Fisheries Research 240 (2021) 105966

Contents lists available at ScienceDirect

Fisheries Research

journal homepage: www.elsevier.com/locate/fishres

Flatfish survivors have tales to tell: Cold seawater and reduced deployment duration contribute to the survival of European plaice (*Pleuronectes platessa*) discarded by Belgian beam trawlers

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ARTICLE INFO

Handled by Niels Madsen

Keywords:
Landing obligation
High survival exemption
Stress
Demersal fisheries
Post-capture
RAMP
Vitality assessment

ABSTRACT

The 'high survival' exemption to the European Landing Obligation regulation intensified the relevance of quantifying the survival of commonly discarded European plaice (*Pleuronectes platessa*) within the discard-intensive Belgian beam-trawl fishery, together with the search for ways to maximize discard survival. In this study we worked together with vessel owners and the crews of three Belgian beam trawlers representing the small (≤221 kW) engine power, coastal ($n = 1$ vessel), 'Eurocutter' (1), and large (>221 kW) (1) fleet segments. During 12 commercial trips which included 99 beam-trawl deployments in 2014 and 2015, three scientific observers assessed the survival of 3849 plaice aboard the vessel (by checking for the presence of reflex responses and bleeding injury; on-board survival assessment) and counted how many survived among a sub-sample ($n = 489$ plaice) monitored for at least 9 days in captivity (post-release survival). These fish were monitored alongside 160 captive controls. Only three control fish died (<2%) during daily monitoring. Survival of plaice discarded from conventional trawls of Belgian beam-trawl vessels representing the three fleet segments was estimated to range between 41–58 %, 11–28 %, 2–4 % (95 % confidence interval; Kaplan-Meier models) for trips of the coastal (≤221 kW), Eurocutter (≤221 kW) and >221 kW vessel, respectively. More challenging operational fishing conditions of >221 kW compared to ≤221 kW vessels such as ~150 min gear deployment and ~37 min sorting durations meant that down to only 20 % of undersized plaice were still alive when landed on deck. Such immediate mortality was hardly observed among ≤221 kW vessels. These effects were cumulative to the effect of elevated seawater temperatures of >14 °C during summer, because despite warm waters, immediate mortality among ≤221 kW vessels was low compared to >221 kW vessel-trips. Out of those fish that were still alive after sorting at the point of discarding and monitored for 9 days, on average 23 % (0%–100 %, 95 % CI) survived. Post-release survival was associated with stress and injury sustained during the capture and sorting process (proxied by the reflex impairment and injury index) and seawater temperature. Survival rates can be improved by choosing when to fish, and restricting gear deployments to practicable minimum durations. Without further adaptations to current fishing practices, justifying a high survival exemption for discarded plaice in the Belgian beam-trawl fishery will remain a challenge in compliance with the Landing Obligation.

1. Introduction

In response to widespread concerns about wasting natural resources when large numbers of fish released after catch (by-catch, discards) at sea are either dying or already dead, the European Union introduced a regulation to ban discarding (the Landing Obligation; European Union, 2013; Uhlmann et al., 2019). This regulation requires Member States to both account for and land all catches of regulated species by January 1st, 2019 (European Union, 2013). The aim is to stimulate more selective fishing by minimising the proportion of undersized, commercially less valuable juveniles among the catch (Borges, 2015). However, to not adversely increase fishing mortality by landing and thus killing such

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https://doi.org/10.1016/j.fishres.2021.105966
Received 6 April 2020; Received in revised form 5 March 2021; Accepted 4 April 2021
Available online 12 April 2021
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unwanted catches, a provision for "high survival" species allows exemptions to the Landing Obligation (Article 15 paragraph 4b, European Union, 2013). The requirement stipulates a scientifically corroborated assessment of survival probability after capture and discard (Rihan et al., 2019). The possibility of gaining a species- and fisheries-specific high survival exemption from the Landing Obligation has led to several survival research projects for various species and European fisheries (International Council for the Exploration of the Seas (ICES), 2014).

The Landing Obligation is likely to economically affect discard-intensive fisheries such as the Belgian beam trawl, as unprofitable catches take up valuable on-board holding space and/or fill quotas, ultimately forcing the law-abiding skipper to stop fishing (Condie et al., 2014; Catchpole et al., 2017). Belgian beam trawlers catch and discard large amounts of undersized European plaice (*Pleuronectes platessa*) (Depestele et al., 2011; Vanelslander et al., 2014), which puts this fishery under pressure (Catchpole et al., 2017). In recent years, plaice has become a candidate species for a high-survival exemption (Uhlmann et al., 2016a, b; van der Reijden et al., 2017; Savina et al., 2019). Discard survival has been studied in demersal and other (commercial) fisheries by combining on-board vitality assessments using the Reflex Action Mortality Predictor method (RAMP; Davis and Ottmar, 2006; Davis, 2010) with captive observations (Uhlmann et al., 2016a, b; Methling et al., 2017; van der Reijden et al., 2017). Within this biomarker method, animals are scored for the presence or absence of innate animal reflexes and spontaneous behaviors as well as the severity of injury. An index is generated, which is then correlated with the observed post-release survival probability of the same individual (Uhlmann et al., 2016a; van der Reijden et al., 2017). Such vitality assessments have become a standard procedure to establish correlations between reflex responses (or the lack of thereof, indicating impairment) and a fish's probability of surviving fishing capture and release (Uhlmann et al., 2016a; van der Reijden et al., 2017; Meeremans et al., 2017; Uhlmann et al., 2020).

Plaice under the minimum conservation reference size (<MCRS, 27 cm for ICES Divisions 4 and 7) are least likely to survive when discarded by beam trawlers (survival rate: 5 %–57 % [Uhlmann et al., 2016a, b]; 11 %–19 % [van der Reijden et al., 2017]), as compared to otter trawlers (84 %–93 % [Eskelund et al., 2019]; 84 %–100 % [Methling et al., 2017]; 45 %–63 % [Morfin et al., 2017]; 37 %–52 % [Noack et al., 2020]), Danish seiners (67 %–87 % [Noack et al., 2020]), or trammel netters (61 %–82 % [Catchpole et al., 2015]). The probability of plaice surviving being discarded after trawling has been associated with

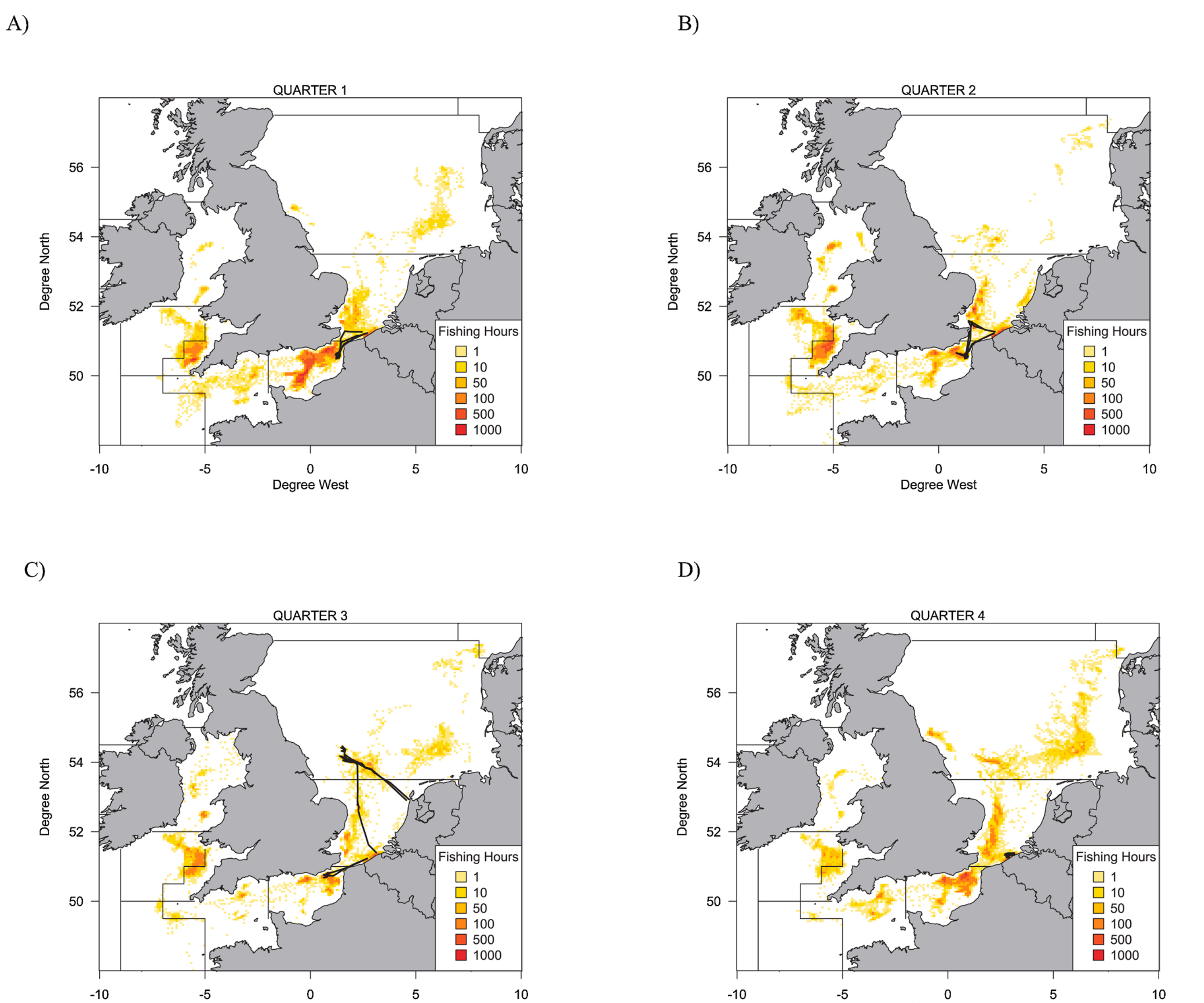

Fig. 1. Heat map of the average total number of fishing hours per quarter (quarter 1 – A; quarter 2 – B; quarter 3 – C; and quarter 4 – D) aggregated over the period 2014-2016 (based on filtered VMS pings of Belgian beam trawlers with a mesh size 70-99 mm filtered on speed). Vessel tracks of participating vessels are represented by black lines.

environmental factors such as (acclimated) environmental seawater temperature (van Beek et al., 1990; van der Reijden et al., 2017; Savina et al., 2019), fishing depth (van der Reijden et al., 2017), or factors related to the fishing operation such as duration of gear deployment or catch sorting (Berghahn et al., 1992) or volumes of total catch (Kelle 1977). Biological factors such as the amount and severity of visible skin damage of individual fish and their vitality when landed on deck and total length (TL) have also been associated with their survival (Kaiser and Spencer, 1995; Depestele et al., 2014; Uhlmann et al., 2016a).

In this study, on-board immediate survival assessments were combined with captive monitoring of a sub-sample of fish to i) estimate on-board, post-release and overall survival of plaice after being discarded from Belgian commercial beam trawlers, and ii) to determine which factors influence the partitioned on-board and post-release survival components, respectively.

2. Material and methods

2.1. Description of the Belgian fishery

While the Belgian fishing fleet is relatively small (64 licensed commercial fishing vessels in 2019) its activity ranges across a large geographical area from the North Sea and the English Channel to Northwestern Atlantic waters and the Bay of Biscay (Fig. 1). The fleet consists mainly of beam trawlers (n = 55 vessels), followed by otter trawlers (7), and trammel netters (2). Beam trawlers exploit different fishing grounds depending on the season and sediment type to target species such as sole, plaice, and several other species (Fig. 2). During this study, the beam trawling took place primarily in the English Channel on predominantly coarse sediments (Figs. 1 and 2).

For fisheries management purposes, the Belgian beam trawl fleet has been segmented by engine power into a small (≤221 kW) and large (>221 kW) fleet segment. The small fleet is further divided into inshore beam-trawl vessels (≤221 kW, ≤70 GT) that are only allowed to fish within 12 nm of the coast for no longer than 24 consecutive hours; and "Eurocutter" beam trawlers (≤221 kW; >70 GT). Among the 55 licensed and active Belgian beam trawlers in 2019, 28 were classified into the small and 27 into the large engine power segment. Of the small segment, 14 vessels belonged to the coastal segment and 14 to the Eurocutter segment. Beam trawling by ≤221 kW vessels was concentrated in the North Sea and English Channel, whereas >221 kW vessels steamed into the Celtic and Irish Seas and the Bay of Biscay (Supporting Table 1). Historically, plaice catches were highest in the North Sea and English Channel, with landings of up to 4722 tonnes (Supporting Table 1). The large (>221 kW) fleet spent up to twice as many hours fishing as compared with the ≤221 kW fleet component in most areas, except for the North Sea (Supporting Table 1). Between 2014 and 2016, on average ~45 % of plaice catches were discarded, except for ICES sub-division 7e, where average plaice discard rates were <8% (Supporting Table 1). For more information about annual effort statistics between 2014 and 2016 per ICES sub-division of Belgian beam trawlers, see Supporting Table 1.

2.2. Selection of participating vessels

Only three commercial vessel operators collaborated out of the pool of ~55 vessel owners who were invited in 2014 via an open letter to participate in this study. The low participation rate is assumed to be due to a lack of motivation and/or lack of sufficient incentives. Each vessel had to meet the following criteria: i) sufficient space to accommodate two scientific observers, their equipment and suitable infrastructure (i.

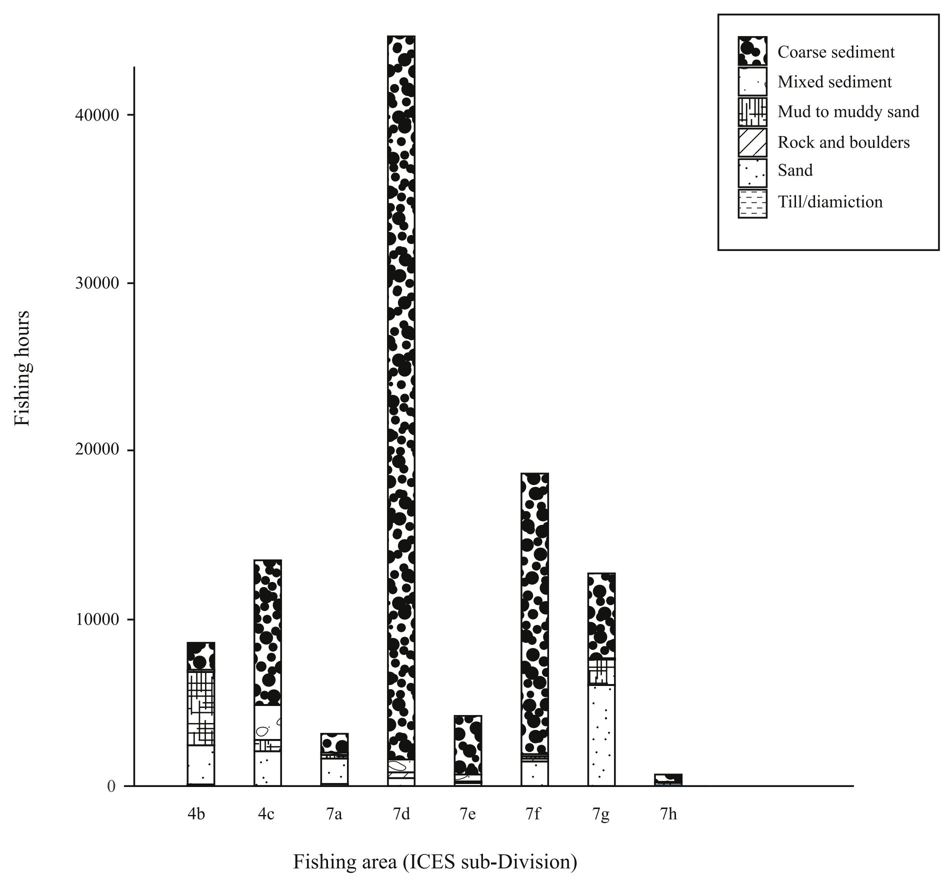

Fig. 2. Mean number of fishing hours per substrate type, according to Eunis Folk 5 (Kaskela et al., 2019) sediment category classification and sediment data derived from EMODnet, and per ICES sub-division between 2014 and 2016 of Belgian beam trawlers fishing with mesh sizes ranging between 70 and 99 mm. Fishing hours were calculated as the sum of the time interval between VMS pings where fishing activity was expected.

e., if applicable, copper-free deck water pumps with a guaranteed continuous >25 l/min discharge volume); ii) fishing gear with 70−99 mm codends; iii) activity within a fishing area where Belgian beam trawlers typically operate with undersized plaice present; and iv) willingness of the crew to co-operate. Vessel owners received monetary compensation for costs accrued due to loss of fishing time and/or catch and the extra effort required by crew members to sort catches.

2.3. Fishing practices

Five trips were made with a commercial coastal Belgian beam trawler (from the ≤221 kW fleet segment of coastal vessels targeting sole in waters of the Southern North Sea), five trips with a Eurocutter (from the ≤221 kW fleet segment fishing in the English Channel) and two trips with a vessel from the >221 kW segment fishing in the North Sea in July/August 2015; Table 1a–1c). Both the coastal and Eurocutter beam trawlers were conventionally rigged with two 4-m beam trawls with chain mats (each weighing ~1200 kg and ~2000 kg, respectively), while the two trips with >221 kW vessels were done with a Sumwing beam of 11.4 m in length and ~5750 kg single gear weight. Codends with 80 mm diamond mesh were used throughout. After fishing, catches were sorted, sampled for biological parameters and a sub-sample of fish were returned to shore for monitoring (Fig. 3). When the net was heaved on deck, both codends were emptied into two separate "hoppers" or "pounders" (i.e., large containers holding the discharged catch). From there, the catch was flushed with surface seawater (supplied from a deck hose) onto a conveyor that lifts portions of the catch onto a moving belt from which marketable catches are separated from unwanted catches by crew members (max. 10–40 min, depending on the catch volume).

Table 1a
Summary of mean ± SD (*n* observations) key technical, environmental, and biological variables collected during each monitored trip of a commercial, coastal beam trawler (vessel 1) with ≤221 kW engine power (small fleet segment), 4-m beam length and 1300 kg single gear weight. Control, plaice from a short research beam trawl (<20 min trawl) captured prior to a monitoring trip. n/a, not available (or in some cases, not measured).

Variable	Trip 1	Trip 2	Trip 3	Trip 7	Trip 11
Month/Year	Nov.' 14	Dec.' 14	Feb.' 15	Jun.' 15	Sep.' 15
ICES sub-division	4c	4c	4c	4c	4c
Total no. of deployments	16	15	15	15	15
Sampled deployments	6	6	3	3	3
No. plaice sampled	61	22	50	65	66
Depth (m)	8.8 ± 2.7 (16)	16.1 ± 4.1 (15)	9.6 ± 3.6 (15)	9.7 ± 3.6 (15)	7.8 ± 4.2 (15)
Gear deployment duration (min)	44.9 ± 12.9 (16)	51.2 ± 9.1 (15)	52.3 ± 9.6 (15)	42.9 ± 14.4 (15)	48.4 ± 10.8 (15)
Sorting duration (min)	23.4 ± 6.2 (6)	25.9 ± 6.7 (3)	13.2 ± 2.4 (3)	17.6 ± 9.3 (4)	11.9 ± 0.7 (3)
Wind force (Bft)	2.1 ± 0.7 (16)	4.8 ± 1.4 (15)	2.6 ± 0.8 (15)	2.7 ± 0.8 (15)	3.9 ± 0.8 (15)
Wave height (m)	0.6 ± 0.1 (9)	1.1 ± 0.5 (5)	0.5 ± 0.1 (12)	0.4 ± 0.1 (4)	1.2 ± 0.2 (3)
Air temperature (°C)	10.9 ± 0.1 (6)	8 ± 0.4 (6)	8.1 ± 0.4 (3)	12.8 ± 0.2 (4)	17.0 ± 0.2 (3)
Seawater temperature (°C)	11.7 ± 0.1 (6)	7 ± 0.1 (6)	5.3 ± 0.1 (3)	14.4 ± 0.2 (4)	16.9 ± 0.1 (3)
Total catch (kg)	482 ± 0 (6)	n/a	481.3 ± 440.9 (3)	333.5 ± 233.7 (4)	349.1 ± 105.1 (3)
Total length (TL, cm)	23.1 ± 2.6 (58)	20.9 ± 3.4 (22)	24.8 ± 2.8 (40)	21.4 ± 3.0 (65)	22.1 ± 3.1 (65)
TL (cm) – control	n/a	22.6 ± 4.0 (20)	23.2 ± 2.9 (20)	n/a (20)	n/a

Table 1b
Summary of mean ± SD (*n* observations) key technical, environmental, and biological variables collected during each monitored trip of a commercial Eurocutter beam trawler with ≤221 kW engine power (small fleet segment), 4-m beam length and 2000 kg single gear weight. *n* observations in brackets. n/a, not available. Control, plaice from a short research beam trawl (<20 min trawl) captured prior to a monitoring trip.

Variable	Trip 4	Trip 5	Trip 6	Trip 8	Trip 12
Month/Year	Mar.'15	Mar.'15	Apr.'15	Jul.'15	Sep.'15
ICES sub-division	7d	7d	7d	7d	7d
Total no. of deployments	52	55	47	43	45
Sampled deployments	7	7	12	9	5
No. plaice sampled	109	111	184	182	78
Depth (m)	43.1 ± 12.4 (7)	36.3 ± 4.4 (7)	36.3 ± 15.9 (12)	35.8 ± 6.5 (9)	31.8 ± 7.6 (5)
Gear deployment duration (min)	75.7 ± 11.8 (6)	72.6 ± 8.2 (6)	86.4 ± 9.6 (11)	69.2 ± 9.4 (8)	69.7 ± 10.5 (4)
Sorting duration (min)	18.6 ± 5.6 (7)	12.4 ± 2.6 (7)	10.8 ± 2.1 (12)	14.9 ± 5.1 (9)	7.4 ± 1.7 (5)
Wind force (Bft)	3.0 ± 0.8 (7)	3.4 ± 0.5 (7)	2.0 ± 1.9 (12)	3.6 ± 0.7 (9)	5.8 ± 0.8 (5)
Wave height (m)	0.7 ± 0.3 (7)	0.6 ± 0.2 (7)	0.2 ± 0.3 (12)	0.4 ± 0.2 (9)	1.9 ± 0.4 (5)
Air temperature (°C)	7.6 ± 1.7 (7)	8.6 ± 1.2 (7)	10.1 ± 1.7 (12)	20.3 ± 3.0 (9)	15.5 ± 1.5 (5)
Seawater temperature (°C)	8.1 ± 0.2 (7)	8.1 ± 0.2 (7)	9.9 ± 0.2 (12)	16.2 ± 0.7 (9)	16.6 ± 0.1 (5)
Total catch (kg)	466.2 ± 270.2 (7)	515.1 ± 299.9 (7)	291.7 ± 296.9 (12)	726.7 ± 481.6 (9)	270.0 ± 163.1 (5)
Total length (TL, cm)	22.9 ± 3.1 (89)	22.5 ± 3.0 (111)	22.7 ± 2.9 (173)	22.6 ± 2.5 (130)	25.9 ± 2.1 (123)
TL (cm) – control	22.6 ± 2.4 (20)	n/a (20)	n/a (20)	n/a (20)	n/a (20)

Table 1c
Summary of mean ± SD (*n* observations) key technical, environmental, and biological variables collected during monitored trips of a commercial beam trawler with >221 kW engine power (large fleet segment), 11.4-m beam length and 5750 kg single gear weight. *n* observations in brackets. n/a, not available.

Variable	Trip 9	Trip 10
Vessel	Vessel 3	Vessel 3
Month	Jul.'15	Aug.'15
ICES sub-division	4b,c	4b,c
Total no. of deployments	88	61
Sampled deployments	19	17
No. plaice sampled	1240	1321
Depth (m)	63.4 ± 15.1 (19)	61.0 ± 16.7 (17)
Gear deployment duration (min)	132.3 ± 17.5 (18)	141.3 ± 18.5 (16)
Sorting duration (min)	45.9 ± 10.9 (19)	33.5 ± 7.3 (17)
Wind force (Bft)	2.4 ± 1.7(19)	2.6 ± 1.1 (17)
Wave height (m)	0.43 ± 0.4 (19)	0.54 ± 0.28 (17)
Seawater temperature (°C)	16.0 ± 0.3 (19)	16.2 ± 0.6 (17)
Total catch (kg)	2600.0 ± 1032.8 (19)	1665.9 ± 487.6 (17)
Total length (TL, cm)	24.0 ± 2.2 (316)	23.6 ± 2.4 (274)
TL (cm) – control	n/a	n/a

2.4. Data collection

All technical, environmental and biological data recorded from each gear deployment were listed in Tables 1a–1c and 2. Apart from the trips with the coastal vessel, catch weights of plaice were estimated in kg and where necessary 'number of boxes' was converted to weight using a factor of 35 kg. Aboard the coastal vessel and during the first trip, catch

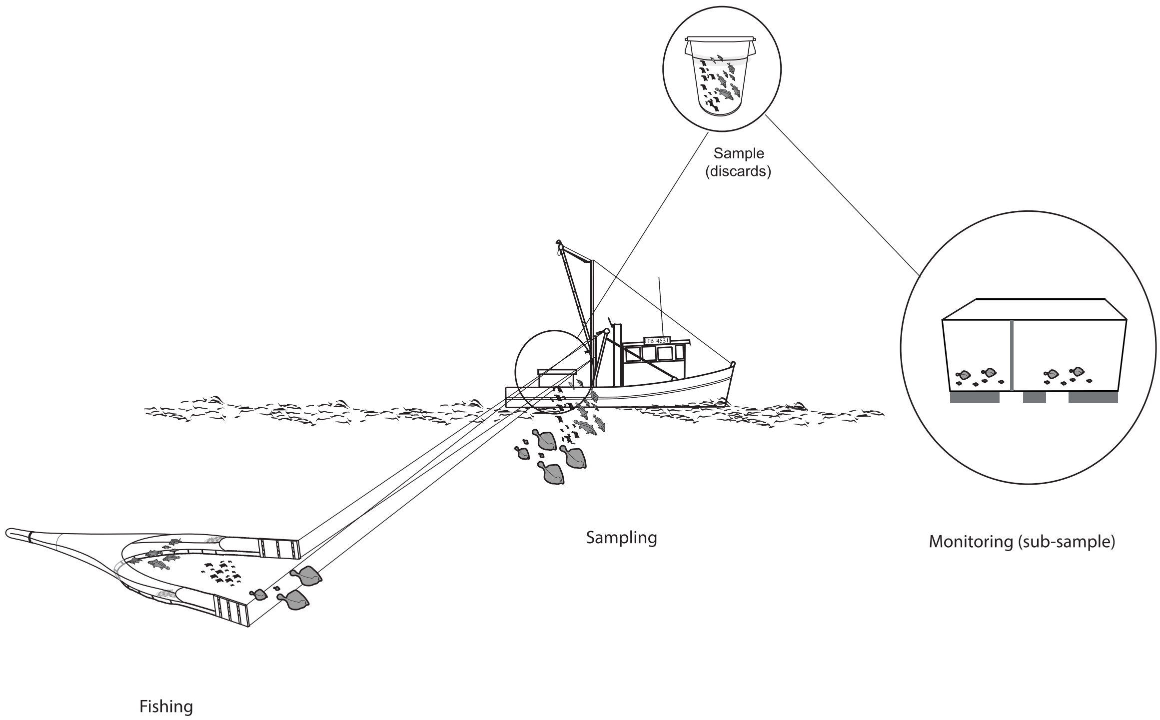

Fig. 3. Schematic diagram illustrating the fishing, catch sorting/sampling, and monitoring phase as part of the data collection (copyright: M. Broadhurst and S. Uhlmann).

weights were estimated based on the ratio between landings and discards of a 35–50 kg catch sample separated into these two fractions by a crew member. This ratio was later raised to a total catch estimate based on the known kg of total landings of that deployment. Additional measurements matching the date and time of a sampled gear deployment, such as maximum wave heights, and surface seawater temperatures, were retrieved from nearby weather stations "Trapegeer", "Westhinder", and "Wandelaar", respectively (Flemish Government, 2015). To represent the discarded component of the plaice catch and evaluate its discard survival probability, assessments were partitioned into estimating on-board and post-release survival.

2.4.1. On-board survival

Throughout the sorting process, undersized (<MCRS 27 cm) plaice were picked either by a crew member or scientific observer and were placed into a white, water-filled, 244-l PVC holding container positioned at the end of the conveyor belt at the point of discard. At the end of the sorting process, ~30 plaice were randomly selected out of the PVC holding container for an assessment of on-board survival. Ten of these individuals were assessed for their reflexes and injuries as described below, and from the remaining 20, the live-dead ratio was determined. The proportion of dead fish among this sample of ~30 plaice drawn from the 244-l holding container was applied to the number of scored and alive fish that were placed into on-board 30-l monitoring containers (see below, section 2.4.2 "post-release survival") to derive the overall proportion of dead individuals among all randomly picked undersized plaice during sorting (Supporting information).

All evaluated fish that were unresponsive to any of the following reflex tests were recorded as dead during the on-board survival assessment. After a reflex was stimulated, each fish was given 5 s to respond. A visible response was scored as present (unimpaired/impairment absent, score = 0). When the response was absent, weak or in doubt, it was recorded as impaired (impairment present, score = 1). Reflex and injury assessments took <1 min per fish. Each plaice was scored for the 'body flex', 'righting', 'head complex' (scored as 'operculum' during the first trip), evasion, stabilize, and tail grab reflexes (Table 2), and a presence/absence of injury (i.e., point bleeding or bruising around the head or body regions; absent = 0; present = 1; Table 2). A reflex impairment and injury index (R&I index) was calculated as the mean score of all impaired reflexes and injuries present. This resulted in values ranging between 0 and 1, where 0 represents an unimpaired (i.e., reflex responsive) and uninjured fish and 1, an impaired and injured fish.

Air exposure of each fish was expressed as the minutes it spent on deck before being placed inside a water-filled container plus one-third of the handling time during reflex testing (because 1/3 of the reflex tests were done in air). All sampled fish were length-measured to the nearest cm of total length (TL).

2.4.2. Post-release survival

As the catch passed by on the sorting conveyor, crew members picked out marketable catch. Upon instruction by the scientific observer, crew members randomly picked approximately five undersized plaice when they would be normally discarded at the beginning, mid- and end-points (in chronological order) of the sorting process. These fish were passed on to the scientific observer who placed them into a 10-l PVC bucket filled with ambient seawater and who immediately (i.e., within ~10 min [mean ± SD, 9.5 min ± 6.8 min]) began scoring them for their reflexes and injury to minimise and standardize handling time. Scored live fish were stored inside stacks of water-filled, 30-l monitoring containers (in total ~20 fish per gear deployment). These fish were T-bar (29 × 8 mm) anchor tagged with Bano'k© guns in the dorsal musculature according to McKenzie et al. (2012). Tagged plaice were transferred into stacks of water-filled, 30-l monitoring containers (60 cm L x 40 cm W x 12 cm H; see Uhlmann et al., 2016a). Upon returning to shore in Ostend, Belgium, the fish were transferred within <1 h to onshore 124-l monitoring containers (five fish per container) for at least 14 days of monitoring. From the two trips of the >221 kW vessel, fish were monitored for the duration of the trip (9 days), but were not brought back to shore. Onshore, fish were fed defrosted brown shrimp (*Crangon crangon*) at <5% of their biomass after the first week of monitoring. Any food leftovers and/or dead fish were removed and the time to mortality noted. Fish were monitored three times per day for the first week and

Table 2
List of variables that were collected either per trip, gear deployment or for each fish considered in the analyses, including as response variable on-board or post-release survival and explanatory variables such as candidate reflex actions and descriptions of a response of European plaice (*Pleuronectes platessa*).

Level	Variable	Description	Type
Trip	Trip code	Unique trip ID	Factor
Deployment	Haul number	Unique gear deployment ID (by combining trip with haul ID)	Factor
Deployment	Gear deployment duration	Time period between the start time of the haul and the time when the gear arrived on deck (in minutes)	Continuous
Deployment	Sorting duration	Time period between time the catch arrived on deck and the end of sorting	Continuous
Deployment	Depth	Average fishing depth (in meters)	Continuous
Deployment	Sediment type in catch	Four-point sediment scale 0: < 25 % stones and/or < 25 % sand; 1: > 25 % sand; 2: > 25 % stones; 3: > 25 % sand and stones	Categorical
Deployment	Total catch	Estimate of the total catch inside the hoppers (in kg; combined estimate from both hoppers).	Continuous
Deployment	Wind speed	Force of wind (Beaufort scale)	Ordinal
Deployment	Wave height	Height of waves (in meters)	Continuous
Deployment	Seawater temperature (°C)	Surface seawater temperatures were retrieved from nearby weather stations and categorized into three categories: <8 °C, 8–14 °C, and >14 °C based on 33 % and 66 % quantiles in the distribution of values of all sampled gear deployments.	Categorical
Fish	TagID	Alphanumeric T-bar anchor tag ID number	Factor
Fish	Air exposure	Air exposure of each fish was expressed as the minutes it spent on deck before being placed inside a water-filled container plus one third of the handling time during reflex testing (because 1/3 of the reflex tests were done in air out of the water-filled container).	Continuous
Fish	On-board survival	Status (status scored as 1=alive; and 0=dead) at the point of discarding (after sorting) on-board a vessel.	Binary
Fish	Post-release survival	Status (status scored as alive = 1; and dead = 0) of a fish after 9 d of monitoring in captivity.	Binary
Fish	Body flex	Fish is held outside the water on the palms of two hands (touching each other) with its belly facing up and its head and tail unsupported. Response: Actively trying to move head and/or tail towards each other, or actively struggling off the hand (impairment absent = 0; impairment present = 1).	Binary
Fish	Righting	Fish is held underwater at the surface on the palms of two hands (touching each other) with its belly facing up and then slowly released. Response: Actively righting itself under water (impairment absent = 0; impairment present = 1).	Binary
Fish	Head complex	Observing the opening of the operculum and/or mouth for breathing (scored as 'operculum' during the first trip) (impairment absent = 0; impairment present = 1).	Binary
Fish	Evasion	Fish is held underwater at the surface in an upright position by supporting its belly with the fingers and holding its back by the thumbs. Then the thumbs are lifted and the fish released, while still supporting its belly by the fingers. Response: The fish swims actively away towards the bottom of the container (impairment absent = 0; impairment present = 1).	Binary
Fish	Stabilize	This reflex is scored immediately after evasion. No extra handling is required. Response: The free-swimming fish tries to find a good position on the bottom by fixing itself and/or rhythmic and swift movement of the fins as if it would bury itself in the sand; no visible displacement, (motionless) resting in one place (within 3 s after reaching the bottom following evasion) (impairment absent = 0; impairment present = 1).	Binary
Fish	Tail grab	The fish was held by the tip of the tail between thumb and index finger. Response: Actively struggles free and swims away (impairment absent = 0; impairment present = 1).	Binary
Fish	Head bruising	Haemorrhage on the head region of a fish (absent = 0; present = 1).	Binary
Fish	Body bruising	Haemorrhage on the body region of a fish (absent = 0; present = 1).	Binary
Fish	Head point bleeding	Multifocal cutaneous petechiae to the head region of a fish (absent = 0; present = 1).	Binary
Fish	Body point bleeding	Multifocal cutaneous petechiae to the body region of a fish (absent = 0; present = 1).	Binary
Fish	Reflex impairment and injury (R&I) index	Mean score of impaired reflexes and present injury (sum of impaired reflex and present injury scores divided by the total number of tested reflexes and injury types). This resulted in values ranging between 0 and 1, whereby 0 would represent an unimpaired, i.e., reflex responsive and uninjured fish and 1, represented an impaired and injured fish.	Continuous

daily during the second week of monitoring. At each monitoring interval, the status of a fish was classified as either alive (1) or dead (0) (Table 2). Seawater temperature (°C) of all holding containers was monitored aboard the vessel as well as in the laboratory with a handheld

YSI Pro 2030 multi-parameter sensor to document that plaice where held under near-natural temperature conditions (within <2 °C deviations; Fig. 4).

To demonstrate that holding fish in captivity did not contribute to any observed mortality, a captivity control group was introduced. Prior to a commercial trip, these fish were sourced during a <20 min short research beam-trawl capture on the *R/V* Simon Stevin, were transferred to 124-l monitoring containers and checked daily for any mortality for at least two weeks until they had recovered from capture and had acclimatized to captivity. Between 10 and 20 healthy captive individuals were brought on-board to control for any effect from captivity, handling and/or transportation. These fish were reflex-tested, tagged and monitored as above.

2.5. Ethics statement

The sourcing of wild-caught plaice was approved by the Flemish Department of the Environment and the handling and housing protocol of plaice was approved by the animal ethics commission of Flanders Research Institute for Agriculture, Fisheries and Food (ILVO, Ref. no. EC 2016/226). Fish were sourced from commercial Belgian beam-trawlers, the *R/V* Simon Stevin and, where applicable, were housed in research aquariums in Ostend, Belgium. The protocol was designed to minimize any stress during the observation phase after capture and sorting. The most invasive research procedure was the T-bar anchor tagging, which was selected for the low risk of tag loss and any induced bruising injury. Any air exposure during the reflex tests was kept to a minimum and was well within exposure times typical for conventional, commercial sorting practices. If fish were held captive, housing mimicked natural conditions, e.g. by providing sediment and natural enrichment features such as empty shells inside the aquariums.

2.6. Statistical analyses

The protocols by Zuur et al. (2010) and Zuur and Ieno (2016) were followed for the exploration of data and reporting of results, respectively, from the following regression-type analyses. First, all data were explored for outliers, homogeneity, normality, relationships, interactions, independence, collinearity and any other confounding effects. To explore relationships between response variables (on-board or post-release survival) with explanatory co-variates, non-parametric Kaplan-Meier (Kaplan and Meier, 1958) survival curves and box plots were made. The curves per trip were segregated by treatment (conventional vs control) to illustrate when survival reached asymptote.

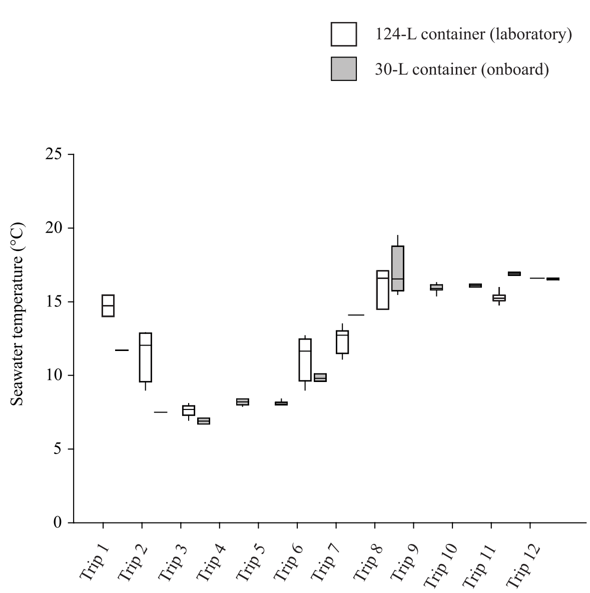

Fig. 4. Seawater temperature (°C) during the holding of fish aboard the vessel and inside containers in the laboratory for the monitoring of post-release survival given as 10th and 90th percentile with median.

Two outliers of gear deployment and sorting durations were manually corrected to eliminate unusual observations (Supporting Fig. 1). These outliers were artefacts of calculating a duration across two dates, when fishing times crossed midnight. An average total catch weight from all >40 min deployments of the coastal vessel (482 kg) was assumed as catch weight per deployment on the first trip, because total catch weights of each deployment were inappropriately estimated on that trip. Wave height was rescaled from m to cm to improve model convergence.

Data were analysed separately for on-board and post-release survival using binomial generalized linear-mixed models (GLMM) that were defined as:

$$Y_{ij} \sim Bin(1,\ p_{ij})$$

$$\eta(p_{ijk}) = \alpha + \beta_1 X_{1,ijk} + \beta_2 X_{2,ijk} + \ldots + \beta_n X_{nijk} + a_j + b_k$$

where η represents the logit-link function; p_{ijk} is the probability that plaice i from unique deployment j within trip k is alive; $X_{1,ijk}, \ldots, X_{nijk}$ represents the fixed effects of the models; $\beta_1 - \beta_n$ are the coefficients that were estimated by the Laplace approximations (Bolker et al., 2009); a_j and b_k represent the random error due to the deployment and trip, respectively, with :

$$a_j \sim N(0, \sigma_a^2)$$

$$b_k \sim N(0, \sigma_b^2)$$

For all (non-predictive) GLMMs, a random effect was included for unique gear deployments (a_{jk}) nested in trips (b_k) to account for the multi-level sampling structure (i.e., multiple deployments per trip, and multiple trips; [1 | Trip / deployment]). Vessel was not included, because most parameters were collected at deployment and trip level and vessel comprised only three levels. Including vessel as a random effect, created issues with model convergence.

Uni-variable GLMM was used to identify any relationship between either on-board or post-release survival (at 9 d of monitoring) and the following explanatory biological, environmental, and operational variables: TL, air exposure, wave height, and seawater surface temperature (categorized into <8 °C, 8 °C – 14 °C, >14 °C, see Table 2), gear deployment duration, sorting duration, total catch weight, fleet segment, vessel and the estimated amount of sediment (i.e., sand, stones or both) inside the unsorted catch. Fleet segment, sorting duration, total catch weight, and depth were collinear with gear deployment duration and therefore not further considered for the model building. Wind speed was highly correlated with wave height. Monitoring of the two trips of the >221 kW segment in summer contributed to a confounding effect of seawater temperature with gear deployment duration, which was collinear for temperatures >14 °C.

All significant and non-collinear explanatory variables and, if applicable, their biologically plausible interactions from these uni-variable analyses were compared in all their possible combinations in candidate models (GLMM – with a random effect for unique gear deployments nested in trips) following an information theory approach (Burnham and Anderson, 2002). The most parsimonious model was the one with the lowest AIC value (Zuur et al., 2007) and ranked based on their highest Akaike weights ω_i, which have most empirical support. Akaike weights were calculated on the basis of Δ_i AIC values. These are based on the difference between an i-th AIC value and the lowest AIC value of all candidate models (AIC_{min}).

To validate the most parsimonious model, the mean on-board or post-release survival probability of a given trip was compared with the predicted average survival probability of that trip in an n-clustered cross validation by splitting the dataset into a training and a validation dataset. By withholding observations from one trip (training dataset), regression parameters (intercept and beta) were calculated and applied to the observations per fish of the left-out trip (validation data) to predict its survival probability. By aggregating values and taking the mean, the average survival probability per trip was calculated. Such a validation is thus based on data that was not used to build the model. This was done *n* times (*n* trips) to compare the mean survival probability of a trip with the predicted survival of that trip. Deviations <10 % were considered to be a good fit. To fit the models, the lmer4 package (Bates et al., 2015) in the open source programming language R was used (R Development Core Team, 2019). A significance level of $p < 0.05$ was used.

For the analysis of an unbiased post-release survival per trip, and to minimise the risk of under- or overestimating survival, the distribution of R&I indices among those fish that were subsequently monitored for at least 9 d was compared with the distribution of R&I indices of all scored fish per trip. This was done to evaluate whether a correction was needed if proportionately more unimpaired fish (e.g., in excellent condition) were monitored than that were actually scored aboard the vessel. In such a case, a weight was applied by dividing the number of fish scored aboard the vessel by the number of fish that were monitored at a given level of the reflex impairment and injury index (10 levels, i.e., 6 reflexes, 4 injury types). The estimation of the post-release survival per trip was done using the estimated marginal means ("emmeans"; Lenth et al., 2015) based on a weighted model. These weighted means were considered when estimating overall survival per trip. Overall, mean survival per trip, unpartitioned into neither on-board nor post-release, was calculated as follows:

$$P(S) = P(A) \cdot P(B|A)$$

where overall survival $P(S)$ is the product of the immediate/on-board survival probability $P(A)$ and the probability of survival post-release, given that the fish had survived the immediate/on-board assessment $P(B|A)$.

3. Results

3.1. Overview of fishing operations

Operational characteristics varied and depended on fishing behavior and engine power. On average, the coastal and Eurocutter vessels of the ≤221 kW fleet segment and the >221 kW engine-powered vessel deployed their gear for ~60 min, ~90 min, and ~150 min; fished in ~10 m, ~40 m and ~60 m deep water; and produced catch volumes of ~450 kg, ~500 kg and ~2250 kg, which took ~15 min, ~15 min and ~40 min to sort, respectively (Table 1a–1c). Trips of the ≤221 kW vessels were monitored throughout the year, while the two trips of the >221 kW vessel took place in summer only (Table 1a–1c). The week-long trip duration and extra deck space of the larger vessel allowed observation of an order of magnitude more plaice than aboard the other two vessels (Tables 1a–1c and Table 3).

Conventionally beam-trawled, undersized plaice typically died within 4 or 5 days after discarding, while all but three of the 160 benign-treated plaice (i.e., controls) survived (Fig. 5). Thus, there was no indication that holding plaice captive in containers substantially and cumulatively contributed to mortality. Excluding the controls, 489 commercially beam-trawled plaice (from 53 deployments; 23.1 ± 2.8 cm TL, mean ± SD) were scored for vitality and injury aboard the vessel and were subsequently monitored for their post-release fate in captivity. In total, 61 observations from two trips were excluded from the analyses of post-release survival, because their monitoring period was reduced to 3 days due to a lack of available monitoring tanks at the shore-based facility (Fig. 5D and E). The remaining 428 plaice were monitored for at least 9 days (average of 15 days) until no more mortality attributable to the catch-and-discarding process was observed (Fig. 5). Across all monitored trips, only three fish died between day 9 and day 35 of monitoring. Considering that all remaining survival curves reached asymptote by day 8 of monitoring, survival at 9 days of monitoring was selected to provide a representative estimate of capture-and-discarding related survival probability.

3.2. On-board survival

Among the 12 trips, 90 % (62–98 %, 95 % CI) of commercially beam-trawled plaice were still alive aboard the vessel. In the summer, survival decreased with increasing deployment duration (Fig. 6). On-board survival was high (>95 %) among trips outside the summer months of July and August, but varied between 20 % and 70 % for trips in July and August across two trips with >221 kW and one trip with a ≤221 kW vessel, respectively (Table 3). Uni-variable analyses revealed gear deployment duration ($p < 0.001$, Table 4) and sea surface temperature ($p < 0.05$; Table 4) to significantly affect the probability of on-board survival of plaice. Both these variables showed a negative relationship with on-board survival, but due to their collinearity (at seawater temperatures >14 °C), they could not be included in the same model. The most parsimonious model therefore included gear deployment duration (AIC = 2686.9; Table 5; Fig. 7). This model was characterized by considerable variability in the random effect component of gear deployment and trip (variance for random effects of unique trawl nested in trip and trip: 1.498 and 2.866, respectively). The random effect for trip contributed to some variation when plotting the relationship between on-board survival with gear deployment duration (Fig. 7A). For

Table 3
Mean on-board, post-release (after 9 days of monitoring; where applicable) and total, overall survival (%) of discarded plaice per monitored commercial beam-trawl trip. The number of assessed plaice per survival component were provided in brackets. n/a, not available.

TripID	Fleet segment	Month	Year	Monitoring period (days)	On-board survival	Post-release survival*	Overall survival
1	Coastal	November	2014	20	100 (61)	45.68 (31)	45.68
2	Coastal	December	2014	22	100 (22)	4.55 (22)	4.55
3	Coastal	February	2015	14	100 (50)	97.33 (30)	97.33
4	Euro	March	2015	17	99.08 (109)	78.84 (30)	78.12
5	Euro	March	2015	3	99.10 (111)	n/a (31)	n/a
6	Euro	April	2015	3	95.65 (184)	n/a (30)	n/a
7	Coastal	June	2015	23	100 (65)	3.4 (30)	3.34
8	Euro	July	2015	14	69.78 (182)	0.1 (44)	0.07
9	Large	July	2015	9	24.11 (1240)	0.31 (84)	0.07
10	Large	August	2015	9	20.21 (1321)	0.27 (97)	0.05
11	Coastal	September	2015	34	98.48 (66)	1.14 (30)	1.12
12	Euro	September	2015	15	94.87 (78)	1.02 (30)	0.97

* , post-release survival was estimated based on weighted least-square means, except for trips 5 and 6 where the monitoring period was cut short. Any observations of post-release survival from these two trips were not considered in the analyses, because of a potential bias to have overestimated post-release survival when asymptote of the survival curve over time was not yet reached.

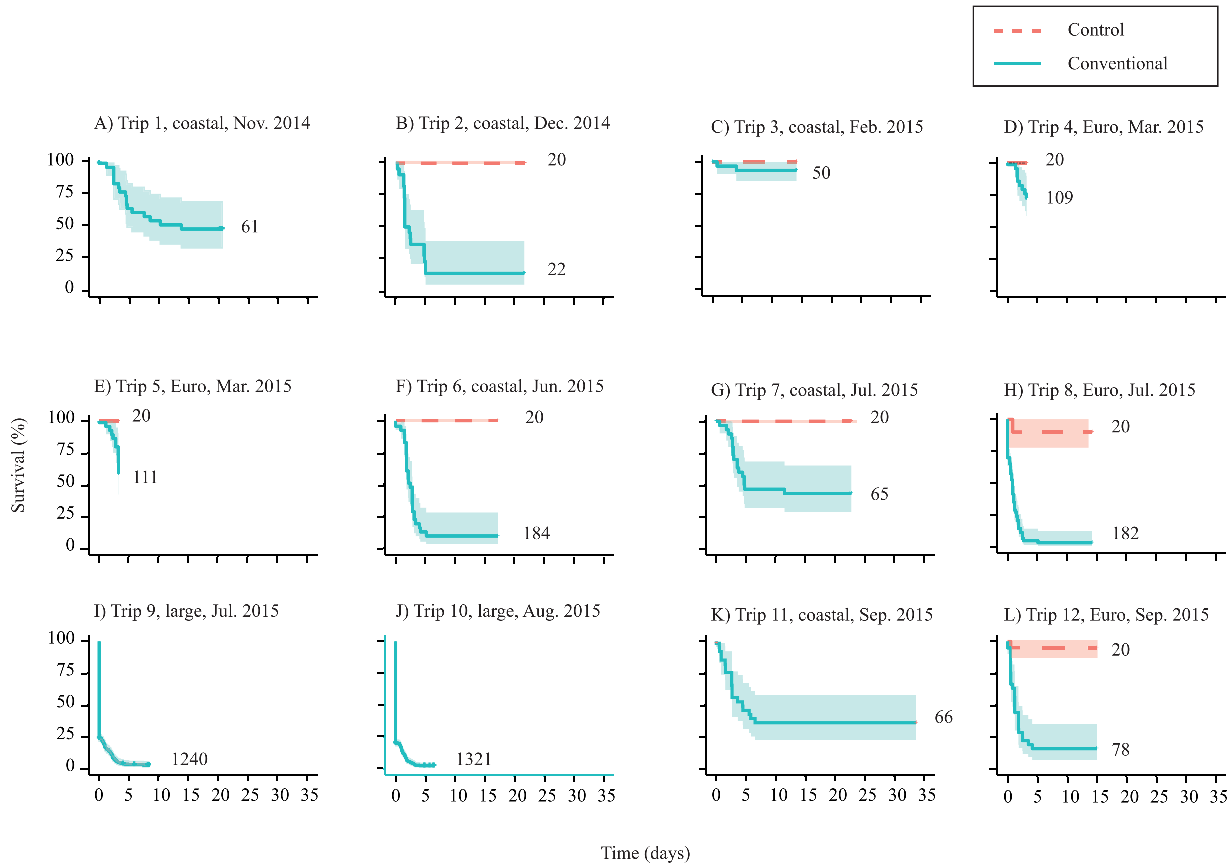

Fig. 5. Non-parametric Kaplan–Meier survival probability estimates over days of monitoring of discarded plaice (*P. platessa*) collected during 12 trips (A–L) from conventional trawls (blue line) by Belgian beam trawlers. Three of the 160 control fish died (dotted red line, B–D). Numbers indicate sample sizes. Shaded areas around each line indicate 95 % confidence intervals. Crosses indicate right-censored data (i.e., fish that were alive when daily monitoring terminated and when these fish left the trial).

example, for gear deployments of 120 min duration, it was estimated that on-board survival can range between ~20 % and 100 % depending on the trip (Fig. 7A). The preferred model appeared to provide a poor description of the data, however, when using clustered cross-validation. Deviations >10 % between observed and predicted on-onboard survival probabilities (aggregated and averaged per trip) were noted for seven out of the 12 trips (Table 6). Notably, among trips of the Eurocutter, on-board survival was predicted to be almost 20 % lower than actual observed survival rates (trips 4–6, 8, 12).

3.3. Post-release survival

Among the sub-set of 428 plaice being monitored in captivity, post-release survival probability varied between <1% and 97 % (Table 3). There was a strongly significant relationship between post-release survival probability and the reflex and injury index ($p < 0.001$), followed by seawater temperature ($p < 0.05$), and gear deployment duration ($p < 0.05$, Table 4). However, due to collinearity of the latter two variables, seawater temperature and gear deployment duration were not considered within the same model. Ten candidate models were built for the analysis, and three received most empirical support (Table 7). The most parsimonious model identified the R&I index and seawater temperature to contribute significantly to the observed variability in post-release survival probability (AIC: 366.2; Table 5). Similar to on-board survival, the most parsimonious model for post-release survival was characterized by considerable variability in the random effect component of trip (best model, variance for random effects of unique trawl nested in trip: 0.064 and 1.011 for deployment and trip, respectively). However, cross-validation of the most parsimonious model indicated >10 % deviations between observed and predicted survival probability among 7 out of 10 trips (Table 6). Predictions at trip level were as inaccurate as those for on-board survival probabilities. In particular, for a winter trip of the coastal vessel (trip 2), predicted values deviated by 55 %. The trip was characterized by >1 m waves, ~15 min air exposures (on average, Table 1a). The random effect of trip contributed to some variation when plotting the relationship between post-release survival with the R&I index for each of the seawater temperature categories (Fig. 7B). More vital plaice were more likely to survive, especially when discarded into 8−14 °C water. Plaice with an R&I index of 0.5 had a ~70 %, ~50 % or ~20 % chance to survive 9d after discarding when acclimated to 8−14 °C, <8 °C or >14 °C of seawater (Fig. 7B).

3.4. Overall survival

Across all sampled trips per vessel and fleet segments, survival of plaice discarded from conventional trawls of Belgian beam trawlers ranged between 41–58 %, 11–28 %, 2–4% (95 % confidence interval; Kaplan-Meier models) for trips of the coastal vessel (trips 1–3, 7 and 11, small), the Eurocutter (trips 4–6, 8 and 12, small) and >221 kW vessel (trips 9 and 10, large), representing the small and large fleet segments, respectively (Fig. 8). Using the weighted post-release survival estimates resulted in an even lower overall survival close to 0% for the vessel of the >221 kW fleet segment (Table 3).

4. Discussion

Between <1 % and 58 % of plaice survive after being caught and sorted aboard Belgian beam trawlers, assuming no predation. Survival

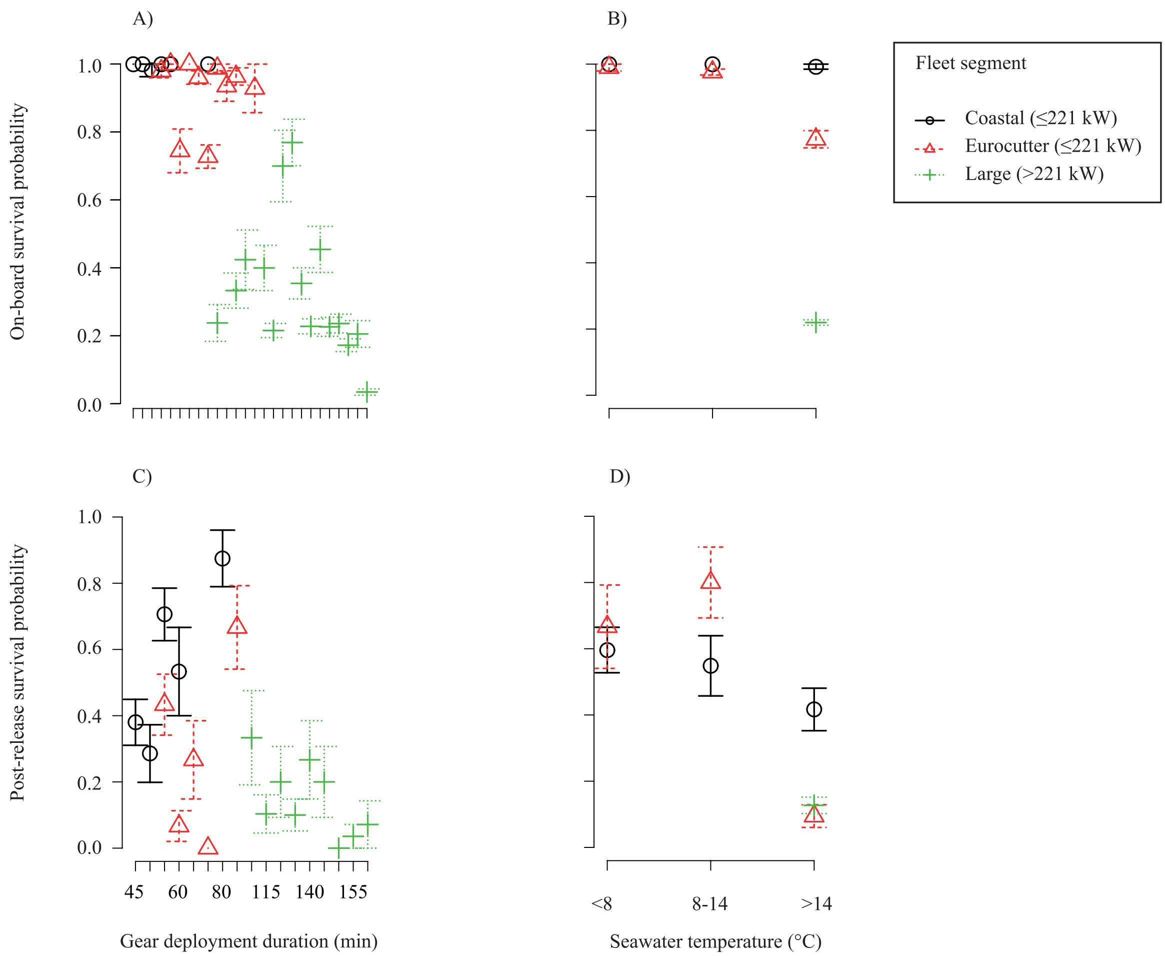

Fig. 6. Mean on-board (A, B) and post-release (C, D) survival probability per fleet segment (coastal, Eurocutter, >221 kW) in relation to gear deployment (A, C) duration and seawater temperature (<8 °C, 8–14 °C, >14 °C; B, D).

Table 4
Significance of variables of uni-variable generalised linear mixed models (GLMM) based on Wald III Chi-square test results. These models were used to investigate the singular effects of environmental and technical variables on survival probability following either the immediate, on-board or delayed, post-release (after 9 d of monitoring in captivity) survival assessment. n/a, not available.

Variable	On-board Chisq	Df	Pr(> Chisq)	AIC	Post-release Chisq	Df	Pr(> Chisq)	AIC
Intercept	0.4918	1	0.4831		3.9647	1	0.04646	
Fleet Segment	22.8654	1	<0.001 ***	2687.5	1.9374	1	0.16395	413.9
Intercept	28.279	1	1.050e-07		0.0026	1	0.9593	
Vessel	34.832	2	<0.001 ***	2683.5	3.7259	2	0.1552	414.5
Intercept	43.508	1	4.221e-11		0.6904	1	0.40604	
Haul Duration	12.467	1	0.0004142 ***	2686.9	3.8886	1	0.04862 *	411.6
Intercept	16.8390	1	4.069e-05		0.1909	1	0.6622	
Wave Height	1.0714	1	0.3006	2698.8	0.7955	1	0.3725	414.9
Intercept	17.6201	1	2.697e-05		0.1855	1	0.66672	
Sea Temp. cat.	7.5238	1	0.02324 *	2625.4	7.0103	1	0.03004 *	412.1
Intercept	14.6201	1	0.0001315		1.3300	1	0.2488	
Sediment Catch	6.5586	3	0.0873792	2626.8	0.8328	1	0.3615	414.8
Intercept	19.7312	1	8.913e-06		0.4412	1	0.5066	
Sorting Duration	0.7227	1	0.3953	2699.2	0.5086	1	0.4757	415.1
Intercept	63.4407	1	1.653e-15		0.1747	1	0.6760	
Air Exposure	0.4844	1	0.4865	224.6	1.6009	1	0.2058	413.9
Intercept	9.0885	1	0.002572		3.6588	1	0.05578	
Length	3.1518	1	0.075845	1103.3	2.0985	1	0.14745	409.0
Intercept	n/a	n/a	n/a		4.8374	1	0.02785	
R&I index	n/a	n/a	n/a		36.6212	1	<0.001 ***	370.4

*** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$.

Table 5
Estimated regression parameters, coefficients, z-values and *p*-values of the most parsimonious models following model selection for on-board (A) and post-release survival probability (B) of beam-trawled plaice, respectively. Fixed effects include: gear deployment duration (S); reflex impairment and injury index (R); seawater temperature category (T); and random effects: deployment (a_{jk}) nested in trip (b_k). Significance threshold, $p < 0.05$.

Model	Estimate	Std. error	z-value	p-value
On-board survival				
$p_{ijk} \sim$ Binomial (μ_{ijk}); E(A_{ijk}) = μ_{ijk}				
Logit(μ_{ijk}) = $S_{ijk} + b_k \mid a_{jk} \sim N(0, \sigma^2)$				
Intercept	6.61827	−1.00336	6.596	<0.001 ***
Deployment duration	−0.03660	−0.01036	−3.531	0.000414 ***
Post-release survival				
$p_{ijk} \sim$ Binomial (μ_{ijk}); E(B_{ijk}) = μ_{ijk}				
Logit(μ_{ijk}) = $R_{ijk} + T_{jk} + b_k \mid a_{jk} \sim N(0, \sigma^2)$				
Intercept	2.5126	0.7413	3.390	0.0007 ***
R&I index	−5.5817	0.9010	−6.195	<0.001 ***
SeaTempCat8−14	0.9222	0.8075	1.142	0.2534
SeaTempCat>14	−2.0003	0.7975	−2.508	0.0121 *

estimates established here corresponded to earlier estimates from comparable studies with respect to fishing conditions, monitoring periods and sampling protocols. For example, between 3% and 57 % of beam-trawled plaice have been estimated to survive from discarding in the North Sea (Uhlmann et al., 2016a, b; van der Reijden et al., 2017; see also the online supplementary review table of discard survival rates by Rihan et al., 2019). Although almost none of the control fish died, arguably some of the conditions during transport and captivity may have contributed to cumulative and chronic stress among captive individuals (Savina et al., 2019). These estimates nevertheless provide a detailed insight into the physical effects of beam trawling on the condition of discarded fish and they support the existing literature about key contributing factors to the survival of discarded plaice after demersal beam- (Kelle, 1976; van Beek et al., 1990; Berghahn et al., 1992; Depestele et al., 2014; Uhlmann et al., 2016a, b; van der Reijden et al., 2017) and otter trawling (van Beek et al., 1990; Methling et al., 2017; Savina et al., 2019). In the present study, discarded plaice were assessed for their condition aboard commercial vessels under a considerable range of biological, environmental and operational fishing conditions that contribute to the variability observed in the survival rates between gear deployments and trips. Variability among discard survival of trawled plaice and the relevance of a reflex impairment and injury index as a proxy for post-release survival (see Table 5) were noted by Kraak et al. (2019), who emphasizes the need to consider the environmental and operational context of scoring the condition of a flatfish.

Overall, our dataset has captured the impact of beam trawling within both mild and extreme environmental and operational fishing conditions. In the present study, on-board and post-release survival of plaice were monitored after discarding by beam trawlers from three fleet segments and in different seasons and after fishing by three fleet segments (coastal, Eurocutter, and >221 kW). In the future, replicated post-release survival estimates of plaice discarded from the >221 kW segment will be needed to disentangle the effects of gear deployment duration and seawater temperature. Discard survival may possibly be overestimated due to the lack of accounting for possible post-release predation (Raby et al., 2014; Depestele et al., 2016).

A key factor negatively associated with both on-board and post-release survival was seawater temperature (van Beek et al., 1990; Savina et al., 2019). It seemed that acclimated environmental temperatures had a predominant effect on vitality and survival observations of

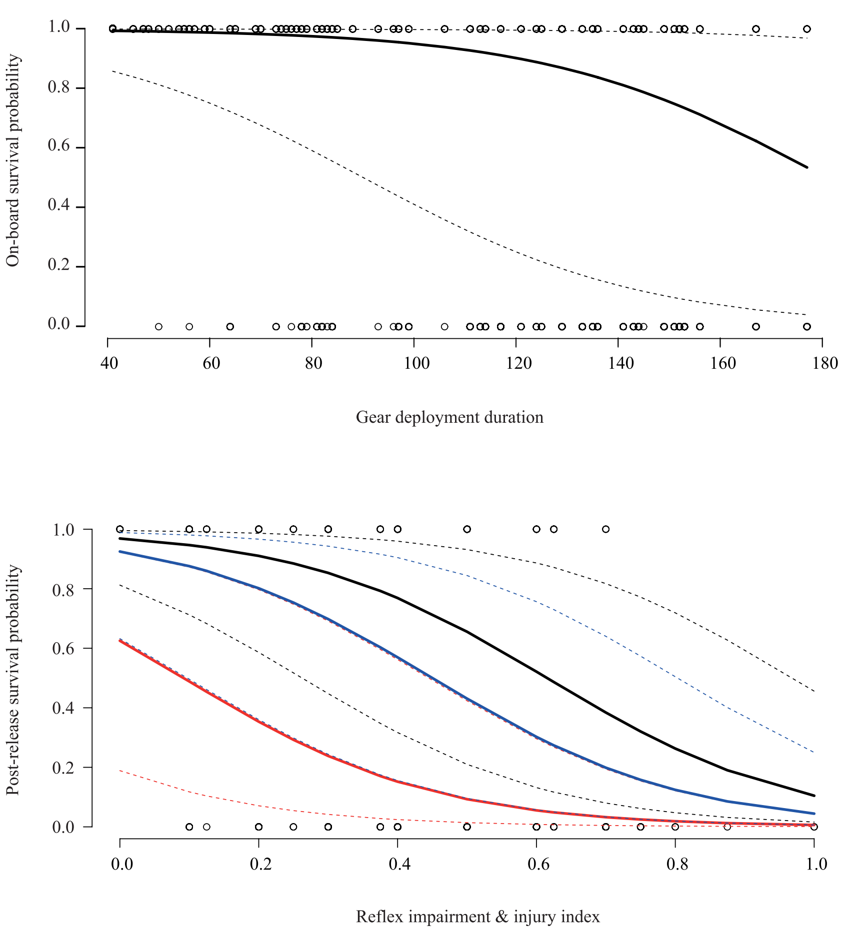

Fig. 7. GLMM predicted on-board (A) and post-release (B) survival probabilities as a function of gear deployment duration and reflex and injury index at three seawater temperatures (<8 °C, 8–14 °C, >14 °C) for trips, respectively. The thick line in the middle represents the predicted values for the 'population of trips', and the other two lines were obtained by adding and subtracting 1.96 × 1.693 (A) or 1.96 × 1.0052 (B) for the random intercept to the predictor function of on-board or post-release survival probabilities, respectively (following Zuur et al., 2009). The space between the dashed lines shows the variation between the predicted values per unique gear deployment or trip for on-board or post-release survival.

Table 6
Differences between predicted and observed survival (in %) of plaice following n-clustered cross validation of the most parsimonious models for on-board and post-release survival, respectively. n/a, not available due to a monitoring period that was cut short to 3 days before survival curves stabilized for trips 5 and 6 (see Fig. 6).

	On-board survival			Post-release survival		
Trip ID	Predicted	Observed	Deviation	Predicted	Observed	Deviation
1	92.6	100.0	−7.4	73.0	54.8	18.2
2	92.7	100.0	−7.3	69.0	13.6	55.4
3	82.8	100.0	−17.2	51.1	93.3	−42.3
4	78.4	99.1	−20.7	61.7	73.3	−11.7
5	80.9	99.1	−18.2	n/a	n/a	n/a
6	69.1	95.7	−26.5	n/a	n/a	n/a
7	91.6	100.0	−8.4	21.5	46.7	−25.2
8	85.6	69.8	15.8	20.0	4.6	15.4
9	35.2	24.1	11.1	19.3	13.1	6.2
10	18.7	20.2	−1.5	16.8	12.4	4.5
11	92.0	98.5	−6.5	19.4	36.7	−17.2
12	83.2	94.9	−11.7	11.1	16.7	−5.6

Table 7
List of relevant candidate logistic regression models fitted to the post-release survival data of discarded European plaice monitored in captivity for at least 9 days. Models (M1–M3) were shown with Akaike weights $\omega_i > 0.05$, calculated on the basis of Δ_i AIC values. Models with higher Akaike weights ω_i have more empirical support.

Model	AIC	Δ_i	AICω_i
M1 − status9d~R&I index + seawater temperature category + (1 | trip / deployment)	366.23	0.00	0.476
M2 − status9d~R&I index + deployment duration + (1 | trip / deployment)	367.016	0.784	0.321
M3 − status9d~R&I index + (1 | trip / deployment)	370.35	4.122	0.476

discarded plaice, in contrast with the <5 °C temperature changes of limited exposure durations (<10 min) between water and air (i.e., temperature shocks) when leaving the water for on-deck handling, travel through thermoclines inside the net, or the return to the seabed after discarding. The occasional <3 °C seawater temperature difference that captive-held fish experienced when being transferred from on-board to laboratory-based holding containers were considered to be non-detrimental, based on high survival rates of captive controls. Increased metabolism at the lower and upper limit of the preferred thermal tolerance of plaice may leave very little capacity to allocate any energy reserves to cope with capture-related, physiological challenges such as burst swimming or injury mediation (Methling et al., 2017). Considering temperature as a categorical term in our models, however, is unlikely to capture the true relationship between temperature and survival, which for plaice is poorly understood. Plaice appear to be more tolerant to fishing capture stress when acclimated to cool water. At the same time, temperature tolerance of plaice has been suggested to shift according to age/size (Fonds et al., 1992). Fonds et al. (1992) states that thermal optima shift from 20 °C to 10 °C as plaice grow older (and larger). Although reallocating fishing effort to cooler waters in summer would effectively improve discard survival, other measures such as reducing gear deployment duration may provide more practical and acceptable options for fishers and managers.

By partitioning survival into an on-board and post-release survival component, the effects of conventional operations that occurred both during capture and on-board handling as well as after discarding were documented. Such combined effects of both the capture-and-sorting and discarding phases all showed detrimental yet varying effects on fish. Capture by >221 kW fatally injured fish and contributed to the low (<25 %) on-board survival rate. Undersized plaice simply did not cope with challenging environmental and operational fishing conditions by >221 kW vessels such as ~150 min gear deployment, ~37 min sorting durations and, in our case, fishing in ~16 °C warm seawater. Such low levels of on-board survival were rarely observed among ≤221 kW vessels. Our results confirm earlier findings, i.e., that any efforts to improve post-release survival of flatfish discarded from beam trawls need to focus on capture rather than post-release stressors (van der Reijden et al., 2017). Trials that attempted to increase survival by reducing air exposure during sorting have provided no conclusive evidence of the efficacy

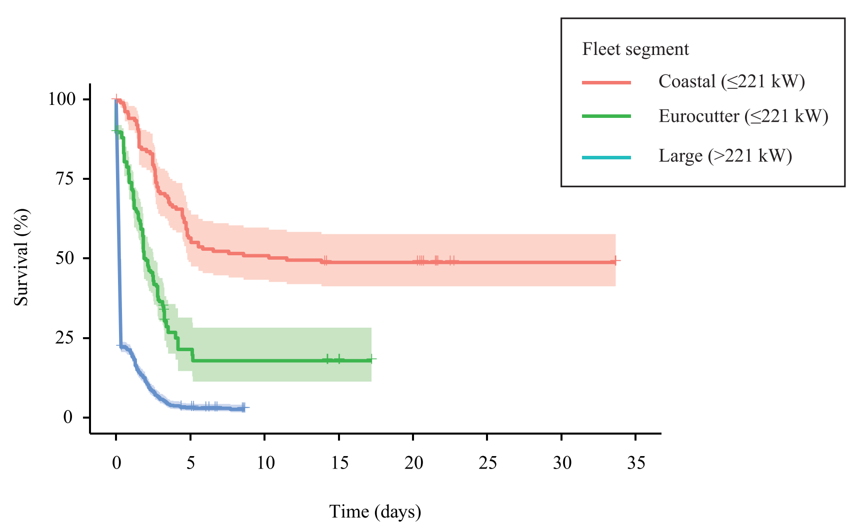

Fig. 8. Non-parametric Kaplan–Meier survival probability estimates over days of monitoring of discarded plaice (*P. platessa*) aggregated per fleet segment. Crosses indicate right-censored data (i.e., fish that were alive when daily monitoring terminated and these fish left the trial).

of such measures in a multi-stressor setting (Schram and Molenaar, 2018), although if tested in singularity, a negative relationship between air exposure and survival was demonstrated for trawled plaice (Methling et al., 2017). Even though shorter sorting durations may have the potential to improve on-board survival, post-release survival as observed in this study is mainly driven by seawater temperature and on-board condition after capture (R&I index).

If a fish survives capture and sorting and is returned to the sea (discarded), in the absence of predation, its post-release survival probability can be associated with the stress experienced throughout the capture process, e.g. the physical trauma inside the net. Especially during periods of adverse weather with elevated wave heights (Uhlmann et al., 2016a). Such trauma can vary depending on what type of gear was used, the duration of deployment and the environmental conditions. Given the fixed structure of beam trawls and attached wires, the gear moves up and down under stormy conditions and thereby exacerbates a pumping motion of the codend, which adds to the compression of any entrapped individuals (O'Neill et al., 2003; Winger et al., 2010). This interaction was not significant in the present dataset.

The combined assessment of reflexes and injury provided the best-fitting model of post-release survival probability (Uhlmann et al., 2016a,b; van der Reijden et al., 2017). Aggregating observations from individual fish to trip level allows for predictions around an overall average, as long as observations were made within a representative spectrum of fishing conditions. However, the exact cause of death could not be established here – for example, fish can be either impinged against meshes of the net or compressed and scraped against abrasive objects inside the codend such as sand, stones, starfish or (empty) shells (van Beek et al., 1990). Underwater observations would be required, including knowledge of which individual fish was subjected to which conditions when it entered the gear, to associate mechanical impact with stress and injury. Accurate dose-response relationships are lacking for the majority of stressors evaluated here, which in many cases were not measured at fish level (i.e., exposure durations, interactions with gear and/or catch, experienced temperature profiles). In the absence of such information, measurement of environmental and operational parameters during fishing and evaluating responsiveness and extent of injury remain the best available options.

Another option may be to demonstrate a more generic, linear relationship between on-board and post-release survival probability (e.g., as Bell and Lyle, 2016 did for some Tasmanian gillnet fisheries). Our dataset does not support this. The context of each observation within the prevailing environmental and operational conditions imply that, if there were such a relationship existed, it is unlikely to be linear because of the potential synergies, antagonistic effects and interactions among contributing factors. The contribution of some (unknown) variable to survival may be absorbed by the random effects for deployment and trip. Possibly, some variables at deployment and/or trip level or interactions are not accounted for, such as an effect of fishing location on catch compositions with abrasive properties, recovery potential (especially when fish were kept in water-filled containers prior to being tested for reflex impairments, van der Reijden et al., 2017), physical condition (i.e., Fulton K index) or scoring ability by different observers, which may contribute to a lack of model fit when using n-clustered cross validation and considerable variability between trips. Variation in survival of trawl-caught plaice between trips was also observed by van der Reijden et al. (2017).

Given the magnitude with which Belgian beam trawlers discard plaice (see Supplementary Table 1), plaice discard survival estimates of 3–58 % could equate to ~30 and ~2700 tonnes of discarded plaice surviving from the 1000–4722 tonnes that were discarded in the North Sea and English Channel, respectively (Supporting Table 1). The likely effects of discard mortality on plaice stocks was estimated recently (International Council for the Exploration of the Seas (ICES), 2020); however, a consistent framework that facilitates the provision of a definitive answer to what constitutes 'high survival' and could assist the European Commission in justifying its decision-making is still lacking.

Credit author statement

Sebastian Uhlmann: Conceptualization, Methodology, Data Collection, Investigation, Analysis, Writing-Original draft preparation. **Bart Ampe:** Data curation, Software, Analysis. **Noémi Van Bogaert:** Visualization, Investigation, Writing-Original draft preparation. **Christian Vanden Berghe:** Data collection. **Bart Vanelslander:** Visualization, Investigation.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

The authors would like to thank Ruben Theunynck, Eddy Buyvoets, and Coenraad Deputter for collecting and entering data and the vessel owners, skippers and crew members of all participating vessels for their co-operation. We thank Maarten Soetaert, Daan Delbare, Hans Polet, David Vuylsteke, and Mattias van Opstal for overseeing the ethically correct handling and housing of beam-trawled flatfish. Additionally, we thank Martine Velghe (Agriculture & Fisheries Department of the Federal Belgian Ministry) for her help in providing recent vessel composition statistics of the Belgium fleet. Also, we would like to thank the Working Group on Methods for Estimating Discard Survival (WGMEDS) of the International Council for the Exploration of the Sea (ICES) for facilitating this research, and all of its members for the useful discussions. Some of the information contained here has been derived from data that is made available under the European Marine Observation Data Network (EMODnet) Seabed Habitats initiative (http://www.emodnet-seabedhabitats.eu/), financed by the European Union under Regulation (EU) No 508/2014 of the European Parliament and of the Council of 15 May 2014 on the European Maritime and Fisheries Fund. We are grateful to Jochen Depestele, David Fletcher, Miriam Levenson, the two anonymous reviewers, and the editor of this journal, whose comments helped us to greatly improve this manuscript. The work was supported by the European Maritime and Fisheries Fund (Grant Numbers: Vis/14/B/01/Div, 17/UP1/01/Div, and 18/UP1/30/Div). The funder or any other stakeholder have had no role in the study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.fishres.2021.105966.

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