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Original Article

Internal injuries in marine fishes caught in beam trawls using electrical versus mechanical stimulations

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To improve the ecological and economic sustainability in the Dutch beam trawl fishery, tickler chains were replaced by electrical pulse stimulation to drive common sole (*Solea solea*) out of the seabed. Because electrical stimulation may cause internal injuries, we quantified this risk by sampling fish species from commercial beam trawlers and recording spinal injuries and haemorrhages from X-radiographs and autopsy. To distinguish mechanically-induced and electrical-pulse-induced injuries, we compared injuries in ten species sampled from pulse (PUL) and tickler-chain (TCK) trawlers and four species sampled from PUL trawlers with the stimulus switched on or off. Co-occurrence of a major spinal injury and major haemorrhage at the same location was only observed in PUL samples, and were frequently (40%) observed in Atlantic cod (*Gadus morhua*) and in low numbers (0–2%) in whiting (*Merlangius merlangus*), grey gurnard (*Eutrigla gurnardus*), and greater sandeel (*Hyperoplus lanceolatus*), but not in flatfishes and other species. In cod, injury occurrence correlated with fish length, with lower probabilities for small fish. Major spinal injury or major haemorrhage occurrence in PUL (range: <1–16%) was lower than in TCK (range: <1–42%) in eight of the ten species studied. Population level consequences of pulse-induced injuries are considered negligible.

Keywords: bottom trawling, electro-trawling, haemorrhage, North Sea, pulse fishing, spinal injury, tickler chains.

Introduction

Bottom trawling is used globally to capture demersal and benthic organisms, contributing 25% of the global landings (Amoroso *et al*., 2018). Dragging fishing gears over the seafloor results in physical disturbance of seabed habitats and mobilisation of sediment into the water column, which affects the structure and functioning of the ecosystem (Amoroso *et al*., 2018; Pitcher *et al*., 2022) and coincides with a high fuel consumption and large CO_2 emission (Parker and Tyedmers, 2015; Sala *et al*., 2022). In the North Sea, beam trawls are used to catch common sole (*Solea solea*) and other flatfish species. Tickler chains are towed in front of the trawl to drive the flatfish from the seafloor and to increase the catch efficiency (Rijnsdorp *et al*., 2008). The tickler chains disturb the structure of the seafloor and may damage or kill organisms in the path of the trawl (Lindeboom and de Groot, 1998; Depestele *et al*., 2019). The small cod-end mesh size (i.e. 80 mm), that is required to retain the slender sole, results in a high bycatch of bottom dwelling species and benthos, which are discarded with a low survival probability (van Beek *et al*., 1990; Uhlmann *et al*., 2014; Uhlmann *et al*., 2016). These effects, in combination with the high fuel consumption (Cheilari *et al*., 2013; Poos *et al*., 2013), jeopardise the ecological and economic sustainability of the fishery (van Balsfoort *et al*., 2006).

Replacing the mechanical stimulation of tickler chains with electrical stimulation is a promising technological innovation to improve the ecological and economic sustainability of the flatfish fishery for sole (van Marlen *et al*., 2014; Soetaert *et al*., 2015). Between 2009 and 2021, part of the Dutch beam trawl fleet was granted temporary derogations to use electrical stimulation (Haasnoot *et al*., 2016; Poos *et al*., 2020). The pulsed electric field induces involuntary muscle contractions that immobilise fish in front of the trawl (Stewart, 1977; Soetaert *et al*., 2019). This so-called pulse (PUL) trawling has several advantages over tickler-chain (TCK) trawling, including increased selectivity and reduced discard rates (van Marlen *et al*., 2014; Poos *et al*., 2020; Van Overzee *et al*., 2023), higher discard survival rates (van der Reijden *et al*., 2017), reduced fuel consumption (van Marlen *et al*., 2014; Poos *et al*., 2020), reduced physical disturbance of the sea floor (Depestele *et al*., 2019; Rijnsdorp *et al*., 2021b), reduced impact on benthic organisms (Bergman and Meesters, 2020; Tiano *et al*., 2020; Boute *et al*., 2021) and the benthic ecosystem (de Borger *et al*., 2020; Rijnsdorp *et al*., 2020b; Tiano *et al*., 2021) and higher revenues (Turenhout *et al*., 2016). Replacing mechanical stimulation with electrical stimulation could thus substantially reduce the ecological footprint of bottom trawling for sole.

Electrical stimulation may also have adverse effects. It is well known that electrical stimulation may inflict spinal injuries (e.g. fractures or dislocations) and haemorrhages in freshwater electrofishing (Snyder, 2003) and in the stunning of fish in aquaculture practice (Roth *et al*., 2003; Nordgreen *et al*., 2008). Marine electrofishing is likewise known to inflict internal injuries (Soetaert *et al*., 2015). Relatively high spinal injury occurrences (7–11%) have been reported in Atlantic cod (*Gadus morhua*) caught in PUL trawls or trawls with

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electrified benthos release panels (van Marlen *et al.*, 2014; Soetaert *et al.*, 2016c) and between 0–37% in controlled laboratory conditions depending on fish length and electric field strength (de Haan *et al.*, 2016; Soetaert *et al.*, 2016a; Soetaert *et al.*, 2016b). By comparison, injury occurrence in whiting (*Merlangius merlangus*) was low. Van Marlen *et al.* (2014) reported a single injured whiting out of 57 filleted specimens sampled from pulse gear catches, whereas Boute *et al.* (2022), in a more extensive study with X-radiography, showed that < 2% of the whiting sampled from commercial PUL trawl catches showed a spinal injury. In experiments where fish were exposed to a commercial pulse stimulus in controlled laboratory conditions no spinal injuries were found in sole, dab (*Limanda limanda*), European seabass (*Dicentrarchus labrax*), lesser sandeel (*Ammodytes tobianus*), and greater sandeel (*Hyperoplus lanceolatus*) (de Haan *et al.*, 2015; Soetaert *et al.*, 2016b; Soetaert *et al.*, 2018; Schram *et al.*, 2022b).

Injuries may also be inflicted by mechanical stress when fish come into contact with the netting or other components of the gear, or during the processing of the catch on deck (Suuronen, 2005; Broadhurst *et al.*, 2006). Mechanical stimulation generally results in external damage to the skin of the fish, such as gear marks, bruises and blood marks, pressure damage on the flesh of the fish, loss of scales and mucus layer, and localised petechial haemorrhages and suffusion of the head or body region caused by the rupture of capillaries (Digre *et al.*, 2010; Veldhuizen *et al.*, 2018; Sistiaga *et al.*, 2020).

The internal injuries caused by electrical stimulation are expected to be different from the injuries caused by externally applied mechanical stress. The double-sided muscle contractions induced by electrical stimulation may cause internal lesions, such as a fracture of the spinal column or in the haemal and neural arches. As a consequence, electrically-induced spinal injuries may rupture arteries and result in major haemorrhages inside the body (Snyder, 2003; de Haan *et al.*, 2016; Soetaert *et al.*, 2016a).

So far, only a few fish species have been studied for pulse-induced injuries in the North Sea flatfish fishery. To fill this knowledge gap, we (i) tested the hypothesis that the co-occurrence of a major spinal injury and major haemorrhage at the same body location is indicative of a pulse-induced injury by comparing injuries in fish sampled from PUL trawlers and from conventional TCK trawlers, and in fish sampled from PUL trawlers with the electrical stimulus turned on (PUL-on) and off (PUL-off); (ii) studied which fish species are sensitive for pulse-induced injuries and estimated the occurrence of pulse-induced injuries in thirteen fish species that dominate the catch of the beam trawl fishery for sole; (iii) studied whether the occurrence of pulse-induced injuries is related to fish body length; and (iv) discuss the ecological consequences of the injuries inflicted by PUL trawling and conventional TCK trawling.

Materials and methods

Dutch beam trawl fleet

A description of the Dutch beam-trawl fisheries is given in Rijnsdorp *et al.* (2020b). The fleet comprises small (engine power ≤ 221 kW) and large vessels (engine power > 221 kW) operating in the North Sea. Small vessels use beam trawls of 4.5 m when trawling in coastal waters. Large vessels operate offshore using beam trawls of 12 m and contribute about 95% of the sole landings (van Overzee *et al.*, 2023). The minimum mesh size is 80 mm when fishing for sole south of a line running from west to east at 55°N shifting to 56°N east of 5°E. The horizontal net opening is fixed by a beam that rests on two shoes. Since 2008, most vessels have replaced the beam and shoes with a hydrodynamic wing reducing the fuel consumption by 16% (Turenhout *et al.*, 2016).

To chase the flatfish up from the seabed, beam trawlers deploy either conventional TCK trawls or PUL trawls. In TCK trawlers a row of transverse chains are attached to the shoes or the ground rope. In PUL trawlers a rectangular matrix of electrode arrays, fitted between the beam/wing and ground rope, creates a heterogeneous electric field in front of the ground rope (de Haan *et al.*, 2016; Soetaert *et al.*, 2019). Most PUL trawlers use the pulse system of HKF Engineering B.V. that generates a pulsed bipolar current (PBC) at a frequency of 30 Hz (SD = 2.2), a peak voltage at the seafloor of 55.6 V (SD = 1.8), a pulse width of 336 ms (SD = 23), and a duty cycle, as defined by Soetaert *et al.* (2019), of about 2% (SD = 0.09) (ICES, 2020). The pulse stimulus has a rectangular shape with a short rise time and fall time (de Haan *et al.*, 2016; Soetaert et al., 2019). When passing through the electric field, fish are exposed for about 1.5 s to a variable field strength which depends on the animal's position and orientation relative to the electrode arrays. A fish that is located close to the electrode array may be exposed to a field strength ≥600 V m^{-1} whereas a fish that is located on the sediment halfway between two electrode arrays may be exposed to a field strength of ≥70 V m^{-1} (Schram *et al.* 2022b).

Collection of animals

Fish were sampled from catches on board commercial vessels (>221 kW) targeting sole during 2016–2019 by scientists from Wageningen Marine Research and the Experimental Zoology Group of Wageningen University & Research (Table 1) as described in Boute *et al.* (2022). Vessels and fishing trips were selected based on availability of scientists and space on board for an additional person. Sampling occurred during tows throughout the trip, except for three trips where the pulse stimulus was switched off (see below), when the fish were on the conveyor belt before gutting by the fishermen. Sampling occurred during as many hauls as possible, before handling by fishermen. Fish samples were stored in sealed plastic bags on ice. After landing, all fish were stored at –20°C in freezer facilities at Wageningen University.

Specimens were collected during sixteen fishing trips made by nine PUL trawlers, and during five trips by three TCK trawlers (Table 1). Fish were randomly sampled, except for cod, for which all specimens were collected to prevent a potential sampling bias, as pulse-induced injuries were visible due to dark skin discolouration (de Haan *et al.*, 2016; Soetaert *et al.*, 2016a). Two vessels (V2 and V9) fished for a single tow with the pulses simultaneously turned off on both starboard and portside. The third vessel (V1) fished with the pulses turned off, either on starboard or portside, for seven tows, allowing the collection of PUL-on and PUL-off samples from the same tow. In the 21 fishing trips, we collected 16 989 specimens of which 8 923 were sampled from PUL-on catches, 2 969 from PUL-off catches, and 5 097 from TCK catches.

The sampled PUL trawlers used a PulseWing from HKF Engineering B.V. and sampled TCK trawlers used a SumWing (Rijnsdorp *et al.*, 2021b). All vessels used the towing speed

Table 1. Overview of sampled fishing trips (anonymized vessel coding) with year, week, gear/treatment, number of collected animals and species, towing speed, and electrical pulse settings.

Vessel code	Year	Week	Gear/Treatment	Number of species	Number of specimens	Towing speed (mean ± SD) [kn]	Electrical pulse settings (mean ± SD)			
							Peak amplitude [V]	Frequency [Hz]	Width [μs]	Duty cycle [–]
V1	2016	29	PUL-off	4	576	5.1 ± 0.1				
V2	2018	4	PUL-off	4	1 075	5.0 ± 0.1				
V9	2018	8	PUL-off	3	1 318	5.0 ± 0.1				
V1	2016	29	PUL-on	10	1 035	5.1 ± 0.1	54.3 ± 2.9	30 ± 0	349.3 ± 2.5	2.1%
V2	2016	41	PUL-on	2	566	5.0 ± 0.1	55.5 ± 3.0	30 ± 0	350 ± 0	2.1%
	2017	36	PUL-on	1	11	5.0 ± 0.1	58.3 ± 3.1	30 ± 0	340 ± 0	2.0%
	2018	4	PUL-on	6	108	5.0 ± 0.1	54.3 ± 3.1	30 ± 0	300 ± 0	1.8%
	2018	36	PUL-on	2	107	5.0 ± 0.1	58.3 ± 3.0	30 ± 0	330 ± 0	2.0%
	2018	46	PUL-on	1	64	5.0 ± 0.1	55.6 ± 3.0	30 ± 0	350 ± 0	2.1%
V3	2017	6	PUL-on	2	126	4.7 ± 0.1	58.7 ± 3.0	30 ± 0	300 ± 0	1.8%
V4	2017	7	PUL-on	4	239	4.9 ± 0.1	55.3 ± 2.9	30 ± 0	350 ± 0	2.1%
V5	2017	24	PUL-on	11	2 898	4.9 ± 0.3	58.3 ± 2.9	30 ± 0	350 ± 0	2.1%
	2017	33	PUL-on	9	1 986	4.9 ± 0.3	58.3 ± 3.1	30 ± 0	350 ± 0	2.1%
V6	2017	24	PUL-on	6	566	5.0 ± 0.1	56.0 ± 3.1	30 ± 0	335.3 ± 5.0	2.0%
	2017	44	PUL-on	6	404	5.0 ± 0.1	55.5 ± 3.0	30 ± 0	330 ± 0	2.0%
V7	2018	4	PUL-on	5	238	5.0 ± 0.1	54.6 ± 3.1	30 ± 0	350 ± 0	2.1%
	2019	5	PUL-on	2	112	5.0 ± 0.1	54.8 ± 3.1	30 ± 0	350 ± 0	2.1%
V8	2018	6	PUL-on	4	177	5.0 ± 0.1	54.8 ± 3.2	30 ± 0	330 ± 0	2.0%
V9	2018	8	PUL-on	7	286	5.0 ± 0.1	56.1 ± 2.9	22.5 ± 0	390 ± 0	1.8%
V10	2018	23	TCK	9	1 425	6.1 ± 0.1				
	2018	26	TCK	9	2 079	6.1 ± 0.1				
V11	2018	47	TCK	7	1 266	6.5 ± 0.3				
	2019	9	TCK	2	301	6.5 ± 0.3				
V12	2019	8	TCK	1	26	6.4 ± 0.3				

that they would use without sampling, which was typically lower for PUL than for TCK (Poos *et al.*, 2020). Electrical-pulse settings were highly similar between trips and vessels and matched those of 33 PUL trawlers in the fleet using the HFK system (ICES, 2020; Rijnsdorp *et al.*, 2020a). The vessels V10, V11, and V12 used conventional TCK trawls with 6–8 shoe tickler chains and 12–14 net tickler chains, respectively.

All vessels used 80 mm diamond-shaped mesh cod-ends, which are the standard in sole-targeting trawl fisheries (Rijnsdorp *et al.*, 2008). To increase sample size of small fish that might have escaped from the cod-end, PUL trawler V1 was equipped with 40 mm mesh cover nets that spaciously fitted over the cod-end and specimens were sampled from both the cod-ends and cover nets, for the PUL-on and PUL-off catch method (Rijnsdorp *et al.*, 2021a).

Collection of fish was approved by the Animal Welfare Body of Wageningen University, the Animal Ethics Committee of Wageningen University & Research, and the Central Authority for Scientific Procedures on Animals (application number AVD1040020184945). Collection of fish smaller than the minimum landing size, and the use of cover nets was approved by the Netherlands Enterprise Agency.

X-ray photography and autopsy

For X-ray photography and autopsy, we followed the methodology described by Boute *et al.* (2022). Briefly, sampled fish were defrosted and subsequently X-rayed using a Philips X-ray machine (SRM 0310 tube s/n 923436) with a 46401 G housing (2.3 mm Al total filtration), Philips XD6028 collimator (0.2 mm Al total filtration), generator Philips Super CP 80 (s/n 953031), Philips Super CP 50 control panel, and a Philips Optimus M200 frame. Flatfish species were X-rayed laterally only, other species were also X-radiographed dorsoventrally, except for fish collected from V1. Depending on fish size, X-ray settings varied in the range of 40–71 kV and 32–71 mAs, and images were captured by either a 35.2 × 42.8 cm phosphor plate (4 020 × 4 892 px, pixel pitch 87.5 μm, 12 bit) or a 23.8 × 29.7 cm mammography phosphor plate (5 440 × 6 776 px, pixel pitch 43.75 μm, 12 bit) and read out with a Konica Minolta Regius 110HQ digitizer. Distance between X-ray source and plate was 127 cm. After X-radiography, fish standard length was measured to the nearest millimetre (Rabone Chesterman No 47R mounted on a measuring board). For autopsy, each fish was filleted on the left and right side, and subsequently photographed with a Nikon D700 digital camera with a NIKKOR lens (JAA782DA type). These protocols were established after the first batch of samples for V1, where only lateral X-rays were taken and no inspection for internal haemorrhages was included yet. In total, we processed 26 266 X-ray images and 30 756 photographs of filleted fish.

Injury scoring system

Internal injuries were scored following Boute *et al.* (2022). Internal injuries that are possibly pulse related comprise major spinal injuries (s2) and major haemorrhages (h2). Major spinal injuries ranged between a subluxation or compression of several vertebrae (e.g. spinal misalignment) and fractured, or clearly dislocated vertebrae, as regularly observed in laboratory exposure experiments in the context of marine electrotrawling (de Haan *et al.*, 2016; Soetaert *et al.*, 2016a; Soetaert *et al.*, 2016b) and in freshwater electrofishing studies (Fredenberg, 1992; Hollender and Carline, 1994; Snyder, 2003). Major haemorrhages (h2) covered a substantial area as typically found in pulse-exposed cod (de Haan *et al.*, 2016; Soetaert *et al.*, 2016a; Soetaert *et al.*, 2016b). Injuries that are likely unrelated to pulse exposure were deformations of one or multiple vertebrae, including a minor subluxation (minor spinal injuries; s1) and minor haemorrhages (h1) that covered a small area and were highly localised. Skeletal deformities that were clearly unrelated to acute injuries inflicted in the catch process, such as the presence of additional spines, spinal curvature linked to developmental luxation, and block vertebrae, were not taken into account. Haemorrhages caused by filleting or blood in the haemal canal were always clearly distinguishable and were not scored. Examples of the spinal injury categories for cod and sole are provided in Figure 1.

The locations of the injuries were determined along the anteroposterior axis of the fish relative to the tip of the snout (0) and the base of the tail (posterior end of the mid-lateral portion of the hypural plate; 1) to reveal patterns of localisations that might indicate a common cause for the observed injuries, as previously reported for cod (de Haan *et al.*, 2016; Soetaert *et al.*, 2016a; Soetaert *et al.*, 2016b).

All data were gathered and stored using a custom-made software database system in `Python` (Python Software Foundation, n.d.), in combination with `OpenCV`, and `SQLiteManager` in `Mozilla Firefox`.

Data analyses

Two metrics for possible pulse-induced injuries were estimated. For the first metric (s2h2), we scored fish with both an s2 and h2 injury occurring at a similar body position (within 0.1 units standard length). This metric is related to the hypothesis that the co-occurrence of a major spinal injury and major haemorrhage at the same body location is indicative of a pulse-induced injury. This co-occurrence is consistent with the knowledge that the muscle contractions caused by electrical stimulation may cause a fractures or dislocation of the spinal column and/or haemal and neural arches, which may result in a major haemorrhage at the location of the spinal injury due to the rupture of the artery running through the haemal canal (Snyder, 2003; de Haan *et al.*, 2016; Soetaert *et al.*, 2016a).

The second metric (s2|h2) included fish with either an s2 or an h2 injury as a possible pulse-induced injury. This metric is consistent with the results of laboratory experiments showing that some of the cod exposed to a pulse stimulus developed an h2 injury in absence of a spinal injury (de Haan *et al.*, 2016; Soetaert *et al.*, 2016a).

Although the above metrics correspond to the injuries observed in fish exposed to an electrical pulse stimulus, the methodology will not provide an exact determination of a pulse-induced injury because injuries may also be caused by externally applied mechanical stress during the catch process or handling of the catch. To support the interpretation, we therefore compared the injury occurrence between PUL (pulse-induced and mechanically-induced injuries) and TCK samples (mechanically-induced injuries) and directly compared the injury occurrence in fish caught by PUL trawlers with the pulse stimulus switched on (PUL-on) and off (PUL-off).

The effect of gear type (PUL and TCK) and treatment (PUL-on and PUL-off) on injury probability was studied by fitting a

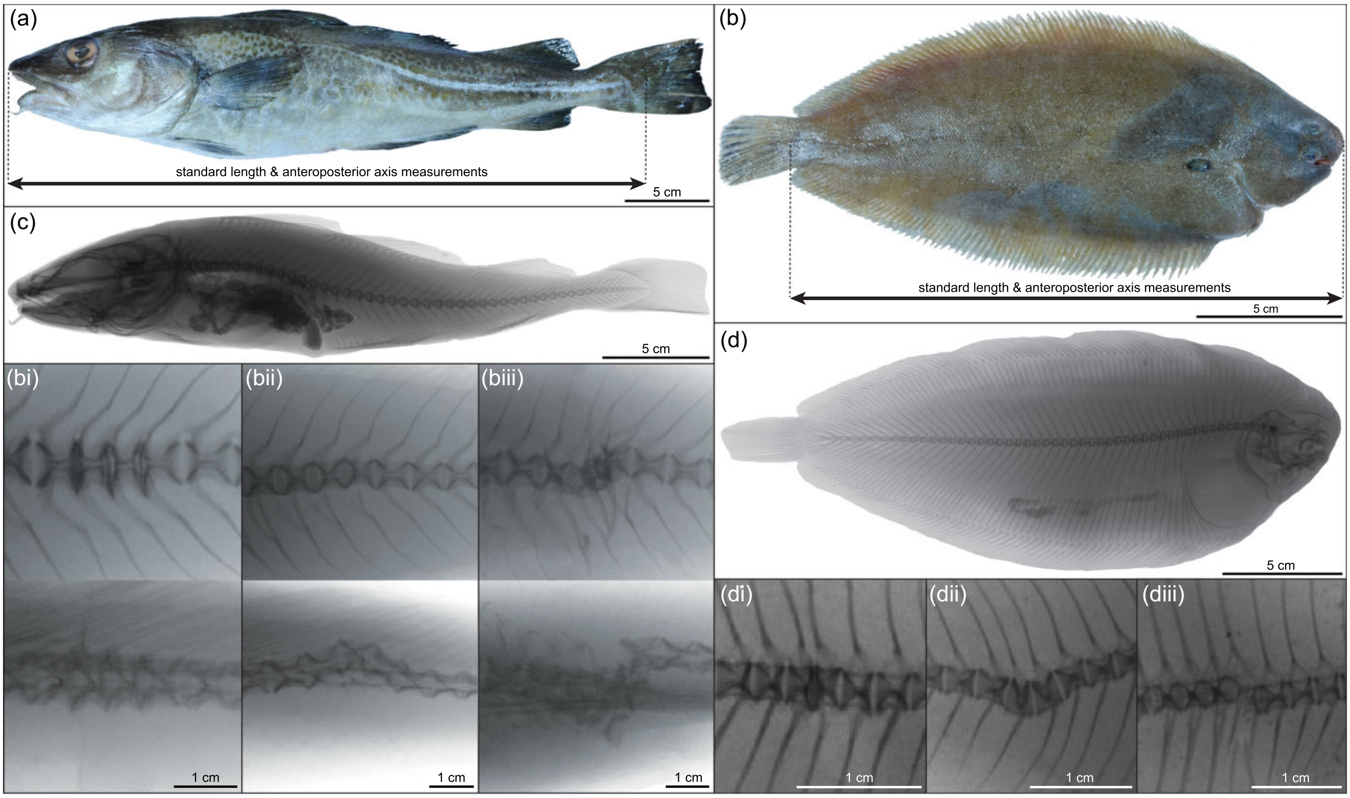

Figure 1. Spinal injury categorisation types in (a and b) cod and (c and d) sole. (a and c) The location of spinal injuries was quantified on the anteroposterior axis of the fish relative to the snout and caudal fin as indicated by the black double arrow. (b and d) Lateral X-radiograph of a specimen without injury. Spinal injuries were subdivided into (bi and di) minor and (bii, biii, dii, and diii) major. Top and bottom images are lateral and dorsoventral X-radiographs of the same fish, respectively. For flatfish only lateral X-radiographs were made.

binomial generalized linear model:

$$\text{(m1)} \qquad P_j \sim Bin(1, p_j), logit\left(p_j\right) = \alpha + \beta_1 C_j,$$

where P_j is the observed injury probabilities by trip *j*, and C is the gear type or treatment. To take account of the different sampling levels, the number of specimens per trip was used as weight factor. The analysis was done for species with at least 25 specimens sampled per catch method.

The contrast between the injury probability by gear type or treatment was estimated for species, for which catch method significantly affected the log odds ratio = ln [(*p*/(1-*p*))/(*q*/(1-*q*))], where p = injury probability of catch method C_1 and q = injury probability of catch method C_2 using the `R` library `emmeans` 1.6.1.

To assess, which species were sensitive or insensitive for pulse-induced injuries we studied the co-occurrence of s2 and h2 in individual fish using 2 × 2 contingency tables and a two-tailed Fisher's exact test (`fisher.test` from `R` library `stats` 3.6.1) of the count data for gear type (PUL and TCK) and treatment (PUL-on and PUL-off) separately.

For species, that were found to be potentially sensitive for pulse-induced injuries, we analysed the effect of fish length on the injury probability. To allow for non-linear dependencies of injury probability on fish length, as found in laboratory-exposed cod (de Haan *et al.*, 2016), we used a generalized additive model (GAM) (Wood, 2017), including a covariate for gear type or treatment [C], a non-linear smooth function of standard length [*s*(SL)], and their interaction:

$$\text{(m2)}\ P_{i,j} \sim Bin(1, p_{i,j}), logit\left(p_{i,j}\right) = \alpha + \beta_1 C_{i,j} + \beta_2 s\left(SL_{i,j}\right) + \beta_3 C_{i,j} \times s\left(SL_{i,j}\right),$$

where $P_{i,j}$ corresponds to the proportion of spinal injuries per length class (*i*) in sampled trip (*j*). SL is the standard length class (1 cm bin). The number of specimens per 1 cm length class per trip was used as weight factor. Model selection was based on the Akaike Information Criterion (AIC) (Akaike, 1973). The model with fewer predicting variables was selected when $\Delta AIC < 2$ (Burnham and Anderson, 2002).

All statistical analyses were performed in `R` v3.6.1 (R Core Team, 2019). GAMs were fitted using the `mgcv` package (Wood, 2017). Model fitted values and confidence intervals were calculated using the `predict` function in the `car` package (Fox and Weisberg, 2019) and back-transformed to the response scale with the inverse logit.

Results

Internal injury occurrence

Table 2 presents the number of fish with a spinal injury or haemorrhage as recorded in the samples from the PUL (PUL-on and PUL-off) and TCK gear. The number of fish sampled varied across species, generally exceeding 500 specimens of the dominant flatfish and roundfish species in the catch. Most of the injured fish had a minor spinal injury (s1) or a minor haemorrhage (h1). Major spinal injuries (s2) and

Table 2. Overview of the occurrence of spinal injuries, haemorrhages, and the combination of spinal injuries and haemorrhages by species (common name and FAO 3-Alpha Species Code) sampled from commercial pulse (PUL) trawls with the pulse stimulation switched on (PUL-on) and off (PUL-off), and commercial tickler-chain (TCK) trawls.

Species		Gear/Treatment	Spinal injuries				Haemorrhages				Spinal injuries and haemorrhages			Number of sampled trips
Common name	Code		s1	s2	s	*n*	h1	h2	h	*n*	s2|h2	s2h2	*n*	
Sole	SOL	PUL-on	24	5	28	824	7	0	7	727	5	0	727	6
Dab	DAB	PUL-on	29	1	30	765	12	9	21	625	9	0	625	4
Plaice	PLE	PUL-on	28	4	30	1 684	7	4	11	1 509	8	0	1 509	4
Cod	COD	PUL-on	29	191	216	475	50	141	183	409	163	123 (2)	409	12
Whiting	WHG	PUL-on	62	25	86	2 616	85	40	122	2 235	54	11	2 235	12
Bib	BIB	PUL-on	7	2	9	352	11	0	11	310	2	0	310	6
Grey gurnard	GUG	PUL-on	19	4	22	1 071	25	8	33	982	10	2	982	10
Tub gurnard	GUU	PUL-on	8	4	11	200	6	8	14	164	9	2	164	7
Lesser sandeel	ABZ	PUL-on	2	6	8	49	2	1	3	48	7	0	48	3
Greater sandeel	YEZ	PUL-on	73	75	143	538	21	31	52	512	82	11 (5)	512	5
Dragonet	LYY	PUL-on	1	0	1	148	0	0	0	112	0	0	112	4
Seabass	BSS	PUL-on	1	1	2	103	1	11	12	102	11	0 (1)	102	3
Lesser weever	TOZ	PUL-on	2	1	3	98	0	0	0	1	0	0	1	2
Dab	DAB	PUL-off	24	4	28	636	18	5	23	444	6	0	444	3
Plaice	PLE	PUL-off	43	5	48	1 631	123	15	138	1 572	19	1	1 572	3
Whiting	WHG	PUL-off	12	5	17	586	13	15	26	321	18	2	321	3
Grey gurnard	GUG	PUL-off	0	1	1	116	3	0	3	56	1	0	56	2
Sole	SOL	TCK	37	6	43	353	0	4	4	353	8	2	353	2
Dab	DAB	TCK	46	6	51	812	3	10	13	812	15	0 (1)	812	3
Plaice	PLE	TCK	41	4	45	1 007	12	12	24	1 007	15	1	1 007	3
Cod	COD	TCK	7	1	8	103	15	0	15	103	1	0	103	4
Whiting	WHG	TCK	35	28	63	1 148	30	3	33	1 148	31	0	1 148	4
Grey gurnard	GUG	TCK	48	1	49	1 033	62	22	83	1 022	23	0	1 022	3
Tub gurnard	GUU	TCK	24	6	28	469	24	15	38	469	19	1 (1)	469	3
Lesser sandeel	ABZ	TCK	9	30	37	112	0	0	0	112	30	0	112	2
Greater sandeel	YEZ	TCK	2	13	14	33	0	3	3	33	14	2	33	2
Dragonet	LYY	TCK	0	0	0	27	0	0	0	27	0	0	27	2

Columns present the number of fish with a minor (s1, h1), major (s2, h2), minor or major (s, h) injury, and the number of fish with a major spinal injury or major haemorrhage (s2|h2) and the number of fish with a major spinal injury and major haemorrhage at the same body location (s2h2). Number of sampled fish is denoted with *n*. The s2|h2 and s2h2 injuries are used as metrics for pulse-induced injuries (see text). The numbers between parentheses in the column "s2h2" denote the number of fish where an s2 and h2 co-occurred but not at the same location.

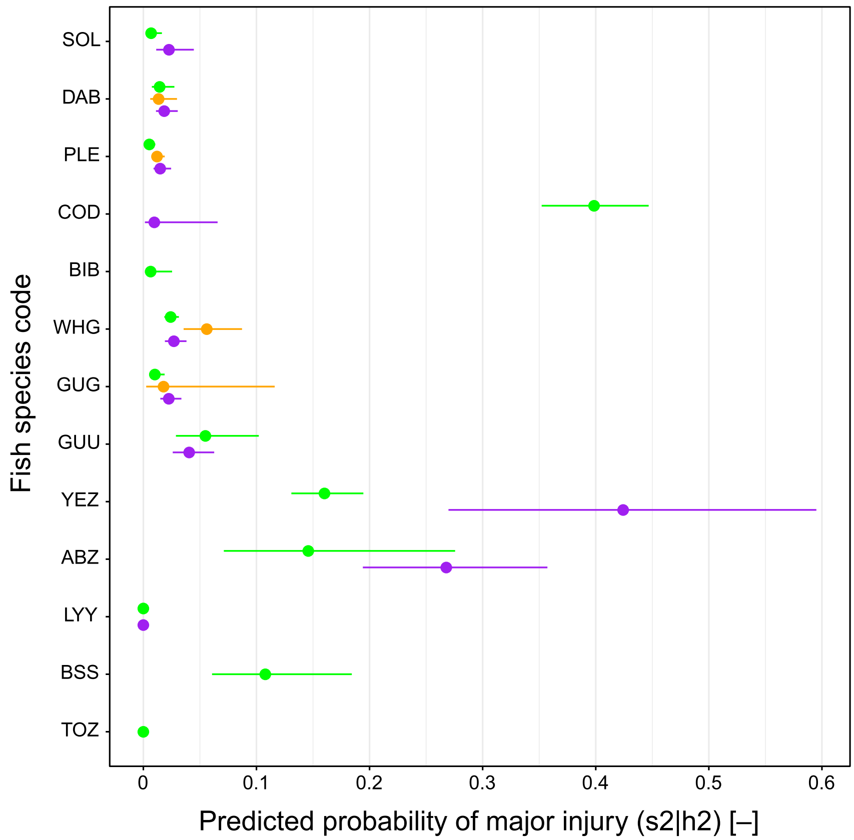

Figure 2. Probability and 95% confidence interval of major injuries (s2|h2) in fish species caught by PUL with PUL-on (green) and PUL-off (orange) and by TCK (purple).

major haemorrhages (h2) occurred less. Minor and major injuries were independent as the sum of the number of fish with both a minor and major spinal injury (s1 + s2), or haemorrhage (h1 + h2), was generally close to the number of fish with a spinal injury (s) or haemorrhage (h). The Fisher's exact test corroborated the independent occurrence (Supplementary Material 1). Only in cod ($p = 0.0027$) and plaice ($p = 0.0016$) sampled from PUL-on was the number of specimens with both a minor and major spinal injury larger than expected.

The occurrence of major injuries (s2|h2) for the different species sampled from PUL-on and TCK gear is shown in Figure 2. Injury occurrence was low (<6%) in 9 out of 13 species sampled from PUL catches. High injury occurrences were recorded for cod (COD: 40%), sandeel species (ABZ: 15%; YEZ: 16%) and seabass (BSS: 11%). Comparison of the s2|h2 injury occurrence between PUL-on and TCK showed that the injury occurrence was lower in PUL-on with the exception of cod and tub gurnard. The contrast between PUL-on and TCK injury occurrence was significant in cod and lesser sandeel (Table 3). Similar results were obtained when evaluating the contrast between the PUL-on and TCK injury occurrences of s2 and h2 separately, although whiting showed a significant lower injury occurrence in PUL-on for s2 and a significant higher injury occurrence for h2.

The differences in major injury occurrences (s2, h2, and s2|h2) between fish from PUL tows with the pulse stimulus switched on and off was studied in four species with a sufficiently high sample size (plaice, dab, whiting, and grey gurnard). Except for whiting, injury occurrence was not significantly different between PUL-on and PUL-off samples. Whiting showed a significantly lower h2 and s2|h2 injury occurrence in PUL-on samples (Table 3).

Consistent with the hypothesis about the diagnostic for pulse-induced injuries, a significant, or almost significant, association of a major spinal injury (s2) and major haemorrhage (h2) was observed in PUL-on catches but not in TCK catches in five of the 10 species studied (cod, whiting, grey gurnard, tub gurnard, greater sandeel) (Table 4). A comparison of the location of the s2 and h2 injury in the same fish showed that the injuries occurred at the same location along the body axis as expected for species that are sensitive for pulse-induced injuries (Figure 3). Only in greater sandeel did the h2-location differ ≥0.1 unit of body length from the s2-location for four of the fourteen specimens. A significant association of an s2 and h2 injury among TCK sampled species was observed in sole.

Fish-length dependence of pulse-induced injuries for cod, whiting, grey gurnard, and greater sandeel (i.e. species that showed potential sensitivity to electrical pulses and for which sufficient samples were obtained) were also analysed for the relationship between injury occurrence and body length. For this analysis, we used the injury occurrence for combined major spinal injuries and haemorrhages (s2h2), as these are most likely to result from electrical exposure. The GAM analysis showed that including a smoother for body length [s(SL)] improved the model fit as the AIC was reduced by more than 2 units, although the p-value of the smoother was only significant in cod (Table 5). The significant injury-probability—size relationship for cod showed a clear peak at intermediate

Table 3. Contrast (log odds ratio with standard error) between occurrence of major spinal injuries (s2), major haemorrhages (h2), and major spinal injury or major haemorrhage (s2|h2) in samples from PUL-on and TCK, and samples from PUL-on and PUL-off.

Catch method comparison	Species code	s2			h2			s2|h2		
		log odds	SE	*p*-value	log odds	SE	*p*-value	log odds	SE	*p*-value
PUL-on vs. TCK	SOL	−1.041	0.609	0.087	−24.13	36 418	0.999	−1.208	0.574	0.035
	DAB	−1.738	1.081	0.242	0.159	0.463	0.937	−0.253	0.425	0.822
	PLE	−0.516	0.708	0.747	−1.512	0.579	0.024	−1.043	0.440	0.047
	COD	4.228	1.009	0.000	18.999	1192	0.987	4.213	1.010	0.000
	WHG	−0.952	0.277	0.002	1.939	0.600	0.003	−0.114	0.228	0.871
	GUG	1.353	1.119	0.448	−1.004	0.415	0.041	−0.806	0.381	0.087
	GUU	0.454	0.651	0.485	0.440	0.448	0.326	0.319	0.415	0.443
	ABZ	−0.964	0.485	0.047	19.741	7604	0.998	−0.762	0.461	0.098
	YEZ	−1.389	0.377	0.000	−0.439	0.633	0.488	−1.352	0.372	0.000
	LYY	−0.716	1 14 801	1.000	−1.212	79947	1.000	−1.212	79947	1.000
PUL-on vs. PUL-off	DAB	−1.576	1.119	0.337	0.249	0.561	0.897	0.064	0.531	0.992
	PLE	−0.256	0.672	0.923	−1.288	0.564	0.058	−0.831	0.423	0.121
	WHG	0.114	0.492	0.971	−0.990	0.309	0.004	−0.875	0.279	0.005
	GUG	-0.841	1.122	0.734	15.91	2 586	1.000	−0.569	1.058	0.852

Bonferroni corrected significant contrasts are underlined.

Table 4. Contingency table showing the frequency of occurrence of major spinal injuries (s2 = 0, 1) and major haemorrhages (h2 = 0, 1) in the PUL-on and TCK samples ignoring the similarity in the location of the s2 and h2 injury.

Gear/Treatment	Species code	Total number of specimens	Injury type combination				Fisher's exact test *p*-value
			s2 = 0, h2 = 0	s2 = 1, h2 = 0	s2 = 0, h2 = 1	s2 = 1, h2 = 1	
PUL-on	SOL	727	722	5	0	0	1.0000
	DAB	625	616	0	9	0	1.0000
	PLE	1 509	1 501	4	4	0	1.0000
	COD	409	246	22	16	125	<0.0001
	BIB	310	308	2	0	0	1.0000
	WHG	2 235	2 181	14	29	11	<0.0001
	GUG	982	972	2	6	2	0.0003
	GUU	164	155	1	6	2	0.0061
	ABZ	48	41	6	1	0	1.0000
	YEZ	512	430	51	15	16	<0.0001
TCK	SOL	353	345	4	2	2	0.0014
	DAB	812	797	5	9	1	0.0719
	PLE	1 007	992	3	11	1	0.0469
	COD	103	102	1	0	0	1.0000
	WHG	1 148	1 117	28	3	0	1.0000
	GUG	1 033	1 010	1	22	0	1.0000
	GUU	469	450	4	13	2	0.0133
	ABZ	112	82	30	0	0	1.0000
	YEZ	33	19	11	1	2	0.5473
	LYY	27	27	0	0	0	1.0000

Association between the presence of spinal injuries and haemorrhages was assessed with a two-tailed Fisher's exact test per catch method. Bonferroni corrected significant contrasts are underlined.

body lengths between 25–30 cm, with occurrence probabilities reaching the 0.5 level (Figure 4). Injury probability quickly dropped to a level <0.1 in cod <20 cm, declined to about 0.25 in cod between 40–60 cm and further declined in cod >60 cm. A separate analysis of the s2 and h2 injury occurrences in relation to body length and gear gave similar results (Supplementary Material 2).

Internal injury locations

The locations of the internal injuries, which may be indicative for the underlying cause, were compared between PUL-on and TCK catches for the species that are likely to be sensitive for electrical stimuli (Figure 5). For cod, the injuries in PUL-on caught fish were highly localised at the posterior part of the abdominal region and anterior part of the caudal region (0.55–0.65), especially when s2 injuries co-occurred with h2 injuries (Figure 5a and b; samples shown in red). In TCK caught fish, the localisation was less clear, but the number of injuries found were rather low (Figure 5c and d).

In whiting, the s2 and h2 injuries in PUL-on caught fish were distributed over a wider area along the body axis (0.3–1.0) with a small peak around 0.65. The locations of the s2h2 injuries (red) showed a more narrow distribution between 0.5–0.75 (Figure 5e and f). The s2 injuries in TCK caught fish seem concentrated in the anterior part (0.3–0.5) (Figure 5g).

In greater sandeel caught with PUL-on, the s2 and h2 injuries show a broad distribution over the body axis with a peak around 0.5 (s2) and 0.7 (h2). The locations of the

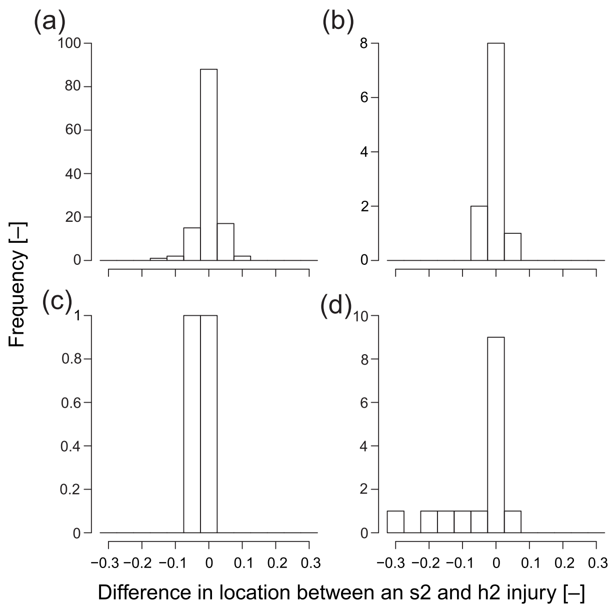

Figure 3. Frequency distribution of the difference in location along the body axis of an s2 and h2 injury in fish specimens with a co-occurrence of an s2 and h2 injury: (a) cod, (b) whiting, (c) grey gurnard, and (d) greater sandeel.

s2h2 injuries showed a broad distribution between 0.25–0.8 (Figure 5i and j). The location of the injuries recorded in TCK caught fish showed a similar pattern, although the number of fish sampled from TCK was rather low (Figure 5k and l). Two of the TCK caught fish showed an s2h2 injury at the same location.

Discussion

Pulse-induced injuries

The s2h2 metric determined the number of fish with an s2 and h2 injury at the same body location. This metric is related to the knowledge that pulse-induced injuries are caused by muscle cramp in response to electrical pulse stimulation. Pulse-exposure may result in double-sided muscle contractions that can overload the vertebral column and result in a spinal injury or dislocation of vertebrae. Such dislocations are likely to co-occur with a major haemorrhage due to the rupture of blood vessels running through the haemal canal (de Haan *et al.*, 2016; Soetaert *et al.*, 2016a; Soetaert *et al.*, 2016b). Similar correlations have been observed in freshwater electrofishing studies (Holmes *et al.*, 1990; Hollender and Carline, 1994; Ruppert and Muth, 1997). The co-occurrence of an s2 and h2 injury at the same location was uniquely observed in PUL-on, and did not occur in TCK sampled fish, corroborating the hypothesis that the s2h2 injuries are related to pulse stimulation. For cod, the s2h2 occurrence showed a relatively high sensitivity for pulse-induced injuries, which corresponds to high occurrences in controlled exposure experiments (de Haan *et al.*, 2016; Soetaert *et al.*, 2016a; Soetaert *et al.*, 2016b). For whiting, gurnards, and sandeels, sensitivities estimated by the combined s2h2 injuries were low, which for sandeels was corroborated in a laboratory exposure study (Schram *et al.*, 2022b). Sole, dab and seabass were found insensitive, in line with previous results (de Haan *et al.*, 2015; Soetaert *et al.*, 2016b; Soetaert *et al.*, 2018).

The s2h2 diagnostic, however, may underestimate the occurrence of pulse-induced injuries because exposure to a pulse stimulus may also result in either an s2 or h2 injury. Tank experiments with cod showed an h2 in absence of an s2 in four out of 101 (de Haan *et al.*, 2016) and three out of five injured fish (Soetaert *et al.*, 2016a), suggesting that a temporary dislocation of vertebrae may rupture a blood vessel in the haemal canal, after which the vertebrae resumed their normal position (Soetaert *et al.*, 2016a). Our results indeed showed that 18 (11%) cod had an h2 in absence of an s2 and 22 (13%) had an s2 in absence of an h2, while 123 (75%) of the 163 cod with a major injury (s2|h2) had an s2h2 injury. Because mechanically-induced major injuries appear to be rare (only 1 of the 103 cod sampled from TCK had s2|h2 injury), this suggests that the s2h2 diagnostic underestimated the pulse-induced injury occurrence in cod by about 25% [(163–123)/163].

On the other hand, an s2h2 injury may also overestimate the pulse-induced injury occurrence, as these could in theory be inflicted by a mechanical cause. This seems unlikely, however, because an s2h2 injury was only observed in a very small percentage of the plaice (0.1%), tub gurnard (0.2%), and sole (0.7%) sampled from TCK, while the non-pulse-induced mechanical stress is expected to be higher in TCK gear than in PUL-on gear, due to the higher towing speeds.

The other metric (s2|h2), however, will have included fish that were injured due to mechanical stress during the catch process as we regularly observed separate s2 and h2 injuries in fish caught in TCK as well as in PUL-off. The s2|h2 metric, therefore, likely overestimated the occurrence of pulse-induced injuries. Because the non-pulse-induced mechanical stress may be highly species dependent, and may also differ between gear types, quantification of pulse-induced injuries beyond these upper (s2|h2) and lower limits (s2h2) remains speculative.

In addition to estimating injury occurrences due to pulse stimulation, we can also directly compare injury occurrences between PUL-on and TCK gears. Tickler chains are currently the main alternative to electrical pulses for sole-targeting bottom trawling in the North Sea. The comparison of major injury occurrences between PUL-on and TCK will therefore provide an indication of relative impact of gear type on internal injuries (Table 6). If the s2|h2 injury occurrence in PUL-on is much higher than in TCK, we expect major injuries to be dominated by pulse-induced injuries, whereas if the s2|h2 injury occurrence in PUL-on is much lower than in TCK, we expect a predominant contribution of mechanical damage. As already shown, the s2|h2 injury occurrence of cod in PUL-on (40%) was substantially higher than in TCK (1%), supporting the conclusion that this species is particularly sensitive to electrical stimulation. For the two sandeel species and grey gurnard, the opposite was found. The s2|h2 injury occurrence in TCK was ≥2 times higher than in PUL-on, suggesting predominantly mechanically-induced injuries. The high s2|h2 injury occurrence of sandeel in TCK indicates a high sensitivity for mechanically-induced injuries. The estimated injury occurrence in sandeel is likely overestimated, because most sandeel will, given their slender body shape, pass through the trawl and escape through the meshes of the cod-end, whereas sandeel that are injured during the catch process may have a higher chance of being retained. The estimated pulse-induced injury occurrence of s2h2 for greater sandeel (2.1%) is close to the worst case estimate (4%) of pulse-induced injury

Table 5. Generalized additive models of the s2h2 injury occurrence (P_{s2h2}) as a function of standard length (SL) for cod (COD), whiting (WHG), and greater sandeel (YEZ) with the pulse stimulus switched on (PUL-on)

Species code	Null: $P_{s2h2} \sim \alpha$		$P_{s2h2} \sim \alpha + s(\text{SL})$						
	AIC	*df*	AIC	*df*	α	SE	*p*-value	*p*-value of *s*(SL)	Deviance explained
COD	375.0	1	350.9	6.956	−1.258	0.264	<0.001	0.0016	12.1%
WHG	80.21	1	77.17	2.677	−5.573	0.443	<0.001	0.11	11.1%
YEZ	53.84	1	51.55	3.219	−4.171	0.616	<0.001	0.29	19.8%

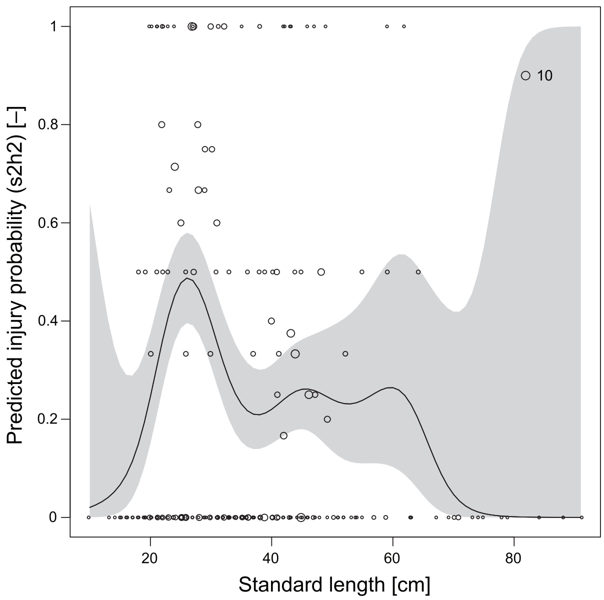

Figure 4. Effect of body length on the probability of an s2h2 injury in cod caught in commercial PUL-on gear. Bubbles show the observed probabilities per cm-bin per trip. The size of the bubbles is proportional to the square root of the number of sampled fish. The reference size is plotted in the upper, right-hand corner. Shaded area shows the 95% confidence interval.

occurrence obtained from of a tank experiment (Schram *et al.*, 2022b) and much less than the injury occurrence of s2|h2 (16%).

In whiting (PUL-on: 2.4%; TCK: 2.7%) and tub gurnard (PUL-on: 5.5%; TCK: 4.1%), the injury occurrences were close to equal between PUL-on and TCK. In this case, part of the injuries might be pulse-induced if the PUL gear inflicts fewer mechanically-induced injuries (Schram *et al.*, 2020) due to a lower towing speed (PUL-on = 5.0 knots; TCK = 6.5 knots; Poos *et al.*, 2020) and the smaller catch volume containing fewer hard objects that may damage fish (van Marlen *et al.*, 2014). For whiting, the s2|h2 injuries in TCK were dominated by spinal injuries, whereas in PUL-on these were dominated by h2, suggesting that most of the h2 injuries may be pulse-induced (Boute *et al.*, 2022).

The overall comparison of major injuries, either a spinal injury or a haemorrhage (s2|h2) between PUL-on and TCK shows that in most species that are potentially sensitive to pulse-induced injuries (i.e. that show cases of co-localised s2 and h2 injuries), this sensitivity is compensated by a lower sensitivity to mechanically-induced injuries in PUL gear, with cod as the only and clear exception.

The data on cod showed that the pulse-induced injury occurrence varied significantly with body length, with highest rates observed for intermediate length classes. The estimated injury—length relationship is in agreement with the length dependence observed in tank experiments (de Haan *et al.*, 2016). The lack of support for an effect of body length on the injury probability in the other species with combined s2 and h2 injuries may be due to the rather low number of injuries. A separate analysis of s2 and h2 injuries provided support for an increase in the occurrence of h2 injuries with body length in whiting sampled from PUL-on and a decrease in s2 in PUL-on and TCK (Boute *et al.*, 2022).

Species-specific differences in sensitivity for pulse-induced injuries

The pulse-induced injury occurrence estimated for the dominant species in the North Sea beam trawl fishery for sole showed large inter-specific differences with eight species considered to be insensitive, four species considered to be potentially lightly sensitive, and one species considered to be highly sensitive. This calls for a mechanistic explanation for the differences in sensitivity. Although it is clear that muscle cramp may overload the vertebral column resulting in the dislocation or fracture of vertebrae and neural and haemal arches (de Haan *et al.*, 2016; Soetaert *et al.* 2016a), it is unknown why for instance cod seems much more sensitive than whiting and why flatfish species seem insensitive.

Interspecific differences in sensitivity could be related to the differences in insulating properties of the skin, characteristics of the vertebrae (number, size, mineral content), strength and flexibility of the ligaments, and the interaction between muscle power and vertebrae strength (Soetaert *et al.*, 2016b; Boute, 2022). Analyses of vertebral column characteristics (spinal angle, number of vertebrae, vertebrae width and height, and inter-vertebra distance) and muscle-to-vertebra ratio (cross-sectional area) alone did not explain the high sensitivity of cod (Boute, 2022). Soetaert *et al.* (2016a) investigated the potential role of the origin of the experimental fish (farmed, wild), number of vertebrae, mineral content of the vertebrae, strength of the intervertebral ligaments, but did not find a conclusive factor that could explain the observed differences in spinal injury occurrence across experimental studies in cod.

A more likely explanation may be found in the typical location of pulse-induced injuries in cod. Injuries occurred in the transition area between the abdominal and the caudal region where the compression force imposed by the lateral muscles during swimming is presumed to be strongest (de Haan *et al.*, 2016; Soetaert et al., 2016a) and where lordosis is most frequently observed in farmed cod (Opstad *et al.*, 2013). In this area, a large change occurs between the relative size of the epaxial muscles and hypaxial muscles (Figure 6). In the abdominal region, the epaxial muscles are relative large as compared to the hypaxial muscles, whereas in the caudal region the epaxial and hypaxial muscles are of about equal size. A

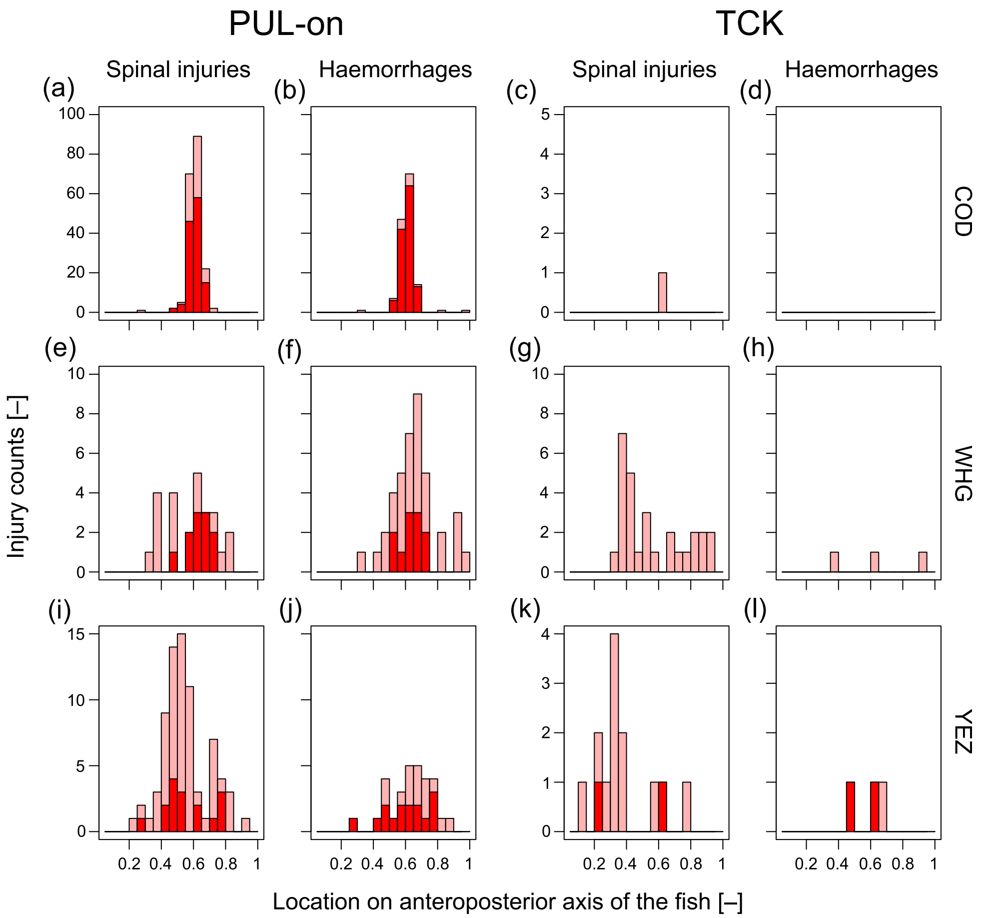

Figure 5. Frequency distribution of the locations along the anteroposterior body axis of the major spinal injuries (s2: 1st and 3rd column) and major haemorrhages (h2: 2nd and 4th column) for fish sampled from PUL-on (1st and 2nd column) and TCK (3rd and 4th column) for COD (top row), WHG (middle row), and YEZ (bottom row). Fish with both a major spinal injury and a major haemorrhage (s2h2) are in red.

Table 6. Percentages of internal injuries occurrence observed in the catch of PUL (pulse stimulus on) and TCK trawlers by individual fish species and for all bony fish. Internal injury occurrence was estimated for the co-occurrence of major spinal injuries and haemorrhages (s2h2) and the total injury occurrence of major spinal injuries or major haemorrhages (s2|h2). The overall injury occurrence, that is representative of 89% of the discard numbers, was calculated as a weighted mean over the numerical proportion of the species in discard fraction of the catch in the Dutch beam trawl fishery for sole (80 mm mesh size) between 2009–2017 (ICES, 2018). ND denotes no data.

Species		PUL-on		TCK		Discard numbers
Common name	Code	s2h2	s2|h2	s2h2	s2|h2	
Sole	SOL	0.0	0.7	0.6	2.3	2.1
Plaice	PLE	0.0	0.5	0.1	1.5	34.7
Dab	DAB	0.0	1.4	0.0	1.8	44.7
Cod	COD	30.1	39.9	0.0	1.0	0.1
Whiting	WHG	0.5	2.4	0.0	2.7	3.9
Grey gurnard	GUG	0.2	1.0	0.0	2.3	1.5
Tub gurnard	GUU	1.2	5.5	0.2	4.1	0.4
Dragonet	LYY	0.0	0.0	0.0	0.0	1.3
Lesser sandeel	ABZ	0.0	14.6	0.0	26.8	0.1
Greater sandeel	YEZ	2.1	16.0	6.1	42.4	0.4
Other flatfish		ND	ND	ND	ND	7.9
Other roundfish		ND	ND	ND	ND	2.7
Elasmobranchs		ND	ND	ND	ND	0.2
All bony fish		0.1	1.0	0.1	1.7	

full body muscle contraction of epaxial and hypaxial muscles on both sides of the body will, therefore, create a high and localised bending force on the vertebral column that is unnatural and perpendicular to the force exerted during swimming. We hypothesize that this unnatural force will be maximal at the transition between the abdominal and caudal region and may be responsible for the pulse-induced injuries in round-shaped fish species.

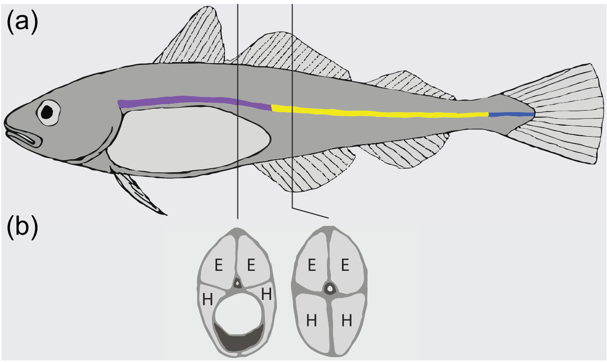

Figure 6. (a) Schematic drawing of the vertebral column of a cod with the vertebrae regions marked with the following colours: abdominal—purple; caudal—yellow; ural—dark blue (based on Fjelldal *et al.*, 2013). (b) Cross sections in the abdominal and caudal region illustrating the change in relative size of the epaxial (E) and hypaxial muscles (H).

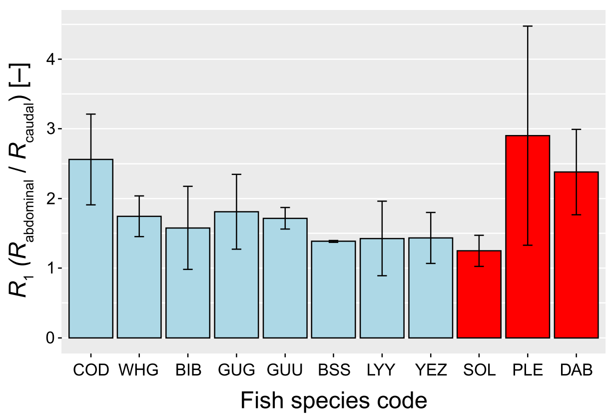

Figure 7. Degree of asymmetry between the size of the epaxial and hypaxial muscles in the abdominal and the caudal region of round-shaped fish species (light blue) and flatfish species (red). The metric shows the mean and standard deviation of $R_1 = \frac{R_{abdominal}}{R_{caudal}}$, where R is the ratio of the mean cross-sectional area of the epaxial ($\overline{Ep}$) and hypaxial ($\overline{Hp}$) muscles in the abdominal and caudal region, respectively.

A preliminary analysis of the degree of asymmetry in the epaxial and hypaxial muscle ratio ($R = \overline{Ep}/\overline{Hp}$) between the caudal ($R_{caudal}$) and abdominal ($R_{abdominal}$) region for a selection of species (Supplementary Material 3) indicated that among the round-shaped fish species, the asymmetry was highest for cod, whereas the asymmetry tended to be intermediate in species that were considered to be less sensitive (whiting, gurnards). Although we also found asymmetries for some flatfish species (Figure 7), the analysis of muscle asymmetry in flatfish is probably less relevant, due to a completely different mode of swimming, and an inherent asymmetry in upper and lower axial musculature that prevents unnatural bending (i.e. flatfish are laterally flattened with more muscles on the eyed side compared to the blind side). Further investigation of the difference in morphometry between flat-shaped and round-shaped fish species is required to elucidate the mechanism that is responsible for the observed interspecific pulse-induced sensitivity differences.

Sensitivity for pulse-induced injuries may also be related to the behaviour of the fish. Because the field strength declines with increasing distance to the electrodes following the inverse-square law, the strength of the pulse stimulus experienced by a fish will depend on its position and orientation in the electric field (de Haan *et al.*, 2016; Boute, 2022; Schram *et al.*, 2022b). Fish that are buried in the sediment will experience a lower field strength as the sediment provides some electrical insulation (ICES, 2020; Boute, 2022). A fish swimming just above the sediment will be internally exposed to a higher field strength than a fish higher up in the water column, or buried deeper into the sediment. Cod tends to dive to the seafloor in response to an oncoming trawl (Main and Sangster, 1985; Krag *et al.*, 2010), while haddock and whiting tend to swim upwards and enter the net higher than many other groundfish species (Main and Sangster, 1985; Catchpole and Revill, 2008). These differences in behaviour may therefore contribute to their differences in sensitivity for electrically-induced injuries.

The increased injury occurrence with body length could be expected from the larger voltage difference over its body (Dolan and Miranda, 2003; Soetaert *et al.*, 2015). Smaller fish would thus require higher external voltages to reach an internal threshold for involuntary muscle contractions. This, however, contradicts a reduced sensitivity for the largest fish (de Haan *et al.*, 2016; Soetaert et al., 2016a). Other factors might therefore play a significant role as well, for example regionally different growth rates of vertebrae, resulting in age-dependent size differences between abdominal and caudal regions (Fjelldal *et al.*, 2013), or differences in behaviour as there is evidence from gear trials that small cod may rise inside the trawl and escape if given the opportunity (Catchpole and Revill, 2008). Differences found in laboratory experiments may also be related to different origins and hence rearing histories of fish used in the experiments (Soetaert *et al.*, 2016a).

Management implications

What consequences has replacement of mechanical stimulation by electrical stimulation on survival for species caught in the beam trawl fishery for sole? Although experimental exposure studies showed little evidence for direct mortality due to electrical pulse stimulation (summary in ICES, 2020; Schram *et al.*, 2022a), internal injuries may result in delayed mortality. This is particularly relevant for the smaller length classes that constitute the discard fraction of the catch and fish that escape through the cod-end meshes. Pulse-induced injuries in larger length classes that are landed will not affect the population dynamics, although the occurrence of pulse-induced injuries in landed fish could be relevant from an animal welfare and economic perspective.

Of the fish species that were considered potentially sensitive for the adverse effects of electrical stimulation, high pulse-induced injury occurrences that could potentially impact the dynamics of the population were only observed in cod. To judge the effect of pulse stimulation on cod populations, one should specifically look at cod length classes which can escape the cod-end meshes. Discarded cod already has a low survival probability due to barotrauma and mechanical damage inflicted during the catch process (Lindeboom and de Groot, 1998; Depestele *et al.*, 2014). The retention length of the 80 mm mesh size used in the beam trawl fishery for sole is about 18 cm total length (Reeves *et al.*, 1992). Under the assumption that the mortality probability of the cod that escape through the cod-end meshes is equal to the observed s2|h2 injury occurrence (40%), the population level effect was negligible (<1%) for the total North Sea cod stock, and very small (~2%) for the cod stock in the southern North Sea due to the limited overlap in distribution of the cod populations and fishing fleet (ICES, 2020; Rijnsdorp *et al.*, 2020a). These numbers can be considered worst-case estimates. Although the number of small specimens sampled was rather low, the injury occurrence in cod, which are sufficiently small to escape through the cod-end meshes, increased with body length from 0% to about 20% at 20 cm standard length. A lower sensitivity for pulse-induced injuries in small fish is also in line with the results of laboratory exposure experiments (de Haan *et al.*, 2016), showing that none of the 132 small cod (11–17 cm total length) exposed to a commercial pulse stimulus developed a spinal injury and all survived. Hence, despite the high pulse-induced injury occurrences in cod, population level effects seem to be negligible.

The estimated s2h2 and s2|h2 injury occurrences of the sampled fish species in PUL-on and TCK catches is summarised together with the numerical proportion in the discard fraction of the beam trawl fleet (ICES, 2018) in Table 6. Pulse-induced injuries were restricted to species with a roundfish body shape, which together contributed to about 10% of the number of discarded fish in the beam trawl fishery for sole. The only species showing a high sensitivity for pulse-induced injuries, cod, contributed only 0.1% of the discard numbers. The percentage pulse-induced injured fish in the discard fraction was estimated at <0.1%. The overall percentage of fish with a major injury (s2|h2) in the discard fraction of the PUL-on was estimated at 1.0%. This percentage is lower than the 1.7% of fish with a major internal injury in the discards of TCK.

The difference in s2|h2 injury occurrence between TCK and PUL-on can be ascribed to the larger mechanical impact during the catch process caused by the faster towing speed of TCK in combination with the larger amount of benthos and debris, which may damage fish in the cod-end (van Marlen *et al.*, 2014; Schram *et al.*, 2020; Rijnsdorp *et al.*, 2021b). This interpretation is supported by the difference in condition and reflex impairment found among undersized flatfish caught in TCK and PUL-on (Uhlman *et al.*, 2016; Schram *et al.*, 2020). Discard survival experiments suggested a higher discard mortality in TCK than in PUL-on (van Beek *et al.*, 1990; van der Reijden *et al.*, 2017) in line with the knowledge that injuries inflicted during the catch process and the handling of the catch on deck are the main cause of mortality among discarded fish (Davis, 2002; Benoit *et al.*, 2013; Depestele *et al.*, 2014).

Conclusion

PUL trawling was shown to inflict pulse-induced injuries in round-shaped fish species, but not in the flatfish species. The sensitivity for pulse-induced injuries differed between fish species and was high in cod (40%) and low (<2%) in whiting, grey gurnard, tub gurnard, and greater sandeel. In contrast, sole, plaice, and dab were found to be insensitive. Despite the high injury occurrence in cod, the population level effect will be small due to the low numbers of cod encountered in the sole fishery on the North Sea. The proportion of fish with a pulse-induced injury in the discarded fraction of the catch was negligible (0.1% of the discards). Because major injuries were more frequent in TCK than in PUL samples, replacement of the conventional TCK with a PUL trawl will, therefore, improve the sustainability of the beam trawl fishery for sole by reducing the proportion of injured fish in the discarded catch due to reduction in the mechanical impact.

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Supplementary data

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

Author contributions

All authors contributed to the conception and design of the study; PGB and RPMP processed the dead fish; MJL programmed the database program; PGB collected the data from the X-ray and autopsy images. PGB and ADR performed the statistical analyses. All authors interpreted the data and discussed the results; and PGB drafted the initial manuscript and figures, with contributions by ADR, JLvL, RPMP, and MJL. All authors contributed to the critical revision of the manuscript and figures, and approved the final version.

Data availability statement

The data are available on the Dryad Digital Repository: https://doi.org/10.5061/dryad.sj3tx9691 (Boute *et al.*, 2023).

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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