electrodes. However, sawfish 1 turned back 20% of the time (Fig. S3), and sawfish 2 swam parallel to the electrodes 42% of the time (Fig. S4; Table 4).

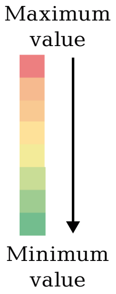
The treatments affected the 2 individuals differently. The pulse most likely to repel sawfish 1 was the 500 µs, as the sawfish turned back 100% of the time (Table 4). The Baseline treatment could also be considered as potentially effective, as only the 2 favourable behaviours were observed (turning back and swimming parallel to the electrodes) (Table 4). The 10 Hz, Exponential, AC, and 50 V treatments led to the most unfavourable behaviours of freezing and/or swimming between the electrodes. In contrast, the larger individual exhibited the freezing behaviour more often (7 times) than the smaller individual (once), and data suggest that the 10 Hz pulse induced the optimal escape behaviour (Table 4).

The conditional inference tree identified the use of an electric deterrent (i.e. treatment) as the variable that most explains sawfish reaction, separating the Control settings from the electrified treatments (Fig. 4). This split was due to sawfish most often swimming between the electrodes in the Control treatment (67% of the time) compared to the electrified treatments (11% of the time). Further, sawfish displayed the turning back behaviour more often in the electrified treatments compared to the Control setting (52 vs. 8% of the time). Each individual behaved differently under Control settings as, when not swimming between the electrodes, sawfish 1 turned back while sawfish 2 swam parallel the electrodes (Fig. 4).

For the electrified treatments, a secondary split separated the 2 individuals. Sawfish 1 turned back more often and swam parallel to the electrodes less often than sawfish 2 (62 vs. 46% and 16 vs. 39%, respectively) (Fig. 4). Trial number had a significant effect ($p < 0.001$) on the reaction type for sawfish 2:

Table 4. Proportion of time each behaviour was observed in response to each treatment, calculated for each individual sawfish separately. Colours indicate where each treatment vs. behaviour falls within the observed range of proportions, where red indicates the highest values, dark green the lowest, and yellow represents median values. Other cells are coloured proportionally, in a gradient. n = total number of approaches for each treatment; only approaches made perpendicularly to the electrode arrangement are included as not all reactions (e.g. swimming between electrodes) could be observed from approaches towards the electrode placed in the middle of the tank. The pulses most likely to not lead to capture (for each individual) are in **bold**

	Behavioural response to electrodes (%)				
	Turned back	Swam parallel	Swam between	Freezing	n
	Sawfish 1				
Control	20	0	80	0	15
Baseline	**44**	**56**	**0**	**0**	**9**
AC	67	17	17	0	6
Exponental	46	0	54	0	13
10 Hz	63	25	0	13	8
500 µs	**100**	**0**	**0**	**0**	**6**
50 V	75	0	25	0	8
	Sawfish 2				
Control	0	42	58	0	24
Baseline	34	50	8	8	12
AC	67	11	0	22	9
Exponental	24	59	6	12	17
10 Hz	**63**	**38**	**0**	**0**	**16**
500 µs	56	33	0	11	9
50 V	45	27	18	9	11



freezing behaviour was only recorded in the first 6 trials, and the sawfish also swam between the electrodes more often and swam parallel to the electrodes less often in the first 6 trials than after the sixth trial (Fig. 4). For sawfish 1, the tree separated the Baseline treatment from all others ($p < 0.05$), as freezing and swimming between electrodes were not registered for this treatment, and swimming parallel to the electrodes was the most frequently observed behaviour (Fig. 2).

3.3. Twitching

All electrified treatments led to twitching behaviour, where the sawfish quickly moved its head and sometimes its whole body side to side. Accordingly, the conditional inference tree identified the presence of an electric field (i.e. treatment) as the most important factor explaining the presence of twitching, separating the Control treatment from all others (Fig. S5). For the electrified treatments, a secondary split separated the data according to reaction distance, where twitching was observed more frequently at distances of ≤~80 cm (84% of the time) than at greater distances (19% of the time). Twitching was also more vigorous when sawfish moved more into the electric field. When further away, sawfish could still react to the electric pulse by a sudden change in direction or speed, without the twitching behaviour (see Figs. S3c,d & S4b,f). For cases when sawfish reacted at ≤80 cm distance, a third split on the tree shows that sawfish twitched more frequently in approaches towards the area between the electrodes than when approaches were towards the electrode placed in the middle of the tank. Finally, for the approaches towards the area between the electrodes, trial number also had a significant effect on twitching, as up to Trial 8, sawfish showed twitching behaviour 98% of the time, whereas from Trial 9 onwards, sawfish only twitched 59% of the time (Fig. S5).

Twitching behaviour lasted from 1 twitch up to prolonged twitching over a 6.4 s period. On 8 occasions, the electric field overwhelmed the sensory system of the sawfish to the extent that the animal was immobilised (i.e. freezing) and the electrodes had to be removed from the water. This was observed only once for sawfish 1 (for the 10 Hz treatment), but 7 times for sawfish 2 (once for Baseline, 50 V, and 500 µs treatments, and twice each for the Exponential and AC treatments). Conditional inference tree analysis found that none of the explanatory variables considered could explain twitching duration.

3.4. Inter-approach times

In general, the time between 2 consecutive approaches to the electrodes (inter-approach times, IATs), did not differ between the Control and electrified treatments (Figs. S6 & S7). The conditional infer-

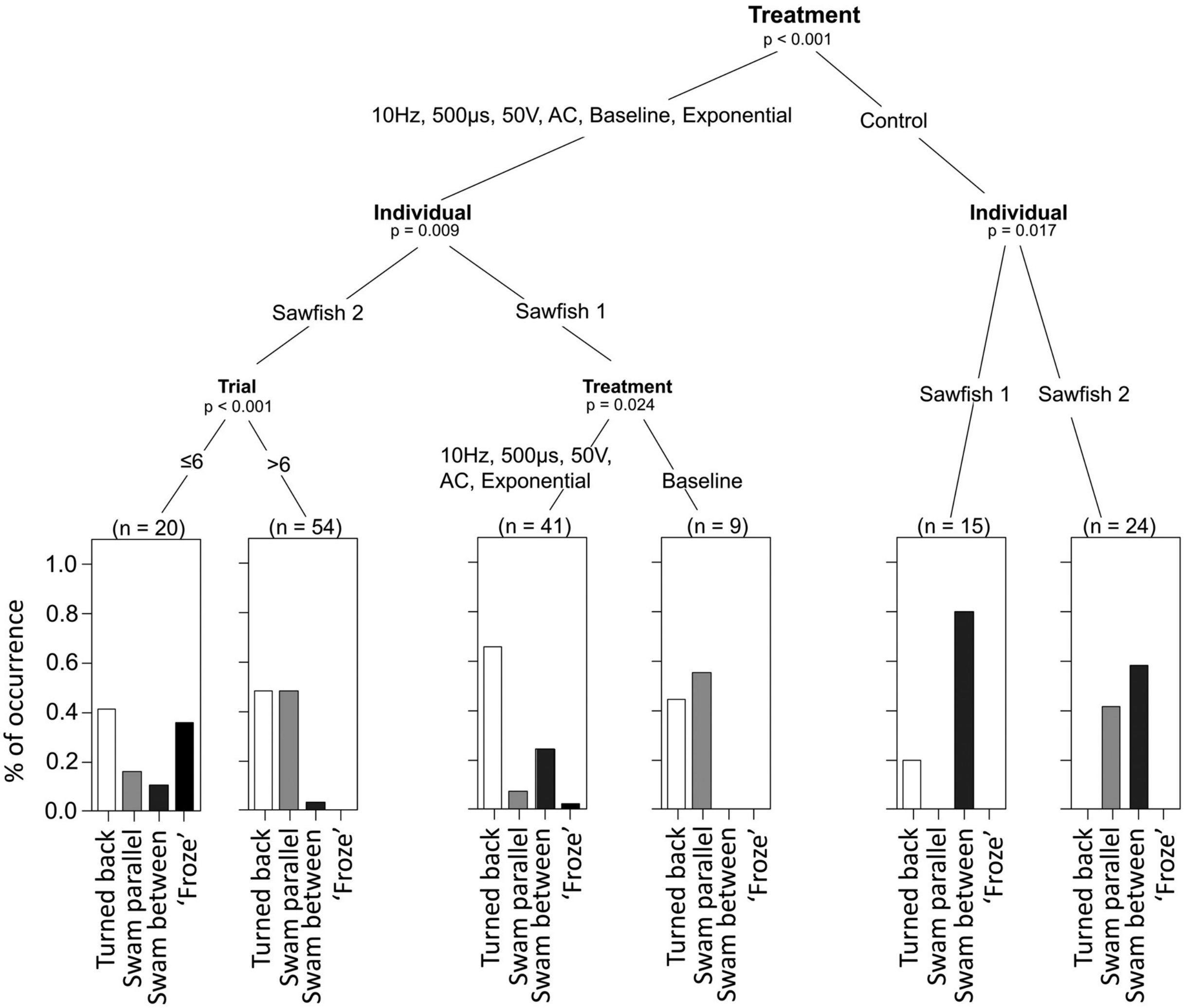


Fig. 4. Conditional inference tree model for the contribution of various factors on sawfish reaction to the electrode arrangement. Bars are the proportion of times each behaviour was recorded for that group. Only data from approaches made perpendicularly to the electrode arrangement were included

ence tree identified individual as the most important factor explaining the time between consecutive approaches to the electrodes, as sawfish 1 had longer time periods between approaches than sawfish 2 (Figs. S6 and S7). For both individuals, the tree identified an effect of time (i.e. experience) on IAT, although this effect was not the same for the 2 individuals: while for sawfish 1, IATs were shorter in the first sessions of the day, for sawfish 2, IATs were the longest in the earlier trials (Fig. S7). Accordingly, there was a significant negative relationship between session number and number of approaches per minute for sawfish 1, and a significant positive relationship between trial number and number of approaches per minute for sawfish 2 (Fig. S8).

4. DISCUSSION

Both sawfish clearly sensed and reacted to the electric fields tested. However, none of the waveforms used could repel from a distance likely to be sufficient to deter sawfish from entering trawl nets. In fact, reaction distances were typically <1.2 m, smaller than the estimated ~5.5 m distance needed to avoid capture by the NPF nets. Nevertheless, the obtained reaction distances are useful to inform future research on electric field-based BRDs, e.g. by giving information on the distance an electric signal must precede a moving net.

One of the most noticeable reactions to the electric fields was twitching, a behaviour that has been observed in other elasmobranchs (Marcotte & Lowe 2008). Twitching involves moving the head and saw side to side, a movement that leads to sawfish becoming increasingly entangled in nets (L. Squire, A. Barnett, pers. obs.), stressing the need for deterrents to avoid contact with the nets, e.g. by being placed well ahead of the moving nets.

Sawfish sometimes reacted to the electric field by rapidly changing swimming speed or direction without twitching, and twitching occurred more often on trials run on the first experimental days than on the last experimental days. This was likely related to a combination of habituation to the electric field and of the smaller reaction distances in the first experiments compared to the last experiments, indicating that sawfish learn to react earlier following initial exposure and avoiding entering the strongest parts of the electric field, decreasing the likelihood of twitching. Reaction distance and reaction type also changed with time, again suggesting that, as observed in other elasmobranchs (e.g. Mourier et al. 2017, Juhel et al. 2019), sawfish are capable of learning to avoid an unpleasant stimulus. Although repeated exposures were needed for sawfish to avoid the electric fields, this learned behaviour could be useful for stationary gear such as gill net fisheries. However, the likelihood of repeated exposure in prawn trawl fisheries is unknown.

It could be argued that temporal changes in behaviour could also be related to muscular or synaptic fatigue. This is unlikely, however, as sawfish were not subjected to the prolonged influence of intense electric fields, e.g. the longest twitching period was 6 s, and observations during experimental trials did not give any indication of fatigue.

Due to equipment failure, it was not possible to describe the voltage field gradients around the electrodes or to measure the field strength for the treatment and distance at which sawfish most reacted. However, the voltage gradient around the Ocean Guardian Freedom7 has been described (Kempster et al. 2016). Since the experimental arrangement used in the present study was based on the Ocean Guardian Freedom7, resulting in similar electrode dimensions, positioning, and distance between electrodes, we can assume that, under the same conditions, our arrangement would lead to a similar voltage gradient. Note that a more recent study (Gauthier et al. 2020) further confirmed similar voltage gradients for Rpela v2 and Ocean Guardian Freedom + Surf, shark deterrent devices with a similar electrode arrangement. Kempster et al. (2016) found the greatest voltage gradient of ≥100 V m^{-1} within 5 cm of each electrode, decreasing sharply with distance from the electrodes. Although our voltage output was lower than that of the Ocean Guardian Freedom7 (100 vs. 115 V), our other waveform parameters (higher frequency and longer pulse duration) would make our pulses stronger and more easily detectable by fish (Dolan & Miranda 2003). Moreover, seawater temperature (15°C) and salinity (37 ppt) in the study by Kempster et al. (2016) mean that conductivity was lower than that estimated based on the average temperature (25°C) and salinity (32 ppt) of the present study (45.1 vs. 49.5 mS cm^{-1}; Lide 2002), and the lower the seawater conductivity, the more voltage is needed to produce the same effect on fish (Lines & Kestin 2004). Additionally, since the produced electricity will dissipate in the available volume of water, under otherwise similar conditions an electrical field would be stronger and more easily detectable by sawfish in our shallow experimental tank than at sea (Thiele et al. 2020). However, despite this more concentrated, stronger field, the pulse stimuli tested did not consistently lead to a fleeing reaction, and reaction distances were smaller than the ~5.5 m needed to avoid capture.

The 2 sawfish tested reacted differently to the different treatments, and the treatments that best worked for sawfish 1 were not favourable for sawfish 2, and vice versa. These differences could be related to animal size. Larger teleosts react more strongly to strong electric fields than smaller fish as their larger dimensions lead to larger potential differences over their body (Dolan & Miranda 2003). Although this size effect becomes minor for fish larger than 14–18 cm (Dolan & Miranda 2003), i.e. at sizes much smaller than the total length of our sawfish, this relationship is still relevant to our experiments because sawfish rostra and heads (which are the parts that first enter the electric field) were narrower than this size threshold.

The differences in reaction between the 2 individuals could also be related to individual behavioural differences, regardless of animal size, as found for white sharks *Carcharodon carcharias* (Huveneers et al. 2013, 2018), for example. Additionally, the relatively large size of the animals in relation to the experimental tank somewhat limits their manoeuvrability, particularly for the larger individual, which could also have contributed to the differences in reaction and IATs between the 2 individuals. It is therefore important to keep in mind that only 2 captive largetooth sawfish were tested, so results might not characterise the typical responses of this species nor the other sawfish species.

4.1. Future directions and possible solutions

Increasing voltage, frequency, or pulse duration could improve the usefulness of an electric field to repel sawfish. However, higher energy pulses (high voltage) would lead to very high field strengths around the electrodes, potentially leading to injury or death of animals (including sawfish) that get too close to the electrodes (Roth et al. 2003, Dolan & Miranda 2004, Soetaert et al. 2016a,b). Such high voltage would also require large amounts of electricity to be produced, making it expensive, potentially dangerous to humans, and unpractical to run. In teleosts, electric fields that elicit strong cramp reactions can lead to haemorrhages and spinal injuries (e.g. Snyder 2003, Soetaert et al. 2016a,b). Although the 2 studies on elasmobranchs available to date (to our knowledge) did not report negative effects (de Haan et al. 2009, Desender et al. 2017) on the small-spotted catshark *Scyliorhinus canicula*, we did not subject the sawfish to stronger electric fields due to ethical concerns.

The use of higher frequencies could also improve avoidance behaviour. However, the pilot tests showed that a higher frequency of 20 Hz led to very fast muscle stimulation, cramping, and immobility, visibly stressing the animals. Given the conservation concern of sawfish species, this is not a positive outcome, particularly if subjecting animals to an electric field would not necessarily stop them from entering fishing nets. Overall, based on our pilot trials and experimental results on reaction types and distance, we suggest that such future studies should focus on rectangular-shaped bipolar pulses of 5–10 Hz, 1500 µs in duration, and 100 V.

To increase the effectiveness of electric fields in reducing sawfish bycatch, electrodes could be placed 5–10 m ahead of the trawling net, perhaps in a V-shape arrangement to encourage avoidance and parallel swimming away from the net mouth. This could give sawfish enough distance and time to swim away from the approaching net. However, the effect of such an arrangement on the target species would need to be investigated. A moving trawl net could also produce a stronger escape response than the stationary electrodes considered in the present study. It would therefore be beneficial to test sawfish behaviour when faced with a moving electrode arrangement. Note that this was trialled but, due to the relatively small tank size, experiments were not successful.

In the NPF, sawfish are captured both when targeting banana prawn aggregations in the water column and when targeting tiger prawns in demersal trawls (Fry et al. 2018). It is possible that the freezing behaviour could lead to a positive outcome when targeting mid-water banana prawn aggregations, as it could lead to sawfish sinking when 'frozen' and escaping under the net. However, it is not known if or how fast sawfish would sink and, if they did, if they would sink fast enough to avoid entering or being entangled by nets travelling at 1.6–1.8 m s^{-1} (Bishop & Sterling 2007). When targeting tiger prawns, freezing would always lead to contact with the demersal nets. In that case, the use of a setup similar to electrotrawling for brown shrimp in the North Sea (Soetaert et al. 2015) could be useful to avoid entanglement (Jordan et al. 2013). In that setup, the ground rope is raised by 10–15 cm and the nets travel above the seabed, with limited contact with the sediment. Electrodes placed at the net entrance produce pulses that cause the shrimps' tail muscles to contract, leading to shrimp jumping out of the sediment and into the water column (Soetaert et al. 2015). This method significantly reduces bycatch of benthic and epibenthic fish (Verschueren et al. 2019), and could reduce sawfish bycatch, allowing the moving net to pass above the animals.

Since the lateral line system of elasmobranchs can detect hydrodynamic disturbances such as water flow direction and velocity, vibrations, and sounds (Montgomery et al. 1995, Collin et al. 2015), the use of water jets ahead of the net mouth could also be useful to reduce elasmobranch bycatch (Jordan et al. 2013). Sawfish have a well-developed lateral line system that extends along the head and rostrum (Wueringer et al. 2011), which should allow them to sense an approaching net. However, to our knowledge, the use of hydrodynamic disturbances to minimise elasmobranch bycatch is yet to be explored. In addition to investigating approaches to reduce sawfish bycatch, it is important that methods that improve post-release survival are used and further developed, and that a better understanding of the spatio-temporal overlap between sawfish distribution and the various fisheries catching them is obtained.

4.2. Conclusion

Reducing bycatch of this highly endangered group of fishes is critically important to their continued survival. Our preliminary results suggest that sawfish can be stimulated to display an escape response using pulsed electric signals. We recommend further research focussing on moving nets, testing a V-shaped electric array preceding the mouth of a moving trawl by ~5 m, and testing a setup similar to the electrotrawling technology used in the North Sea when targeting brown shrimp.

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