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Original Article

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Effect of electrical stimulation used in the pulse trawl fishery for common sole on internal injuries in sandeels

Edward Schram [1,*], Pieke Molenaar [1], Maarten Soetaert [2], Dirk Burggraaf [1], Pim G. Boute [3,4], Martin J. Lankheet [3] and Adriaan D. Rijnsdorp [1]

[1]Wageningen Marine Research, Wageningen University & Research, PO Box 68, NL-1970 AB IJmuiden, the Netherlands
[2]Fisheries and Aquatic Production, Animal Sciences Unit, Flanders Research Institute for Agriculture, Fisheries and Food, Ankerstraat 1, B-8400 Ostend, Belgium
[3]Experimental Zoology Group, Department of Animal Sciences, Wageningen University & Research, PO Box 338, NL-6700 AH Wageningen, the Netherlands
[4]Biomimetics, Energy and Sustainability Research Institute Groningen, Faculty of Science and Engineering, University of Groningen, PO Box 11103, NL-9700 CC Groningen, the Netherlands
[*] *Corresponding author: tel: +31 317 48 70 38; e-mail:* edward.schram@wur.nl

Electric stimulation was used in the North Sea beam trawl fishery for common sole to reduce its environmental impact. Because electrical stimulation may cause internal injuries in fish, a laboratory experiment was conducted to study the effect of pulse exposure on lesser sandeel (*Ammodytes tobianus*) and greater sandeel (*Hyperoplus lanceolatus*), important mid-trophic species in the North Sea ecosystem. We exposed 244 sandeels between two electrodes to a pulsed bipolar current for 2 s in an experimental cage with 5 cm sediment; 221 control fish were handled similarly but not exposed. The occurrence of spinal injuries and internal haemorrhages were scored using X-radiography and dissection. None of the sandeels exposed to a field strength of up to 600 V m^{-1} showed spinal injury or haemorrhage. Equal numbers of minor spinal abnormalities were found in exposed and control fish. In the absence of spinal injuries, we estimated by bootstrapping the field strength below which spinal injuries are unlikely to occur, i.e. the lower limit threshold, and the corresponding limit dose–response relationship between field strength and injury probability. We conclude that it is unlikely that pulse trawl fishery will have an ecologically significant adverse effect on the population abundance of sandeels, because of the low probabilities of exposure and injury.

Keywords: beam trawling, haemorrhage, laboratory experiment, North Sea, pulsed bipolar current, spinal injury.

Introduction

The Dutch beam trawl fishery in the North Sea is a mixed fishery that targets common sole (*Solea solea*) and European plaice (*Pleuronectes platessa*) with other species as valuable bycatches (Gillis *et al.*, 2008). The beam trawls are equipped with tickler chains to mechanically chase flatfish from the seabed into the net. Starting in 2009, part of the Dutch demersal fishing fleet switched to electrical stimulation with pulse trawls when targeting sole, mainly because of the higher catch efficiency for sole, lower fuel consumption, and reduced impact on the seabed due to the reduced gear weight and lower towing speed (van Marlen *et al.*, 2014; Haasnoot *et al.*, 2016; Poos *et al.*, 2020; Rijnsdorp *et al.*, 2020). The electrical stimulus causes a cramp response that immobilizes the fish and facilitates their catch (van Stralen, 2005; Soetaert *et al.*, 2015; Soetaert *et al.*, 2019). Spinal injuries caused by involuntary muscle contractions induced by pulse stimulation have been reported in several species (van Marlen *et al.*, 2014; de Haan *et al.*, 2016; Soetaert *et al.*, 2016a,b). The sensitivity among fish species for pulse-induced injuries was estimated by extensive sampling of target and non-target species from catches of commercial pulse and tickler-chain beam trawlers (ICES, 2020; Boute, 2022; Boute *et al.*, 2022). In most species, relatively low spinal injury probabilities were found in pulse-trawl catches. High spinal injury probabilities, however, were detected for Atlantic cod (*Gadus morhua*), lesser sandeel (*Ammodytes tobianus*), and greater sandeel (*Hyperoplus lanceolatus*). The spinal injuries observed in the sampled cod are caused by pulse-induced muscle contractions as shown in laboratory experiments (de Haan *et al.*, 2016; Soetaert *et al.*, 2016a, b). For sandeels, the cause of spinal injuries is less clear as injury probability was elevated in catches of both pulse and tickler-chain gears, with the highest injury probability in the tickler-chain catches. Spinal injuries in sandeels, thus rather appear to be caused by mechanical impacts due to the catch process. However, experiments are lacking that isolate the effect of electrical stimulation from mechanical disturbance on spinal injuries. We therefore conducted a laboratory experiment with two sandeel species—lesser sandeel and greater sandeel—to study the sensitivity of these important mid-trophic species in the North Sea ecosystem (Rindorf *et al.*, 2000; Clausen *et al.*, 2018) to electrical pulse stimulation used in commercial pulse fisheries for sole. Injury rates were related to electric field strength and a limit dose–response relationship was determined to estimate the probability of pulse-induced injuries of sandeel in the commercial pulse trawl fishery.

Materials and methods

Origin and housing of experimental animals

Experimental fish were collected with a small-meshed otter trawl in Dutch coastal waters. At sea, fish were stored in four

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Table 1. Experimental treatments, pulse parameters, and numbers of tests and fish.

Experiment	Species	Treatment	Pulse generator	Frequency (Hz)	Width (μs)	Peak amplitude (V)	Duty cycle (–)	Total number of tests	Number of fish/test	Total number of fish
1	Lesser sandeel	Pulse 1	LPG	40	263	43.5	2.1%	10	10	103[a]
		Control 1	–	–	–	–	–	10	10	100
2		Pulse 2	Delmeco	30	330	52.5	2.0%	10	10	101[b]
		Control 2	–	–	–	–	–	10	10	101[b]
3		Pulse 3	Delmeco	30	330	43.5	2.0%	4	10	40
4	Greater sandeel	Pulse 1	LPG	40	263	43.5	2.1%	4	5	17[c]
		Control 1	–	–	–	–	–	2	5	10

[a]In three tests, 11 fish were used.
[b]In one test, 11 fish were used.
[c]In one test, 2 fish were used.

75-l circular tanks (Ø 40 × 60 cm height) that were placed inside a 0.5 m^3 tub. The tub and circular tanks were filled with surface seawater which was continuously recycled between the tub and the tanks. Water was pumped into each tank by an external pump submerged in the tub, creating a circular water flow inside the tank. From the tanks, water spilled back into the tub via 22 holes (Ø 10 mm) just under the brim of each tank. Each tank was aerated and filled with a 15 cm layer of coarse sand (grain size 1.0–1.6 mm) as bottom substrate. The total water volume of this system was approximately 0.45 m^3. At sea, the water in the tub was regularly renewed. Upon return in the harbour, the entire tub containing the tanks and collected fish was transported by road to the laboratory. Transport time was ~1 h. During transport, the water was aerated, recycled between the tub, and the tanks but not renewed. In the laboratory, fish were stored in a 2 × 2 × 0.5 m tank with a total water volume of 1.2 m^3 and a 15-cm layer of coarse sand as bottom substrate. Tank water was temperature controlled at 10–11°C and continuously renewed at a rate of ~1 tank volume d^{-1}. Test fish were collected 3 d before the first experiment and fish were not fed during captive housing.

Treatments and experimental design

The pulse equipment consisted of a power supply, pulse generator, and a pair of electrode arrays. Each electrode array consisted of three conductive electrodes of Ø 2.64 × 18 cm length separated by 23.3-cm-long insulated elements. The two electrodes array were spaced 42.5 cm apart on top of a 0.3 m layer of coarse sand (1.0–1.6 mm) in a polyester tank (2.05 × 1.40 × 0.9 m; l × w × h) with a water level of 0.6 m above the sediment.

A pulsed bipolar current (PBC) stimulus was generated by a LPG or Delmeco pulse generator as used in earlier experiments (de Haan *et al*., 2016; Soetaert *et al*., 2016a; de Haan and Burggraaf, 2018). Both pulse systems generated alternating positive and negative rectangular-shaped pulses that were evenly distributed in time (Soetaert *et al*., 2019). Pulse shape, pulse frequency, pulse width, and duty cycle (% of time during which electric current was running) corresponded to pulse stimuli used in the commercial fishery (de Haan *et al*., 2016; ICES, 2020). Details of the pulse characteristics are presented in the Supplementary material (SM1). Exposure duration was 2 s, which is slightly longer than the 1.36–1.5 s in the commercial fishery (de Haan *et al*., 2016; Boute *et al*., 2021).

Lesser sandeel (mean ± *SD* weight = 4.5 ± 3.2 g, mean ± *SD* standard length = 11.0 ± 2.2 cm) and greater sandeel (mean ± *SD* weight = 24.4 ± 14.7 g, mean ± *SD* standard length = 18.9 ± 4.6 cm) were exposed to a PBC representing three pulse settings in four experiments (Table 1) in a nylon cage (35 × 40 × 60 cm; l × w × h) with square meshes (mesh size 4 × 4 mm; nylon Ø 1 mm) that was placed between an electrode pair. A thermostatically controlled cooler kept water temperature between 10.4 and 11.7°C. Dissolved oxygen and salinity were between 7.2–8.9 mg l^{-1} and 32.7–33.4 g l^{-1}. Control groups were included to distinguish between spinal injuries resulting from electrical stimulation and fish handling associated with the capture and experimental procedure. Handling of control groups was identical to exposed groups except for the absence of electrical stimulation. Experiments 1 and 2 each consisted of 20 tests: 10 pulse treatments tests and 10 control tests conducted in alternating order with 10 fish per group (Table 1). The sample sizes in experiments 3 and 4 were limited by fish availability. Experiment 3 consisted of four pulse treatment tests with ten fish each. Experiment 4 consisted of four pulse treatment tests and two control tests with five fish each (Table 1). Each experiment was performed within 1 d and all four experiments were completed within 3 d. The use of experimental animals was in accordance with the Dutch Experiments on Animals Act, as approved by the Animal Welfare Body of Wageningen Research (protocol 2017.D-0012.003).

Experimental procedure

Prior to each test, a batch of experimental fish was netted from the storage tank into a temporary holding container to transfer the fish to the experimental tank. The holding container of 105 l was filled with seawater and a 5-cm sediment layer. The water in the holding container was aerated to maintain dissolved oxygen levels. Prior to each test, the nylon cage was placed between the electrodes at a depth of 5 cm into the sediment. At the start of each test, fish were randomly picked from the holding container and placed in the nylon cage. Electrical stimulation took place within 2 min after fish had been placed in the nylon cage. Directly after electrical stimulation, the nylon cage was gently pulled out of the sediment and gently shaken in the water column to remove all the sediment. Fish were then euthanized by transferring them to a 3% (v/v) diethylphenoxyethanol solution in seawater and stored at −20°C for later X-ray analysis and dissection.

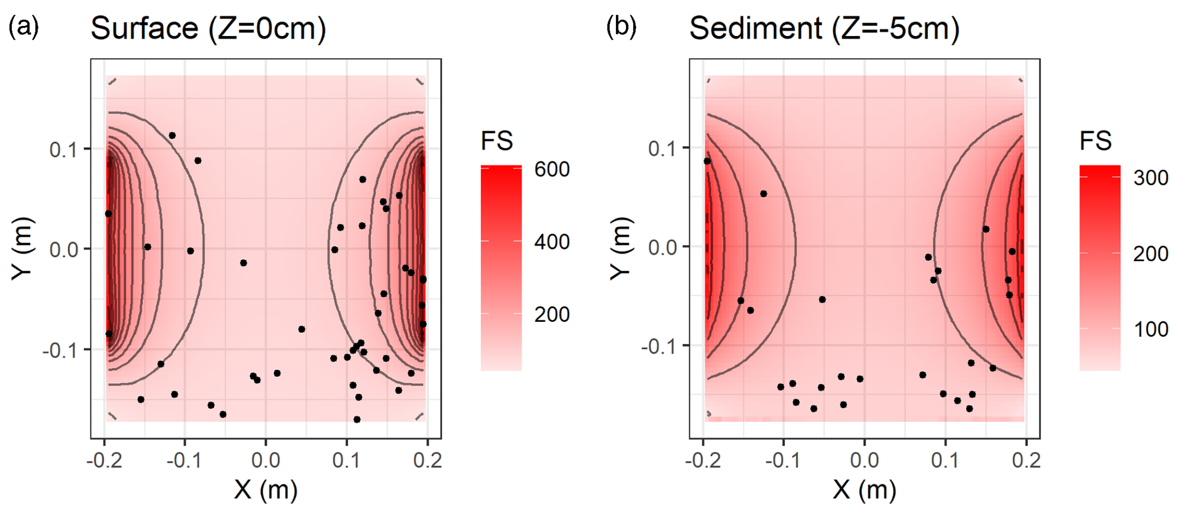

Figure 1. Electric field strengths (*FS* in V m^{-1}) in the experimental cage on top of the sediment (a) and at the bottom of the cage for Pulse 1 (b). Contour lines indicate equal *FS* at 50 V m^{-1} intervals. The dots indicate (a) the positions of sandeel laying on the sediment that are closest to the conductor and (b) the burying positions. X- and Y-coordinates are given in m.

Assessment of spinal injuries and internal haemorrhages

All fish were transported to and stored at −20°C in the freezer facilities of the Experimental Zoology Group in Wageningen. To visualize internal injuries, fish were defrosted and X-rayed in the lateral and dorsoventral axis using a Philips X-ray machine. The X-radiographs were captured by a 23.8 × 29.7 cm mammography phosphor plate (5440 × 6776 pixels, 43.75 µm, 12 bit) and read out with a Regius model 110 HQ digitizer from Konica Minolta. Distance between X-ray source and plate was 127 cm. For processing speed and efficiency, multiple fish were X-radiographed simultaneously per plate. After X-radiography, fish wet body mass to the nearest gram (KERN FCB 12k1) and standard length to the nearest millimetre (Rabone Chesterman No 47R mounted on a measuring board) were recorded, followed by dissection to expose internal haemorrhages. For dissection, each fish was filleted on the left side and photographed with a Nikon D700 digital camera with a 24–120 mm f/3.5–5.6G ED-IF AF-S VR NIKKOR lens.

Internal injuries were categorized to enable standardized and consistent scoring as described by Boute (2022). Spinal injuries were scored in three categories: minor, moderate, and severe. Minor spinal injuries were deformations of one or multiple vertebrae, including minor subluxation. Moderate spinal injuries included a subluxation or compression of several vertebrae (i.e. spinal misalignment) with minor fractures only. Severe spinal injuries were fractured and/or dislocated vertebrae, where the spinal column was either slightly or completely displaced. The presence, severity, and location of spinal abnormalities and haemorrhages were scored on the anteroposterior axis of the fish between the tip of the snout and base of the caudal fin.

Electric field strength simulation

To determine the electric field strengths in the experimental tank, we used the AC/DC package in COMSOL Multiphysics (COMSOL Multiphysics® v. 5.6. www.comsol.com. COMSOL AB, Stockholm, Sweden) to numerically simulate the electric field generated between the electrode pair. The field strength was determined in the steady state, which corresponds to the maximum field strength during a pulse. Electrode voltages were set to +5 V and −5 V. A 3D-coordinate system (X, Y, and Z) was used to define the positions with the X-axis perpendicular to the electrode in the horizontal plane, the Y-axis parallel to the electrode, and the Z-axis perpendicular to the electrode in the vertical plane. The absolute value of the field strength, as well as the components in the X, Y, and Z directions, were simulated for positions at a distance of 5 mm between X (−500, 500), Y (−500, 500), and Z (−300, 300) mm. The origin of the coordinate system was at the centre of the experimental cage, which was positioned between the middle one of the three conductor pairs similar to those used in the experiment and in commercial gears. Electrical conductivity of the water and sediment were set to 4 and 0.04 S m^{-1}, respectively. The cage was simulated as a thin (1 mm) layer with conductivity reduced by 4/9, as determined by the closed surface area of the net. Figure 1 shows the simulated field strength in the experimental cage at the sediment surface and at the bottom of the cage scaled to the conductor voltage of 43.5 V. Simulated field strengths were similar to *in-situ* field strength measurements in the experimental setup using the methodology of de Haan and Burggraaf (2018) (Supplementary material SM2).

Electric field strength exposure of sandeel

The field strength to which the sandeels were exposed to in the experiment was estimated from the simulated field strength at the positions of the sandeel in the experimental cage. Individual positions of sandeels just before pulse exposure were determined from video recordings (GOPRO HERO 4 Black) (Supplementary Figure SM2.1). For sandeels that were visible on top of the sediment, the position closest to the conductor was taken. The unknown position and orientation of sandeels, which were observed to bury in the sediment, were determined by assuming the fish' tail was located at the observed burying position and the head at a random position on the circumference of the circle with a radius of the mean length (11 cm) around the burying position. For

Table 2. Observed spinal injuries in lesser and greater sandeel per treatment.

Experiment	Species	Treatment	Total number of fish	Fish with minor spinal injuries (*n*)
1	Lesser sandeel	Pulse 1	103	6[a]
		Control 1	100	8[a]
2		Pulse 2	101	6[b]
		Control 2	101	4[a,c]
3		Pulse 3	40	4
4	Greater sandeel	Pulse 1	17	2
		Control	10	1

No moderate and severe injuries were observed.
[a]One fish had two minor injuries.
[b]Three fish had two minor injuries.
[c]One fish had three minor injuries.

each buried fish, the highest of the simulated field strengths for the head or tail position was used. The total number of recorded positions was smaller than the number of exposed sandeels because the video stills covered only part of the surface of the experimental cage. The X- and Y-coordinates of the recorded positions were estimated using WebPlotDigitizer (https://automeris.io/WebPlotDigitizer/).

Field strength frequency distributions for the 244 sandeels in the experiment were resampled from the subset of field strengths for 48 sandeels on the sediment and the subset of possible field strengths for 196 sandeels buried in the sediment. As the depth of the buried sandeels was unknown, we estimated three separate frequency distributions representing three burying depths in the experimental cage (deep: Z = –50 mm; random: –10 < Z < –50 mm); shallow: Z = –10 mm).

Field strength simulations did not take account of the GOPRO camera that was placed in the lower right corner of the experimental cage. Because the camera had an insulating cover, the local field strength around the camera will have been higher than the simulated field strengths. Hence, the field strength to which the sandeels in the lower right corner were exposed may have been underestimated.

Estimation of the lower limit field strength threshold and dose–response relation between field strength and injury probability

Because we did not find injuries that are typically observed in fish that are exposed to an electrical stimulus, we estimated the limit field strength threshold F01, i.e. the lowest field strength below which the spinal injury probability was ≤1%, by a simulation of exposure experiments. The probability of pulse-induced injuries (p) increases with field strength (*FS*) (Spencer, 1967; McMichael, 1993; de Haan *et al.*, 2016). This dose–response relation between *FS* and p can be described by a sigmoid curve: $\log(p/1\text{-}p) = \alpha + \beta * FS$, where α is a constant and β is the slope. The field strength at which 50% of the fish is injured, which indicates the species sensitivity for pulse-induced spinal injuries, is given by $F50 = -\alpha/\beta$. To obtain a lower limit *FS* threshold compatible with the experimental results, we determined the lowest F01 for which the corresponding dose–response curve yields zero injuries among sandeel exposed to the electric field strengths in the laboratory experiment. This was done by predicting the number of injured fish in 1000 simulated experiments for all F01 values in the range of 1–1000 (natural numbers only). In each of these 1000 simulated experiments, 244 sandeel (sample size equal to the laboratory experiment) were exposed to 244 field strengths randomly resampled from the observed frequency distribution. The slope of the dose–response curve was assumed to be equal to the slope observed in cod (de Haan *et al.*, 2016): $\beta = 0.043$. This procedure was repeated 1000 times for each of the three assumptions about the depth distribution of the buried sandeel in the experiment (deep, random, and shallow) to obtain frequency distributions for F01 and median F01 value for the three assumptions about the depth distribution.

Estimation of the upper limit of the *in-situ* injury probability

The simulated estimated dose–response relation was used to estimate the injury probability of sandeel exposed to the pulse stimulus in the path of a commercial pulse trawler. Because none of the sandeel exposed in our experiment developed a pulse-induced injury, the simulated dose–response relationship provided an estimate of the lower limit of the sensitivity of sandeel for pulse-induced injuries. The true sensitivity will be higher. Injury probabilities estimated with the limit dose–response relationship therefore provide an estimate of the upper limit of the *in-situ* injury probability.

The upper limit of the injury probability of sandeel exposed to a pulse stimulus in the path of a commercial pulse trawler was estimated by applying the limit dose–response relation to a random sample of *in-situ FS* of 1000 sandeels of a random length (mean = 16 cm; *SD* = 2.4; Sparholt et al., 2015) at a random position and orientation between the conductor pairs at a burying depth between 0 and –5 cm. This was repeated 1000 times to estimate the median and 2.5 and 97.5% percentiles of the injury probability. The *in-situ FS* values were estimated from the COMSOL predictions outside the experimental cage and using the mean conductor voltage (55.6 V) used by pulse trawlers (ICES, 2020).

Results

Spinal injuries and internal haemorrhages

None of the sandeel exposed to an electrical pulse stimulus showed moderate or severe spinal injuries that are often recorded in electro-caught fish (Table 2). Minor spinal abnormalities were recorded in 7% of the exposed lesser sandeel and 12% of the exposed greater sandeel. These frequencies did not differ significantly from the control fish ($p = 0.96$). Examples of the minor injuries observed in lesser sandeel are shown in Figure 2. Spinal abnormalities were mostly located in the posterior part along the body axis in the caudal and ural regions, although we also observed abnormalities in the ab-

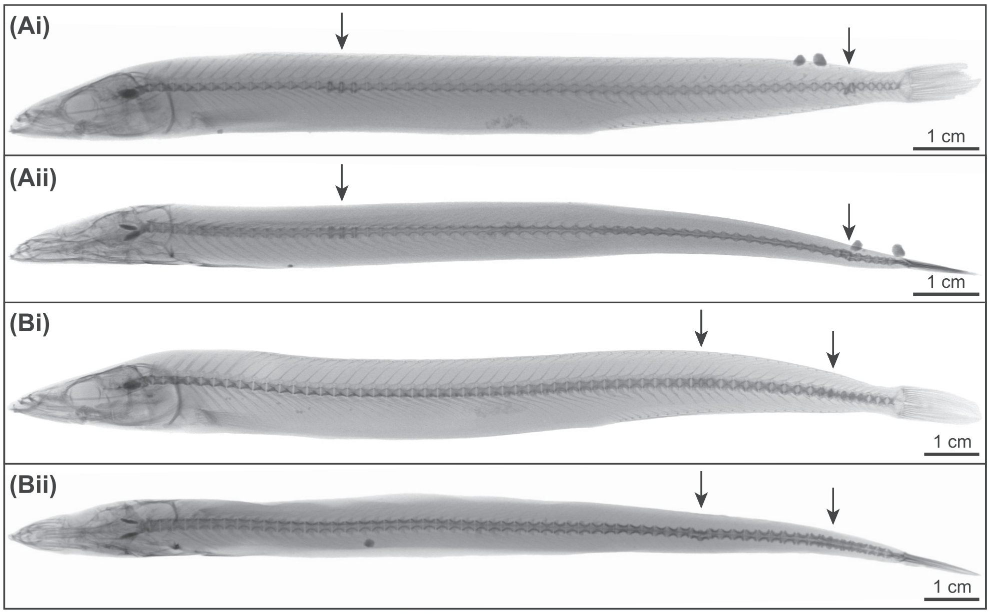

Figure 2. Examples of minor spinal abnormalities observed in two lesser sandeel specimens from a (Ai, Bi) lateral view and (Aii, Bii) dorsoventral view. Abnormalities are indicated with arrows. Both specimens have deformations of two to seven vertebrae with only slight subluxation. The most posterior abnormality observed in (B) could be developing block vertebrae. The dark, irregularly positioned spots on the X-radiographs are contaminations of hard material such as sediment or remains of hard-shelled invertebrates.

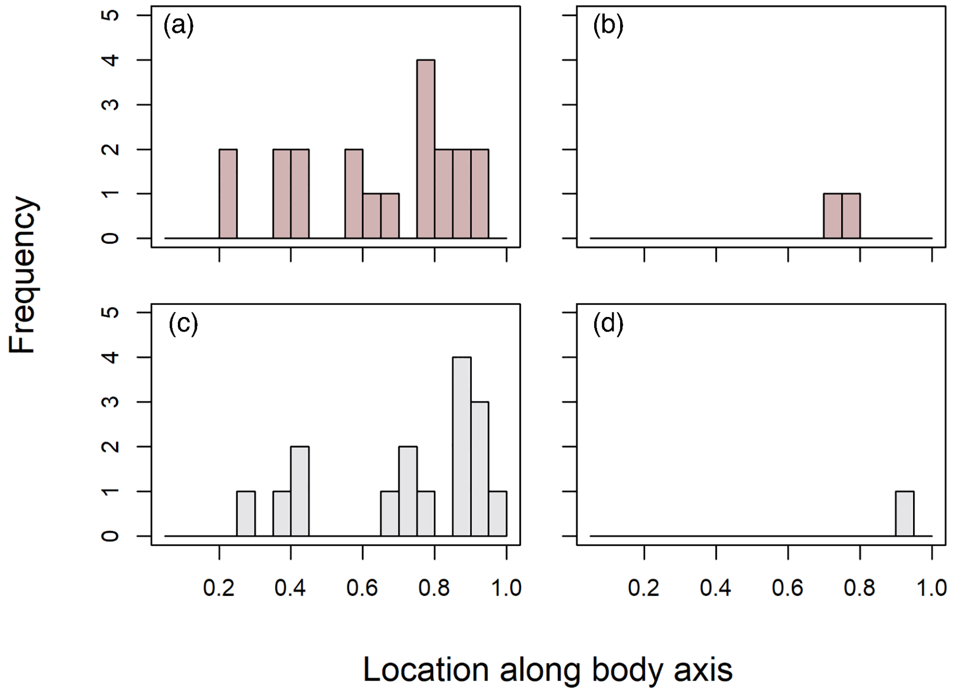

Figure 3. Location of minor spinal abnormalities along the anteroposterior axis observed in lesser sandeel ((a), (c)) and greater sandeel ((b), (d)) exposed to a pulse stimulus (top panels) and in the control specimens (lower panels). Locations are defined as relative distances from snout (0) to caudal fin (1). Multiple injuries may be present in a single specimen. No moderate and severe spinal abnormalities were observed.

dominal region (Figure 3). No internal haemorrhages were observed in the specimens, irrespective of treatment and species.

Field strength estimates

Sandeels in the experiment were exposed to *FS* ranging between 20 and 640 V m^{-1}, depending on their positions relative to the electrodes (Figure 1). Sandeel that buried at the cage bottom (deep) will be exposed to lower *FS* compared to sandeel buried just below the sediment surface (shallow). Sandeel buried at a random depth in the experimental cage will be exposed to intermediate *FS* (random) (Figure 4).

Sensitivity for pulse-induced injuries

The limit *FS* threshold F01, i.e. the lowest *FS* below which spinal injury probability ≤1%, was estimated between 320 and 540 V m^{-1} (Figure 5a). The median threshold was esti-

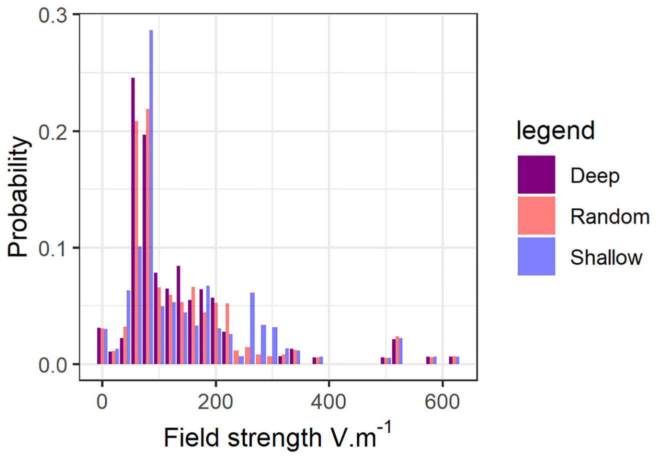

Figure 4. Frequency distributions of *FS* (V m^{-1}) experienced by sandeel in the experiment if the fish were buried at the bottom of the cage (deep), were randomly distributed in the sediment between Z = −10 and Z = −50 mm (random), or buried just below the sediment surface at Z = −10 mm (shallow).

mated at $F01_{deep} \geq 481$ V m^{-1} (95% confidence limits: 419–523 V m^{-1}). The corresponding limit dose–response curve is the worst-case proxy of the sensitivity of sandeel (Figure 5b). The dose–response curve was rather insensitive for the assumption on the depth distribution of the buried fish in the experiment. The limit sensitivity for pulse-induced injuries in sandeel was estimated at $F50 \geq 586$ V m^{-1} (95% confidence limits: 524–628 V m^{-1}).

A worst case estimate of pulse-induced injuries imposed by commercial pulse trawlers

Under the assumption that sandeel on a fishing ground are buried in the sediment at a random depth between the surface sediment and 5 cm deep, the upper limit of the percentage of sandeel that are exposed to a commercial pulse stimulus that could result in a pulse-induced injury was estimated at ≤4.3% (95% confidence limits: 3.2–5.7%). In other words, ≥96% of the sandeel in the path of commercial pulse trawlers are exposed to a field strength at which none of the sandeel in our experiment developed a spinal injury.

Discussion

We exposed sandeel to a PBC electrical stimulus used in the commercial pulse fishery for common sole in the North Sea. None of the exposed sandeel developed injuries such as spinal fractures and severe luxations that may coincide with severe haemorrhages as shown in salmonids, Atlantic herring, and Atlantic cod exposed to an electrical stimulus (Sharber and Carothers, 1988; Sharber *et al.*, 1994; Snyder, 2003; Roth *et al.*, 2004; Nordgreen *et al.*, 2008; de Haan *et al.*, 2016; Soetaert *et al.*, 2016b). Minor abnormalities were observed in similar numbers in exposed and control fish and are therefore unlikely to be electrical-pulse induced. These minor abnormalities may be developmental deformations or old injuries from which the fish have recovered, and therefore are unrelated to electrical-pulse exposure (Sharber *et al.*, 1994; Soetaert *et al.*, 2018; Boute, 2022).

The estimated *FS* threshold should be considered a limit that is consistent with the experimental results where we did not find any evidence of pulse-induced injuries, although we exposed sandeel to field strength >600 V m^{-1}. Higher electric field strengths might result in the typical internal injuries observed in fish exposed to an electrical stimulus. The F01 threshold estimates the lowest *FS* at which the pulse exposure might induce injuries, although it is also possible that sandeel are insensitive for pulse-induced injuries.

Pulse-induced spinal injuries are caused by muscle contractions on both sides of the body, which, in turn, depends on the strength of the external field to which the animal is exposed, the electrical properties of the body, and the conductivity of the medium (Soetaert *et al.*, 2019). In a low conductive medium, e.g. sediment, animals will experience lower internal *FS*, and are therefore presumably less affected than animals in the water column that are exposed to the same external *FS* (ICES, 2020; Boute, 2022). The electrical properties of the body depend on factors such as body shape, insulating characteristics of the skin, body fluids, muscle fibre type, and subcutaneous fat layers (Snyder, 2003; Polet, 2010; Soetaert *et al.*, 2016a; Boute, 2022). These factors may set different thresholds for inducing double-sided muscle cramps. Moreover, differences in body characteristics such as the distribution of muscle mass and number, shape, and size of vertebrae may affect the probability that pulse-induced muscle cramps

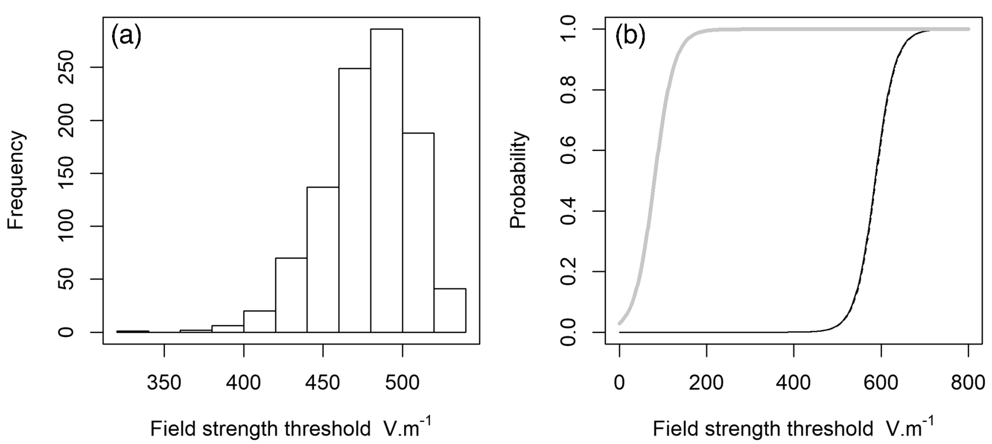

Figure 5. (a) Frequency distribution of *FS* thresholds (F01) compatible with the experimental results showing zero pulse-induced injuries. (b) Simulated limit dose–response curve of pulse-induced injuries of sandeel (black line) and the observed dose–response curve of cod from de Haan *et al.* (2016) (grey line). The limit dose–response curve gives the lower limit of the sensitivity. The true sensitivity will be higher (see text).

lead to internal injuries (Soetaert *et al.*, 2018; Boute, 2022). Interspecific differences in sensitivity to pulse-induced internal injuries are therefore to be expected. Indeed, our results show that sandeels are substantially less sensitive than, for example, Atlantic cod. If sandeels would be sensitive to internal injuries induced at higher *FS* than exposed to in our experiments, their dose–response curve would be shifted to at least 586 V m^{-1} (at the F50 level) while for Atlantic cod the *FS* at which 50% of the fish exposed developed a spinal injury was estimated at F50 = 80 V m^{-1} (de Haan *et al.*, 2016). Also, European seabass and sole appear less sensitive than cod as no spinal injuries were observed in specimens exposed to an external *FS* of 37–155 V m^{-1} in the laboratory (Soetaert *et al.*, 2016a; Soetaert *et al.*, 2018).

In sandeel collected from catches of commercial pulse trawlers, major spinal injuries were observed in 12% of the lesser and 14% of the greater sandeel (Boute, 2022; ICES, 2020). These injury percentages are substantially higher than the injury probabilities estimated from present experimental findings (≤4.3%), especially as the limit dose–response relationship estimated from the experimental data represents an upper injury probability limit. Higher injury probabilities of 27 and 39% were recorded in lesser and greater sandeel caught by conventional beam trawlers using solely mechanical stimulation with tickler chains (Boute, 2022). Therefore, it is most likely that the injuries observed in sandeel from catches of commercial pulse trawlers are not pulse-induced but rather caused by mechanical stressors imposed on the fish during the capture process and on-deck handling (Suuronen, 2005; Veldhuizen *et al.*, 2017; Cook *et al.*, 2019). The high injury incidence recorded among sandeel retained in the codend of commercial beam trawls targeting sole may also be biased as injured specimens may be less likely to escape through the cod-end meshes of 80 mm (Boute, 2022).

To estimate the *in-situ* injury probability, we assumed that sandeels were buried between 0 and 5 cm in the seabed when exposed to a commercial pulse stimulus. Sandeels spend most of their time buried in sandy substrates except during a brief spawning period in winter (Macer, 1966; Gauld and Hutcheon, 1990) and when foraging during part of the daytime in spring and early summer (Rindorf *et al.*, 2000). Sandeel prefer a specific sediment grain size, which allows for pumping water through the sediment pores over their gills (Holland *et al.*, 2005; Behrens *et al.*, 2007). Burying depths in the field have not been documented. Observations in the laboratory suggest sandeel rarely bury deeper than 5 cm (Winslade, 1974). In contrast, we found that upon collection before the experiment specimens tended to bury deeper than 5 cm in the sediment in the storage tank, which could have been an escape response to the handling. If sandeel respond in a similar manner to an approaching gear, the *in-situ FS* and injury probability presented in this paper can be considered conservative.

We conclude that it is unlikely that the pulse trawl fishery for common sole will have a substantial adverse effect on the population abundance of sandeel because of the low exposure probability in combination with the low injury probability; at least 96% of the sandeel in the path of commercial pulse trawlers are exposed to a *FS* at which none of the sandeel in our experiment developed a spinal injury or haemorrhage.

Data availability statement

The data underlying this article will be shared on reasonable request to the corresponding author.

Supplementary data

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

Author contributions

Conceptualization: ES, PM, AR; design and methodology: ES, PM, DB; performing experiments: ES, PM, DB, MS; collection of data: ES, PM, DB, MS, PB, ML, AR; data analysis: ES, PM, DB, PB, ML, AR; COMSOL simulation: ML; writing original draft: ES, AR; and writing, review, and editing: ES, PB, MS, ML, AR.

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Conflict of interest statement

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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