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Original Article

Quantifying the performance of selective devices by combining analysis of catch data and fish behaviour observations: methodology and case study on a flatfish excluder

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This article describes a method for the quantitative analysis of fish behaviour relative to selection devices in trawl gears. Based on video observations, the method estimates probabilities for a given event to happen and establishes behavioural tree diagrams representing and quantifying behavioural patterns in relation to the selection device under assessment. Double bootstrapping is used to account for the uncertainty originating from a limited number of fish observations and the natural variation in fish behaviour. The method is used here to supplement standard analysis of catch data for the performance assessment of a flatfish excluder (FLEX). The Baltic Sea trawl fishery targeting cod (*Gadus morhua*) provides the pilot case. Results obtained by comparing catches with and without FLEX installed revealed that >75% of bycaught flatfish individuals escaped through the device, while no evidence was found that catches of cod in the targeted sizes were reduced. The behavioural analysis produced values of escape efficiency comparable to those obtained in the catch analysis. Furthermore, it revealed that ~80% of the flatfish went calmly into the excluder, while most of the roundfish displayed avoidance swimming reactions. The method provides quantitative information of fish behaviour that can be relevant for developing and optimizing selection devices.

Keywords: behavioural trees, bycatch, flatfish, FLEX, quantitative analysis, selection devices

Introduction

Flatfish are common bycatch species in bottom-trawl fisheries targeting crustaceans or roundfish species (Beutel *et al.*, 2008; Ulleweit *et al.*, 2010; Storr-Paulsen *et al.*, 2012; Lescrauwaet *et al.*, 2013). Often, unintended flatfish catches are of low commercial value for the fishers, being partially or totally discarded (Borges *et al.*, 2006; Lescrauwaet *et al.*, 2013). In fisheries subjected to catch-restricted legislation, bycatch of flatfish with limited quota can represent a challenge for fisheries targeting other species. For example, in US Georges Bank, healthy roundfish stocks are largely under-exploited due to the abundance of flatfish species with limited quota (Beutel *et al.*, 2008; ICES, 2018).

Catches of unintended species often occur due to a mismatch between the selective properties of the trawl and specific morphological characteristics and somatic growth of captured species (Catchpole and Reville, 2008; Wienbeck *et al.*, 2014). In such cases, a common strategy to reduce bycatch is to mount selection devices in the fishing gear able to provide additional escapement possibilities to those non-targeted species that enter the gear (Milliken and DeAlteris, 2004; Catchpole and Reville, 2008).

Traditionally, the effectiveness of selective devices in trawl gears is evaluated based on catch data alone, following well-established methodologies for data collection and for the subsequent statistical analysis (Wileman *et al.*, 1996). However, in most cases, these quantitative methods based on catch data do not provide any detailed information on the contribution of the different components of the device to its overall performance, or about the sequences of behavioural events occurring when the fish interacts with the selection device. This lack of detailed information limits the understanding of the functioning of the device, and therefore, the ability to optimize its performance.

The general development in camera technology that occurred in the last decade has led to the availability of low-cost cameras with high image quality for underwater video recordings, which are therefore becoming an affordable method to assess fish behaviour in selectivity studies (Bayse and He, 2017). Video observations are often used by fisheries technologists to obtain a qualitative picture on how fish interact with a selection device (Queirolo *et al.*, 2010; Chosid *et al.*, 2012; Lövgren *et al.*, 2016; Grimaldo *et al.*, 2018; Larsen *et al.*, 2018). A review of recent literature suggests, however, a growing interest in more detailed descriptions of fish behaviour based on quantitative analysis (He *et al.*, 2008; Krag *et al.*, 2009a; Yanase *et al.*, 2009; Chosid *et al.*, 2012; Hannah and Jones, 2012; Bayse *et al.*, 2014, 2016; Underwood *et al.*, 2015; Queirolo *et al.*, 2019). The methodology applied in quantitative behavioural studies often involves tracking observed fish from their first detection to the final fate (capture or escape), during which the occurrence of behavioural events categorized at different stages of the selection process is identified and counted. While it is reasonable to assume that the fate of the fish can be related to sequences of behavioural events occurring throughout each of the selection stages, with few exceptions (Yanase *et al.*, 2009; Hannah and Jones, 2012), the stage-wise nature of the behavioural data is usually ignored. Instead, events from different stages are analysed together as predictors in regression models (Underwood *et al.*, 2015; Bayse *et al.*, 2016) or separately in contingency tables (He *et al.*, 2008; Krag *et al.*, 2009a; Bayse *et al.*, 2014; Queirolo *et al.*, 2019) and are therefore treated independently to events recorded in previous and subsequent stages. Behavioural responses to selection devices can be influenced by factors intrinsically related to the individual being selected and by extrinsic factors such as fishing conditions varying within and/or between hauls (Winger *et al.*, 2010). Therefore, estimating uncertainties associated to observed behaviours can be relevant information in the assessment and development of selection devices. However, to the best of our knowledge, no selectivity study based on fish behaviour provides such information.

Ignoring the stage-wise nature of the behavioural events and the uncertainty of occurrence preclude answering all the following questions: (i) how often does a given event happen?; (ii) how precise is the estimated probability of occurrence of a given behavioural event?; (iii) does the occurrence of an event condition the events happening next?, which at the same time can lead to more general questions like: (iv) what are the connections between different events being observed before, during, and after the fish contacts the selection device; and (v) could the observed sequences of events be related to the fate of the fish in relation to the selection process?. Therefore, to fully benefit from incorporating the use of underwater recordings in the process of studying, developing, and optimizing the performance of selective devices in fishing gears, it is necessary to be able to provide quantitative answers with uncertainties to the former questions.

This study introduces and applies a new method to quantitatively analyse fish behaviour in relation to selection devices. The method enables (i) quantifying the probability for a observed behavioural event to happen, (ii) quantifying the probability for a given behavioural event to happen, conditioned to the occurrence of events observed in previous behavioural stages, and (iii) establishing behavioural tree diagrams, formed by all the sequences of events displayed by the observed fish towards their final fate in the catch process. Moreover, the method accounts for uncertainties derived from the limited number of fish observations, and the natural variation in fish behaviour (Winger *et al.*, 2010) that potentially influences the between- and within-haul variations in the performance of selection devices (Fryer, 1991).

Applicability of the method is demonstrated here using a flatfish excluder as a case study. The device was conceived in the Baltic Sea, where large amounts of flatfish bycatch such as plaice (*Pleuronectes platessa*), flounder (*Platichthys flesus*), and dab (*Limanda limanda*) frequently occur in cod-directed trawl fisheries (ICES, 2017). Therefore, the present study develops, tests, and assesses the efficiency of such device using the standard analyses of catch data, supplemented with the proposed method for the quantitative analysis of fish behaviour based on video observations.

Material and methods

Development of a simple flatfish excluder for trawls

The design strategy for FLEX (a simple FLatfish EXcluder for trawls) exploits behavioural differences between fish species. According to several studies, cod tend to enter the trawl swimming downwards, after which it starts to redistribute up in the water column as it approaches the gear's aft (Holst *et al.*, 2009; Fryer *et al.*, 2017; Karlsen *et al.*, 2019). At this point in the trawl, the vertical distribution of cod might be length dependent, with small cod more likely to swim closer to the bottom net panel than larger ones (Melli *et al.*, 2019). Flatfish are commonly observed swimming near the floor of the trawl (Bublitz, 1996; Ryer, 2008; Fryer *et al.*, 2017). Based on these behavioural patterns, establishing an outlet in the bottom panel of the extension piece of the trawl could be an efficient strategy to reduce the bycatch of flatfish and undersized cod. This selection concept was adopted as the basis for the development of a simple and adaptive FLEX design that could be activated or deactivated with simple modifications at haul level, therefore providing fishermen with flexibility to switch their fishing strategies and targets in the short term.

The initial version of FLEX was developed on board the German research vessel RV CLUPEA during sea trials in October 2014. The earliest design consisted of an outlet established by a simple cut in the netting of the bottom panel of a four-selvedge extension piece. The cut was made at the mid-length of the 6-m-long extension. Stepwise improvements were achieved during the cruise based on video observations of fish responses near the outlet. Such observations revealed, for example events in which flatfish individuals turned back to the gear after passing through the outlet and losing contact with the bottom panel, or avoidance reactions due to the excessive waving of the net around the outlet. The behavioural information collected guided the development of the concept into the final design (Figure 1). FLEX consists of a

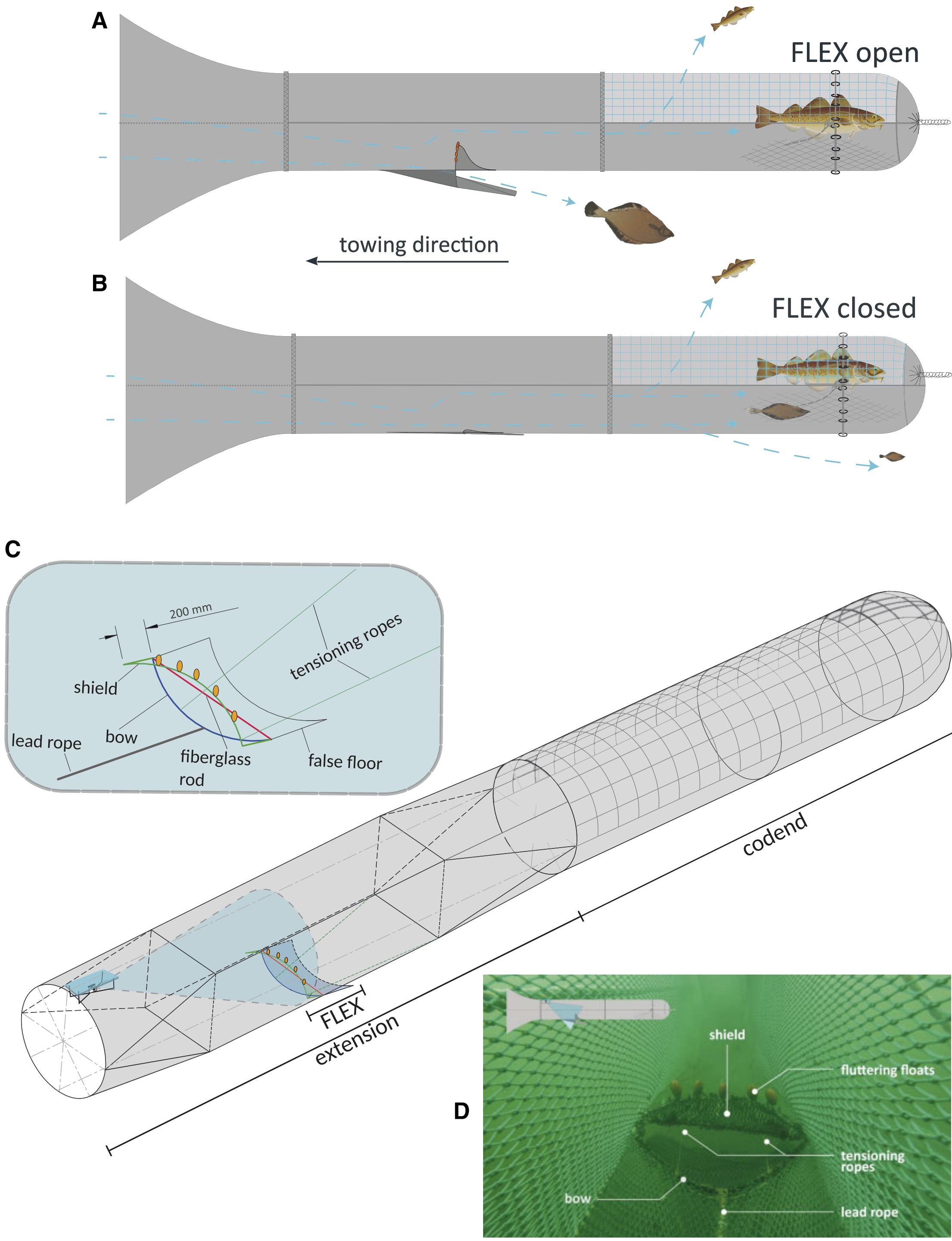

Figure 1. Design and working principle of the FLEX as it is intended for a commercial fishery (a and b). Blue arrows represent the expected swimming paths of roundfish and flatfish. (a) With FLEX open, flatfish escape before entering the codend, while roundfish selectivity occurs in the codend. (The BACOMA codend used in the Baltic Sea is included here only for illustration purposes. It was not used in this study.) (b) FLEX can be closed easily between hauls; with FLEX closed, all fish entering the trawl are size selected in the codend. (c) Construction details and placement of FLEX in the extension piece. (d) Front view of the device [underwater picture taken from the camera position shown in (C)].

half oval-shaped outlet, with the major axis formed by a 90-cm-long, straight fibreglass rod, connected to the rear edge of the net cut, and the tips fixed to the lower selvedges of the extension. The bow of the outlet is oriented downwards and defined by an elastic dentex wire connected to the forward edge of the net cut. A 1.5-m lead rope was connected to the vertex of the bow, running lengthwise through the forward section of the extension to create a furrow on the floor of the net. The furrow should guide the flatfish towards the outlet. Furthermore, a 90 cm × 20 cm rectangular net shield with small floats on top was connected to the fibreglass rod as a deterrent device for cod. In particular, the presence of a net shield with fluttering floats on top should stimulate avoidance reactions in cod swimming close to the floor (Herrmann *et al.*, 2015), reducing the probability of encountering the outlet. In the final design, we also connected a piece of netting to the outside of the bow (a false floor), aiming to guide flatfish further out of the gear. Such device could also create an optical illusion for the fish that the outlet is blocked. This visual effect could motivate the approaching cod to choose the clearer path towards the codend (Figure 1).

Collection and analysis of catch data

Experimental fishing was conducted 12–20 November 2014 on board the 42.40-m, 1780-kW German research vessel RV SOLEA. The experimental design applied was a paired catch comparison set-up (Krag *et al.*, 2015), with two identical four-panel extensions made of 60-mm nominal mesh length (Wileman *et al.*, 1996) on each side of a Double Belly Trawl (DBT; Supplementary Figure S1). The DBT was specifically designed to conduct paired-gear experiments on vessels with no twin-trawl facilities and has no application in commercial Baltic fisheries. FLEX was installed on one side of the DBT, referred to here as the test gear, and the other side remained as control, referred to here as the control gear (Figure 2).

A two-selvedge codend made of the same netting material as the extensions was connected to each gear. To ensure that fish entering the DBT would have an average equal probability of entering either gear, they were switched between sides during the cruise. Catches from the test and control gears were kept separate and sampled one after another at the end of each haul. The catch in each codend was sorted by species before each individual was length-measured to the half centimetre below (total length), using electronic measuring boards.

Estimate of FLEX's escape efficiency

Analysis of the catch data was conducted by species, following the procedure described in this section to estimate the efficiency of FLEX as an excluding device. The mesh length of the codends (60 mm) might not be small enough to retain all individuals from the smallest length classes. Therefore, only fish longer than 15 cm were considered for the analysis. The limit at 15 cm was set based on comparing fish morphology with the codend meshes for samples of fish of different species based on the mesh fall-through method described in Wienbeck *et al.* (2011). Fifteen centimetres was judged by this method to be a safe size limit that guaranteed that none of the species investigated would have been subjected to codend size selection, which potentially could have biased results in case of differences in codend size selection between the two gears used. Such differences in codend size selection could be caused by differences in catch size (O'Neill and Kynoch, 1996) due to the effect of mounting FLEX in the test gear. Furthermore, hauls with fewer than 20 individuals of the specific species studied were not included in the analysis.

In this section, we develop a model and method for quantifying length-dependent escape efficiency based on catch data. The method compares the catches obtained with the two gears (test and control) and relates the observed proportions of the catches to the efficiency of FLEX as an excluding device, $e_{flex}(l)$ (Figure 2). Because both gears fished simultaneously, the collected catch data were treated as paired catch comparison data (Krag *et al.*, 2015).

Based on Herrmann *et al.* (2018), the size selection processes in the two gears can be considered as sequential processes, first with a size selection $r_{front}(l)$ in the part of the trawl ahead of the extension, followed by the size selection in the extension piece $r_{ext}(l)$, and finally the selection process in the codend $r_{codend}(l)$. The only difference between the two gears is that the test gear has FLEX installed in the extension piece. This leads to an additional selection process, which can be expressed as $r_{flex}(l) = 1.0 - e_{flex}(l)$, where $e_{flex}(l)$ is the length-dependent escape probability (escape efficiency) through FLEX for a fish entering the extension. Based on these sequential selectivity processes, the total selectivity for the test gear with FLEX $r_t(l)$ and the control gear $r_c(l)$ can be modelled as:

$$\begin{aligned} r_t(l) &= r_{front}(l) \times r_{ext}(l) \times \left(1.0 - e_{flex}(l)\right) \times r_{codend}(l) \\ r_c(l) &= r_{front}(l) \times r_{ext}(l) \times r_{codend}(l) \end{aligned} . \quad (1)$$

Based on the group of valid hauls h, we can quantify the experimental average catch comparison rate CC_l (Herrmann *et al.*, 2017) as follows:

$$CC_l = \frac{\sum_{i=1}^{h} nT_{il}}{\sum_{i=1}^{h} (nC_{il} + nT_{il})} \quad (2)$$

where nT_{il} and nC_{il} are the numbers of fish in length class l caught in haul i in the codend of the test gear and the codend of the control gear, respectively. The next step is to express the relationship between the catch comparison rate CC_l and the size selection processes (retention probability) for the test gear with FLEX $r_t(l)$, and the control gear $r_c(l)$. First, the total number of fish n_l in length class l entering the DBT is separated into the test or the control gears (Figure 2). The split parameter (SP) accounts for this initial catch separation by quantifying the proportion of fish entering the test gear compared with the total entering the DBT. SP is assumed to be length independent; therefore, the expected values for $\sum_{i=1}^{h} nT_{il}$ and $\sum_{i=1}^{h} nC_{il}$ are:

$$\begin{aligned} \sum_{i=1}^{h} nT_{il} &= n_l \times SP \times r_t(l) \\ \sum_{i=1}^{h} nC_{il} &= n_l \times (1 - SP) \times r_c(l) \end{aligned} . \quad (3)$$

Based on (1)–(3) and Figure 2, the theoretical catch comparison rate CC(l) becomes:

$$\begin{aligned} CC(l) &= \frac{n_l \times SP \times r_{front}(l) \times r_{ext}(l) \times \left(1.0 - e_{flex}(l)\right) \times r_{codend}(l)}{\left(\begin{array}{r} n_l \times SP \times r_{front}(l) \times r_{ext}(l) \times \left(1.0 - e_{flex}(l)\right) \times r_{codend}(l) \\ + n_l \times (1 - SP) \times r_{front}(l) \times r_{ext}(l) \times r_{codend}(l) \end{array}\right)} . \\ &= \frac{SP \times \left(1.0 - e_{flex}(l)\right)}{1.0 - SP \times e_{flex}(l)} \end{aligned} \quad (4)$$

Equation (4) establishes a direct relationship between the escape probability through FLEX $e_{flex}(l)$ and the catch comparison rate CC(l). Therefore, FLEX's length-dependent escape efficiency can be assessed by estimating the catch comparison rate as formulated in (4). The expected equal catch efficiency of both sides of

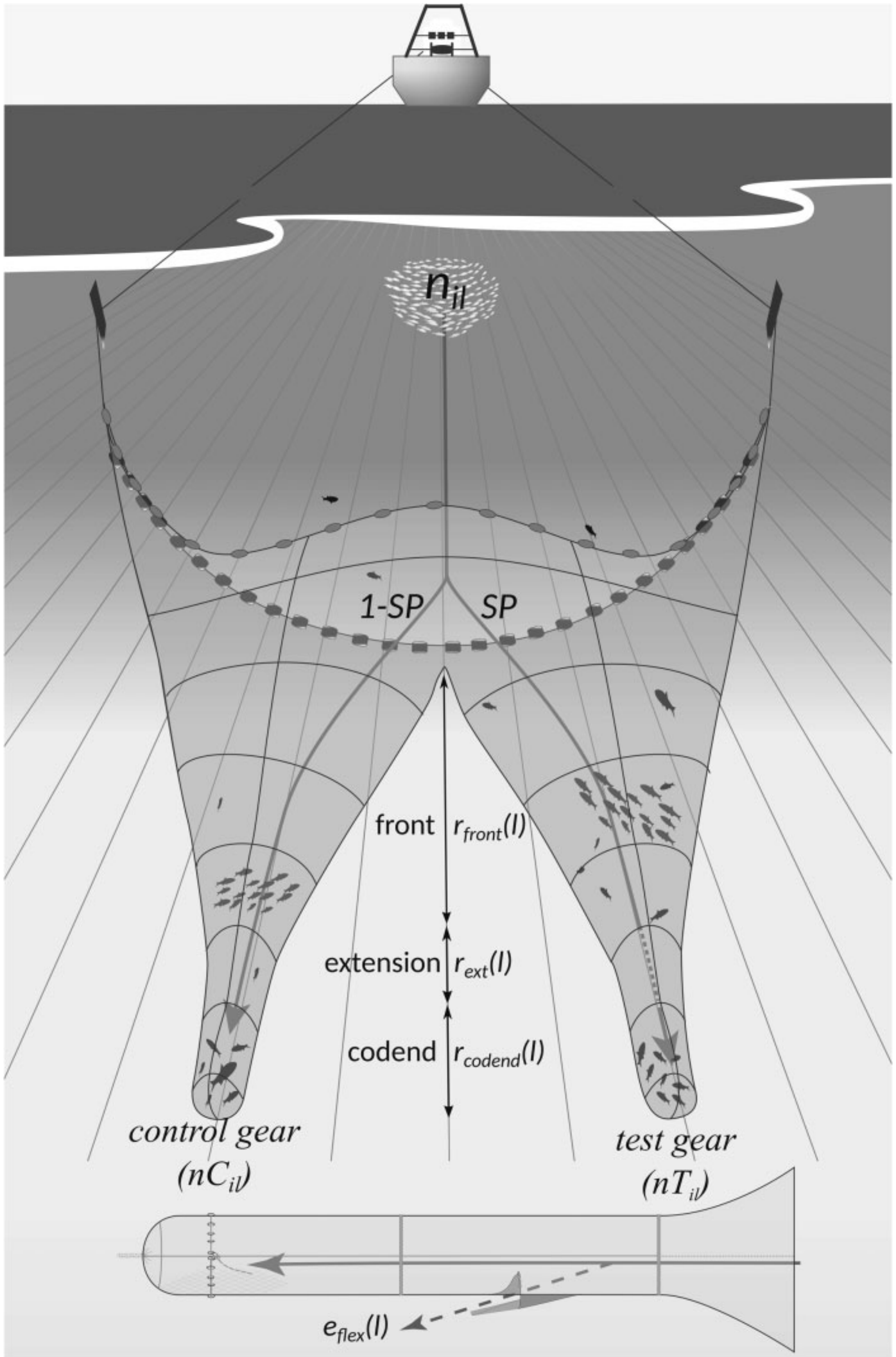

Figure 2. Experimental design applied during the sea trials with RV SOLEA. Test (FLEX) and control gears were mounted on different sides of the DBT. Numbers of fish by length l caught at haul i in the test codend (nT_{il}) and in the control codend (nC_{il}) were used for subsequent analysis. Description of the other mathematical notations showed in the figure can be found in the 'Collection and analysis of catch data' section.

the DBT and the swapping of the test gear between sides during the experiment led to the assumption that fish entering the trawl would have an average equal probability of entering either the test or the control gear; therefore, the parameter SP in (4) was fixed to a value of 0.5.

The escape efficiency of FLEX might depend on species-specific behaviour and length-dependent swimming ability. Therefore, to be able to model $e_{flex}(l)$ for the different species investigated, we used a highly flexible function often used in catch comparison studies (Krag *et al.*, 2015, 2014; Herrmann *et al.*, 2017, 2018):

$$e_{flex}(l, v) = \frac{\exp(f(l, \boldsymbol{v}))}{1.0 + \exp(f(l, \boldsymbol{v}))}, \quad (5)$$

where $f(l,\boldsymbol{v})$ is a polynomial of order 4 with parameters $\boldsymbol{v} = (v_0, v_1, v_2, v_3, v_4)$ (Krag *et al.*, 2015). Therefore, the estimation of the catch comparison rate in (4) is conducted by minimizing the following maximum likelihood equation with respect to the parameters $\boldsymbol{v}$ describing CC(l,$\boldsymbol{v}$):

$$-\sum_i \sum_l \left\{ nT_{il} \times \ln(\mathrm{CC}(l,\boldsymbol{v})) + nC_{il} \times \ln(1.0 - \mathrm{CC}(l,\boldsymbol{v})) \right\}. \tag{6}$$

Leaving out one or more of the parameters v_0–v_4 in (5) led to 31 additional simpler models, which were also considered potential candidates for modelling FLEX escape efficiency and therefore also estimated by (6). The model with the lowest AIC (Akaike, 1974) was selected from among the candidates. Following the guidelines in Wileman *et al.* (1996), the ability of the selected model for CC(l,$\boldsymbol{v}$) to describe the data sufficiently well was based on the calculation of the *P*-value associated with the Pearson's Chi-squared statistic, together with the visual inspection of residual length-dependent patterns. The *p*-value expresses the likelihood of obtaining at least as big a discrepancy between the fitted model and the observed experimental data by coincidence. Therefore, this *p*-value should not be <0.05 for the fitted model to be a good candidate to describe the observed length-dependent escape efficiency.

Efron confidence intervals (95%) of the curves predicted by (4) and (5) were obtained using the same double bootstrap procedure (1000 replications) as in Santos *et al.* (2016). This includes accounting for between-haul variation in FLEX's escape efficiency and the uncertainty in individual hauls related to the finite number of fish caught. In addition, the bootstrap method accounts for uncertainty in model selection to describe $e_{flex}(l,\boldsymbol{v})$ by incorporating in each of the bootstrap iterations an automatic model selection based on which of the 32 models produced the lowest AIC. The analysis of FLEX's escape efficiency described above was carried out using the software tool SELNET (Herrmann *et al.*, 2013; Santos *et al.*, 2016).

Indicators of escape efficiency

To further evaluate the efficiency of FLEX by accounting for the length structure of the population fished, three different escape efficiency indicators were estimated:

$$\begin{aligned} nE_{-} &= 100 \times \left(1.0 - \frac{\sum_i \{\sum_{l<ref} nT_{il}\}}{\sum_i \{\sum_{l<ref} nC_{il}\}}\right), \\ nE_{+} &= 100 \times \left(1.0 - \frac{\sum_i \{\sum_{l\geq ref} nT_{il}\}}{\sum_i \{\sum_{l\geq ref} nC_{il}\}}\right), \\ nE &= 100 \times \left(1.0 - \frac{\sum_i \{\sum_l nT_{il}\}}{\sum_i \{\sum_l nC_{il}\}}\right), \end{aligned} \tag{7}$$

where the summation of i is over hauls and l is over length classes. The escape efficiency indicators in (7) are calculated as one minus the ratio of catches from each of the species studied in FLEX gear (nT) to the catches in the control gear (nC). This is done for the total catch (nE), and for the fractions below (nE_-) and above (nE_+) a given reference fish size (ref). If available, the reference length used was the species Minimum Conservation Reference Size (MCRS), length used for management purposes that replaced the Minimum Landing Size in European fisheries. In general, high values of the three indicators for flatfish and low values for roundfish would indicate that the intended species selection was achieved. Any length dependency in the escape efficiency would be expressed by differences in the values of nE_- and nE_+. If this is the case, high values of nE_- and low values for nE_+ would be the preferred results for cod, indicating FLEX to potentially contribute in the reduction of bycatch of undersized cod without producing losses of marketable sizes. Confidence intervals associated to these indicators were obtained by including the calculations in (7) into the same bootstrap scheme used to obtain the confidence intervals associated to the curves predicted by (4) and (5).

Assessment of fish behaviour based on video observations

Video recordings were collected during selected hauls with a GoPro camera mounted in a protective structure on the upper panel of the extension, in front of FLEX. The camera focused on the selection device, with sufficient depth of field to visually follow the observed fish in the vicinity of FLEX (Figure 1). Only the video footage that provided a clear view of FLEX and surroundings during towing were used in the assessment. Estimation of fish length was not possible due to the limitations of the recording methodology, which only provided a front perspective of the selection device and surroundings. The behaviour of each fish observed was assessed within four different behavioural stages: entry (1), approach (2), contact (3), and reaction (4) stages (Figure 3). At the entry stage, we assessed two different behavioural categories, body orientation and vertical position of the observed fish immediately after entering in the field of view of the camera. Body orientation was categorized with three mutually exclusive possibilities; facing forwards in the direction of towing, facing aft towards the codend, or sideways. Vertical position at entry was assessed relative to a horizontal plane projected from the top of the fluttering floats of FLEX. Fish entering inside the field of view below the projected plane were considered "in" the operative zone of the device; individuals swimming above the projected plane were considered "out" of the operative zone. The path followed by the observed fish from its first detection until it reaches the zone where FLEX was mounted was categorized within the approach stage. Predefined main reactions were "upwards", "steady", "downwards", "sideways", and "forwards". The paths followed by fish "in" the operative zone of FLEX that did not display any evident attempt to avoid contacting the device were categorized as "steady". Paths followed by fish out of the operative zone of FLEX other than downwards were not relevant for this study and therefore also categorized as "steady". More complex approaching paths were also considered by combining two or more of the defined main paths. Infrequent approaching paths (less than five observations) were aggregated into category "others". At the contact stage, it was evaluated to which component of the device the fish made first contact. Three mutually exclusive possibilities were predefined: "outlet", "net shield", and "no contact". The first reaction after contacting FLEX was evaluated at the reaction stage. Predefined main reactions were "upwards", "forwards", "downwards", "sideways", and "no reaction". As in the approach stage, more complex reactions were also categorized by combining two or more of the defined main reactions, and infrequent reactions (less than five observations) were aggregated into category "others". Those individuals that did not contact the device at all were categorized with "no reaction". Finally, the fate of the observed fish (selection outcome, escaped or caught) was recorded once the individual went out of

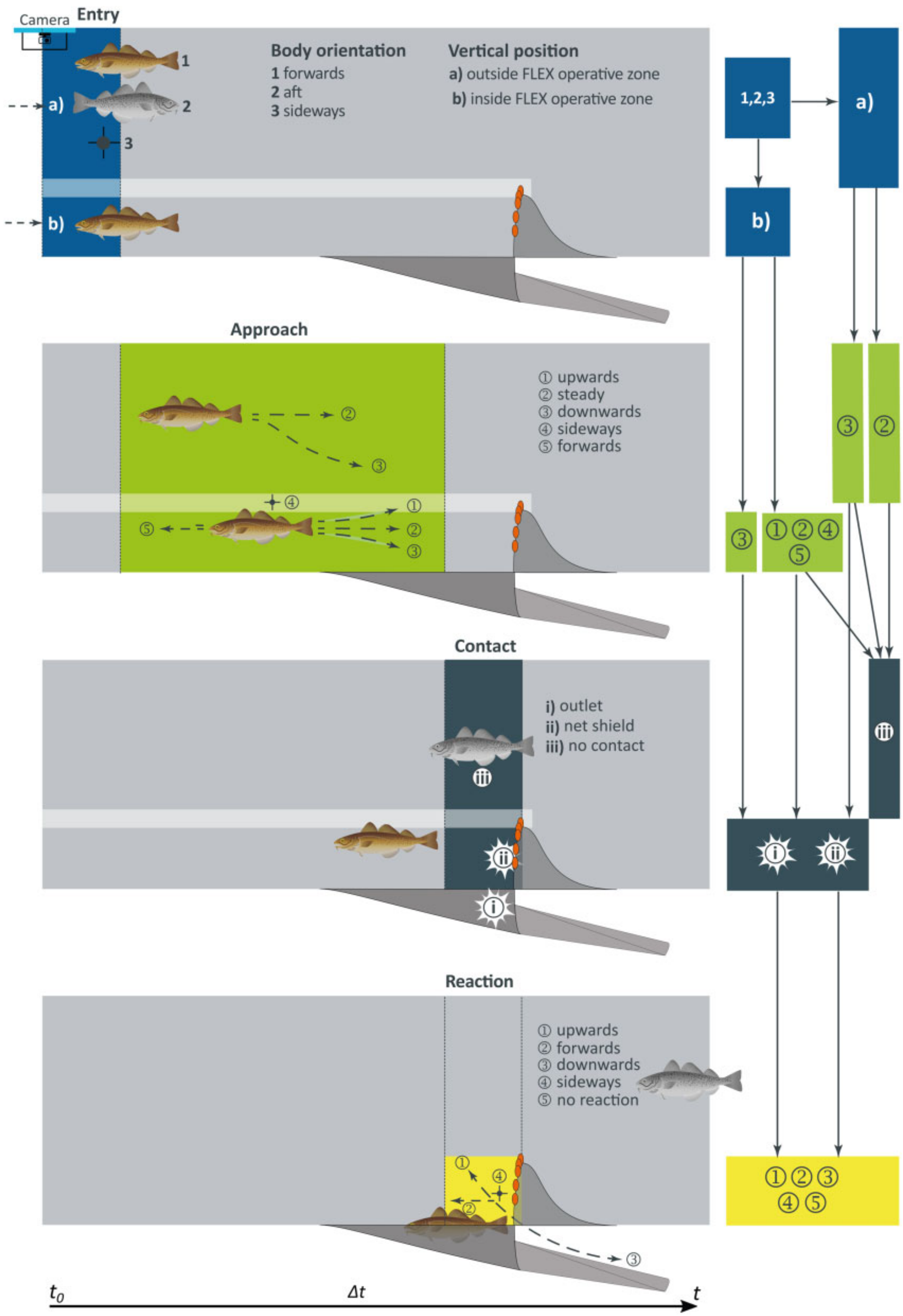

Figure 3. Graphical representation of the methodology applied in the analysis of video recordings for the assessment of fish behaviour in relation to FLEX. The plots illustrate the side view of the fore part of the extension piece where FLEX is mounted. Each plot shows a given behavioural stage highlighted by a coloured rectangle (blue = entry, green = approach, dark grey = contact and yellow = reaction). The behavioural events considered within behavioural stages are represented as items (possibilities) or broken arrows (paths). Horizontal pale band represents the projection of the horizontal plane used to determine if the observed fish enters the field of view "in" or "out" the operative zone of FLEX. Such band is visually projected by the observer from the point of view of the camera. Right margin: flow chart representing all possible connections among behavioural events from successive behavioural stages.

the camera focus. The duration of the selection process in seconds (Δt), from the first detection of the observed fish (t_0) until the moment when the selection outcome occurred (t) was also recorded (Figure 3).

The recorded events (either a possibility or path) displayed in the different behavioural stages characterize a specific behavioural sequence that could be related to the final fate of the observed fish.

Behavioural assessment was conducted following a systematic sampling procedure, whereby the first 30 roundfish and 30 flatfish that entered the field of view of the camera during towing were sampled. The information collected from each fish observed (including the behavioural sequence displayed and the resulting selection outcome) was pooled within and between hauls. The pooled data were arranged in a tree-like structure, departing from a root that represents the total number of individuals observed. The root is connected to behavioural nodes ($N_{Z,j}$, $j \in \{1, \ldots, J\}$), each counting the number of times a specific behavioural event j from stage $Z \in \{1, 2, 3, 4\}$ was observed. The nodes are arranged in four levels related to the four observation stages, with the branches of the tree representing the observed connections among nodes from successive levels. The leaves at the bottom of the tree contain the number of observed fish retained or escaped after following a given behavioural sequence of events.

Using the behavioural tree described above, we calculated two different statistics associated to each of the behavioural events recorded. First, the marginal probability (MP) for a given behavioural event j from behavioural stage Z to happen was calculated as:

$$\mathrm{MP}_{Z,j} = P(N_{Z,j}) = \frac{N_{Z,j}}{\mathrm{Root}}. \qquad (8)$$

In (8), $N_{Z,j}$ is the node representing the total number of fish that displayed the behavioural event j in behavioural stage Z, while Root is the total number of fish observed. Similarly, the conditional probability (CP) that event j from behavioural stage $B \in \{2, 3, 4\}$ could happen, given that the parent attribute k from behavioural stage $B - 1$ happened was calculated as:

$$\mathrm{CP}_{B,j} = P\left(N_{B,j} | N_{B-1,k}\right) = \frac{N_{B,j}}{N_{B-1,k}}. \qquad (9)$$

The total numbers of observed fish retained and escaped were also used to calculate an escape efficiency indicator based on video recordings:

$$nE^{*} = 100 \times \left(\frac{\sum_{i=1}^{h} nEscaped_i^{*}}{\sum_{i=1}^{h} \left(nEscaped_i^{*} + nRetained_i^{*} \right)} \right), \qquad (10)$$

where the sum of h is for hauls used for video observation. For a given group of species studied, the indicator nE^* accounts for the rate of observed individuals that escaped through FLEX, to the total individuals observed. Therefore, values of nE^* are equivalent to nE (7) and can be compared to assess the consistency of escape efficiency indicators obtained with the current video analysis and the analysis based on catch data.

The uncertainty derived from the limited number of fish observed by haul and the natural variation in fish behaviour occurring between hauls were accounted in (8)–(10) using the same bootstrap scheme applied in the previous section. In particular, the double bootstrap technique produced a total of 1000 artificial trees from which it was possible to estimate Efron confidence intervals (95%) associated to probabilities MP, CP, the indicator nE^*, and the average duration of the selection process, Δt.

The video sequences were observed using BORIS (Friard and Gamba, 2016), a free software specifically developed to investigate animal behaviour. Subsequent analyses were conducted using R (R Core Team, 2018), with data.tree (Glur, 2018) and DiagrammeR (Iannone, 2019) packages.

Results

Description of fishing operations and catch data

Altogether, 33 valid hauls were conducted during nine fishing days on two different fishing grounds, in the western Baltic Sea, respectively in ICES Subdivisions 22 and 24. The average haul duration was 84 min [standard deviation (SD) = 30.4] and the towing speed averaged 3.1 (SD = 0.42) knots (Table 1). In total, 15 hauls were conducted with the test gear mounted on the starboard side and 18 hauls were conducted with the test gear mounted on the port side. Catches consisted mostly of dab, cod, whiting, flounder, and plaice, together making up ~90% (in weight) of the total catch. These species were used in the data analysis. Dab was the most frequently occurring species in the catches with 10 339 individuals. However, hauls 20 and 26 were not used in the subsequent analysis for dab owing to problems with the sampling of dab lengths. The second most frequent species was cod with 8848 individuals caught, followed by whiting (*Merlangius merlangius*) with 3219 individuals, flounder with 2718 individuals, and plaice with 410 individuals.

Catch-data analysis

After excluding the hauls with fewer than 20 individuals for specific species, a total of 8, 17, and 21 hauls were used to analyse three flatfish species, plaice, flounder, and dab, respectively. The model estimated by (4)–(6) described well the length-dependent catch comparison rate between the test and control gears for the three species (Figure 4). The models yielded p-values >0.05, implying that the model fitted the experimental data sufficiently well (Table 2). The experimental catch comparison rates reveal that the catches of dab and flounder (the two most abundant flatfish species) were mostly caught in the control codend. The catch comparison curves (4) are significantly below 0.5 (the value expressing equal catch sharing probability) throughout the available length classes (Figure 4). This demonstrates the escape of flounder and dab through FLEX. Both curves exhibit similar patterns, with a slight and positive trend in the range of the most abundant lengths, dropping down across the largest, less abundant length classes. The catch comparison curve for plaice had higher uncertainty as a result of the smaller catches obtained for this species. For flounder and dab, FLEX's escape efficiency was estimated to be >75% for all lengths caught during the trials (Figure 4). For example, the escape efficiency for flounder at its MCRS (23 cm) was significantly >80%, a value slightly higher than for dab at the same length (78%). For plaice, the escape efficiency at MCRS (25 cm) was estimated at 66%, however, with high uncertainty because the 95% confidence band spanned >1–94%.

Altogether, 16 and 21 hauls were used to estimate FLEX's escape efficiency for cod and whiting, respectively. Visual

Table 1. Operational information of the hauls conducted during the experimental trials, and fish caught per species (in numbers) by each gear (test = *nT*, control = *nC*).

Date	Haul	Time (CET)	Duration (min)	Latitude	Longitude	Speed (knots)	Side	Cod		Whiting		Plaice		Dab		Flounder	
								nT	*nC*	*nT*	*nC*	*nT*	*nC*	*nT*	*nC*	*nT*	*nC*
12 November 2014	1	9:53	120	54°12N	011°58E	2.6	Starboard	0	0	0	0	0	0	0	2	0	0
12 November 2014	2	12:44	30	54°12N	011°45E	2.4	Starboard	0	0	2	6	0	0	0	4	1	5
12 November 2014	3	14:06	30	54°11N	011°50E	2.7	Starboard	1	0	0	0	0	0	0	1	2	0
12 November 2014	4	16:01	60	54°11N	011°56E	2.8	Starboard	1	1	0	0	0	0	1	1	0	0
13 November 2014	5	7:132	60	54°26N	011°25E	2.7	Starboard	15	2	68	16	4	9	261	589	22	176
13 November 2014	6	9:11	120	54°26N	011°25E	3.2	Starboard	9	10	69	52	7	30	349	1 534	83	483
13 November 2014	7	12:43	120	54°21N	011°24E	3.3	Starboard	5	5	35	39	7	27	269	1 377	55	325
13 November 2014	8	15:22	60	54°27N	011°25E	3	Starboard	4	1	40	27	3	9	218	696	26	126
14 November 2014	9	7:09	60	54°10N	011°49E	3.6	Portside	549	646	131	127	10	48	33	170	34	150
14 November 2014	10*	9:12	90	54°11N	011°50E	2.9	Portside	46	117	31	193	2	3	3	20	7	34
14 November 2014	11*	12:07	90	54°10N	011°51E	3.5	Portside	47	28	13	23	0	0	4	4	3	8
14 November 2014	12	14:07	90	54°10N	011°43E	2.6	Portside	128	181	25	25	7	31	39	172	18	74
15 November 2014	13	7:08	90	54°42N	013°08E	2.8	Starboard	60	86	1	4	0	3	0	5	4	24
15 November 2014	14	9:42	119	54°42N	013°07E	3.2	Starboard	169	153	1	1	0	3	0	0	2	8
15 November 2014	15	12:40	120	54°42N	013°07E	3.2	Starboard	76	80	1	3	0	3	1	0	4	9
16 November 2014	16	7:07	60	54°13N	011°33E	3.1	Starboard	0	0	3	11	2	1	0	1	0	1
16 November 2014	17	8:57	90	54°10N	011°428E	3.4	Starboard	6	2	28	33	0	1	2	20	1	17
16 November 2014	18	11:13	120	54°12N	011°48E	3.5	Starboard	2	1	3	1	0	0	3	4	0	4
16 November 2014	19	14:26	8	54°17N	011°55E	3.1	Starboard	0	0	2	4	0	0	10	61	0	0
17 November 2014	20	14:07	60	54°26N	011°25E	3.4	Portside	5	3	42	23	3	4	0	588	15	97
17 November 2014	21	15:47	60	54°23N	011°24E	3.1	Portside	1	15	12	53	3	5	47	169	11	26
18 November 2014	22	7:35	90	54°16N	011°39E	3.6	Portside	8	19	35	44	1	6	34	83	3	21
18 November 2014	23	10:11	113	54°20N	011°23E	2.1	Portside	12	11	93	106	1	30	150	1 213	31	357
18 November 2014	24	13:15	60	54°31N	011°19E	3.6	Portside	5	4	44	65	2	37	102	777	25	132
18 November 2014	25	15:05	60	54°31N	011°196E	3.8	Portside	7	2	44	53	25	5	163	661	22	92
19 November 2014	26	7:04	120	54°12N	012°00E	4	Portside	270	435	143	224	0	17	5	66	4	24
19 November 2014	27*	9:41	120	54°11N	011°51E	3.2	Portside	589	1 237	128	165	4	27	20	165	12	85
19 November 2014	28*	13:19	90	54°12N	012°00E	3.3	Portside	382	274	82	29	1	1	2	24	1	4
19 November 2014	29	15:25	75	54°11N	011°53E	3.5	Portside	689	692	239	334	0	3	16	23	0	7
20 November 2014	30	7:03	90	54°12N	012°00E	2.9	Portside	84	212	19	4	1	9	3	41	3	11
20 November 2014	31	9:21	120	54°11N	011°50E	2.9	Portside	773	170	138	52	3	4	7	59	5	15
20 November 2014	32	12:41	90	54°12N	012°00E	2.7	Portside	44	257	2	9	1	4	2	30	0	3
20 November 2014	33*	14:48	90	54°11N	011°53E	3.1	Portside	185	32	6	13	2	1	8	27	2	4
							Total	4 172	4 676	1 480	1 739	89	321	1 752	8 587	396	2 322

The column named "side" provides information about the side of the trawl the test gear was used. Towing speed averaged over continuous measurements automatically taken by the vessel. Videos collected from hauls with (*) were used for the behavioural analysis.

inspection of the catch comparison curves provided a good description of the length-dependent trend in the experimental rates for both species (Figure 5). However, the *P*-value obtained for whiting was <0.05 and, therefore, required a deeper investigation of the model fit. No systematic pattern was found in the length-dependent distribution of residuals around the predicted curve; therefore, the *p*-value of <0.05 was attributed to overdispersion. Because overdispersion does not affect the predictive capability of the model, we found it valid to describe the experimental catch comparison data for whiting by the model. With average values between 0.4 and 0.5, the catch comparison curves predicted for cod and whiting exhibit nearly equal catch shares between both gears (Figure 5). For cod, the average catch comparison curve dropped below $CC = 0.5$ for sizes smaller than 46 cm, whereas the curve estimated for whiting dropped below $CC = 0.5$ within the range of lengths between ∼15 and ∼30 cm. However, there was no statistical evidence of escape through FLEX of any sizes for both roundfish species, because 0.0 escape ($CC = 0.5$) was within the 95% confidence bands for all length classes (Figure 5).

The values of the escape efficiency indicators obtained from the catch data are consistent with the estimated catch comparison curves. The reference lengths used to calculate nE_{-} and nE_{+} were the species MCRS, except for dab. For this species, we used the same reference length as for flounder (Table 3). The highest values were obtained for flounder, with escape efficiencies ∼85% regardless of the indicator considered. Lower values were obtained for dab, especially considering the nE_{+} indicator, ∼5 percentage points lower than the species nE_{-}, however, attending to the wide overlapping of the indicator's confidence intervals, such difference cannot be considered significant. The indicators for plaice resulted in the lowest and least accurate values for the three flatfish species studied. The *nE* indicator for the roundfish species was very similar and below 15%. The average values of nE_{-} obtained for both species (∼18%) was higher than the nE_{+} for cod (∼9%) and whiting (∼5%), indicating higher, but not significant escape efficiency for small roundfish.

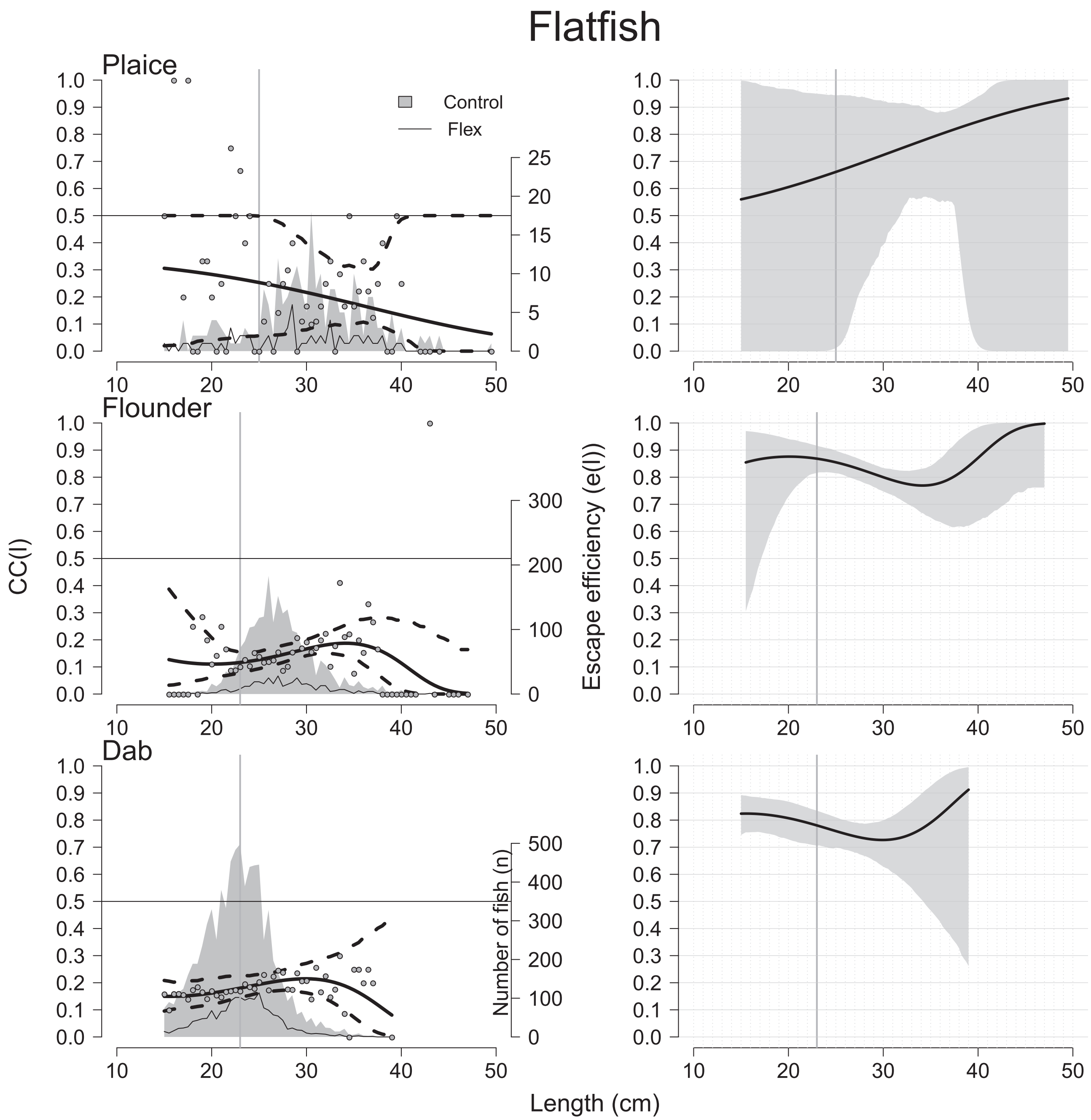

Figure 4. Experimental catches and model results for the three flatfish species analysed [plaice (top), flounder (middle), and dab (bottom)]. The left column shows the catch comparison plots. Grey-filled circles represent experimental catch comparison rates per length class (CC_l) (2). The solid thick line represents the estimated catch comparison curve ($CC(l)$) (4–6); dashed lines represent their respective 95% confidence intervals. Total numbers of fish caught per length class in the test gear (solid thin line) and control gear (grey area) are plotted in the background. The right column shows the predicted escape efficiency curves of FLEX ($e_{flex}(l)$, solid line) and associated 95% confidence intervals (grey band). Vertical grey lines represent species MCRS.

Assessment of fish behaviour based on video observations

A total of 11 hauls had the camera mounted in the position shown in Figure 1. Clear images were obtained in hard-bottom fishing grounds. However, towing on soft bottoms—where most of the flatfish catches occurred—led to dense clouds of sediments, which drastically reduced the visibility and sharpness of the video footage. Therefore, only hauls 10, 11, 27, 28, and 33 (Table 1) could be used for simultaneous assessment of flatfish and roundfish behaviour. Four out of these five hauls had a towing duration of 90 min, while haul 27 had a towing duration of 120 min (Table 1). Turbidity associated to soft grounds impeded reaching the predefined number of 30 flatfish observations per haul and the observations of 12, 8, 30, 5, and 24 individuals respectively were obtained throughout the entire tows. Observations on roundfish reached the predefined number of 30 individuals per

Table 2. Fit statistics for the escape efficiency models for the three flatfish species and the two roundfish species analysed (d.o.f = model degrees of freedom, *n* hauls = number of hauls included in the analysis).

Species	*p*-Value	Deviance	d.o.f	*n* hauls
Plaice	0.60	51.79	55	8
Flounder	0.69	53.12	59	17
Dab	0.96	29.86	45	21
Cod	0.49	101.64	102	16
Whiting	$<$0.01	85.20	54	21

haul and were all collected during the first 50 min of towing. The images obtained were not sufficiently clear to identify fish species accurately; therefore, the assessment was conducted considering two groups of species: flatfish and roundfish. Altogether, 79 flatfish and 150 roundfish were successfully observed, of which 67 [$nE^* = 84.8\%$ (95% confidence interval: 64.3–94.0%)] and six [$nE^* = 4.0\%$ (1.3–8.0%)] individuals escaped through FLEX, respectively. Most of the observed selection processes (Δt) lasted for <2 s, being 35% faster for flatfish than for roundfish (Table 3). Most of the observed flatfish (62 individuals, ~78.5% of the total observed) entered the field of view facing aft towards

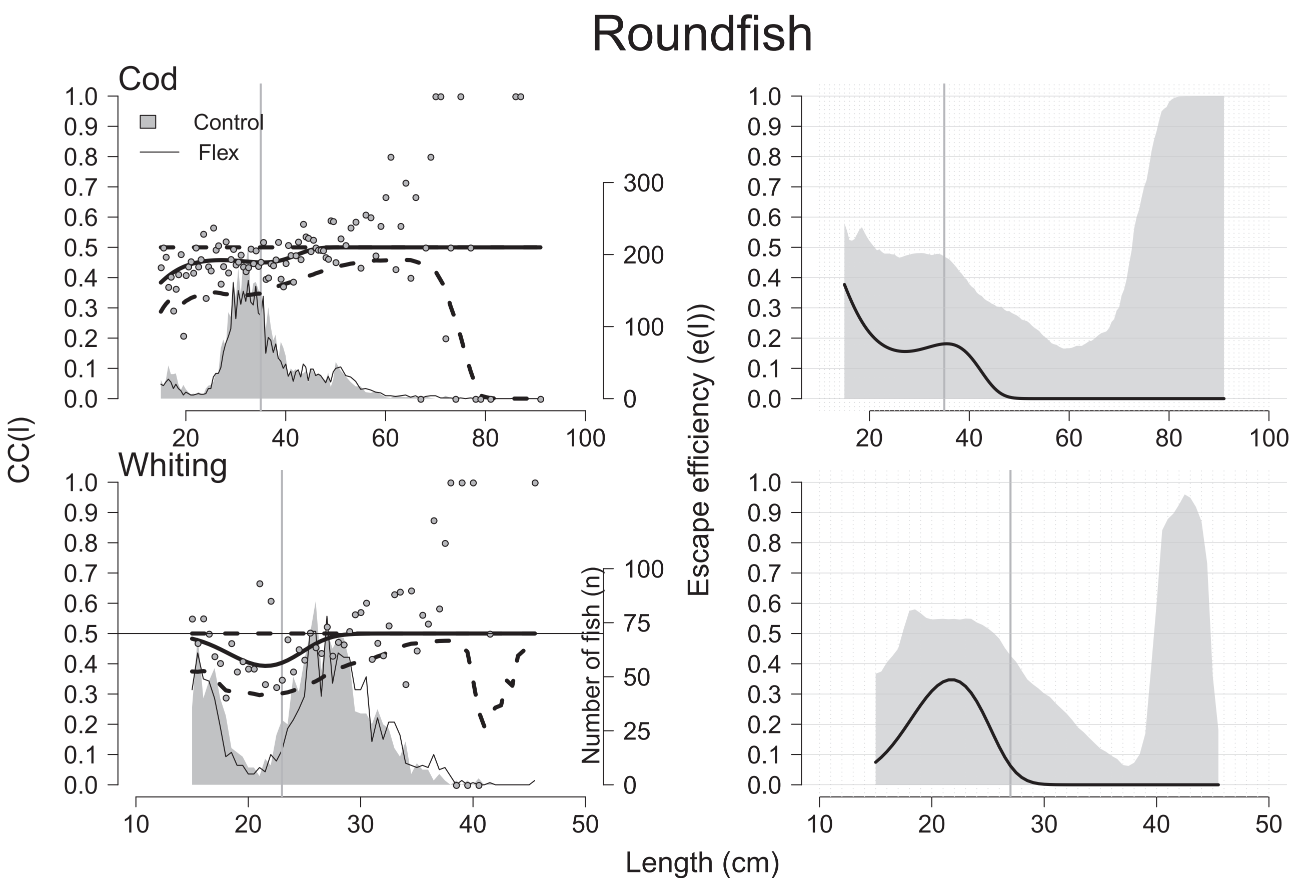

Figure 5. Experimental catches and model results for the two roundfish species analysed [cod (top) and whiting (bottom)]. The left column shows the catch comparison plots. Points represent experimental catch comparison rates per length class (CC_l) (2). Solid thick lines represent the estimated catch comparison curve ($CC(l)$) (4–6); dashed lines represent their respective 95% confidence intervals. Total numbers of fish caught per length class in the test gear (solid thin line) and control gear (grey area) are plotted in the background. The right column shows the predicted escape efficiency curves of FLEX ($e_{flex}(l)$, solid line) and associated 95% confidence intervals (grey band). Vertical grey lines represent species MCRS.

Table 3. Indicators for escape efficiency of FLEX for the different species studied.

Species	Ref length (cm)	nE_-	nE_+	nE	nE^*	Δt
Dab	23	80.66 (72.96 – 86.09)	75.64 (70.51 – 80.14)	78.09 (71.74 – 82.96)	84.81 (64.28 – 93.96)	1.24 (0.88 – 2.24)
Flounder	23	84.97 (77.16 – 91.59)	83.11 (79.13 – 86.17)	83.27 (79.49 – 86.45)		
Plaice	25	62.26 (0 – 91.67)	76.80 (54.46 – 88.43)	73.50 (41.57 – 88.28)		
Cod	35	17.70 (0 – 46.24)	8.84 (0 – 35.59)	14.11 (0 – 41.65)	4.00 (1.31 – 8.00)	1.97 (1.54– 2.53)
Whiting	27	18.37 (0 – 43.99)	4.45 (0 – 37.54)	13.35 (0 – 42.17)		

The three first indicators, nE_-, nE_+, and nE, were calculated by applying (7). The fifth and sixth columns of the table contains the escape indicators obtained from the video observations (nE^*), and the average duration of the observed selection processes (Δt) in seconds. Efron confidence intervals (95%) in brackets.

the codend, while 11 and 6 individuals entered facing forwards and sideways, respectively. Contrary, most roundfish (109 individuals, ∼73% of the total observed) entered the field of view facing forwards, while 25 and 16 individuals entered heading aft and sideways, respectively. Altogether, 37 fish (2 flatfish and 35 roundfish) entered the field of view swimming outside the operative zone of FLEX. From these, only two roundfish and one flatfish interacted with FLEX, and all of them were finally retained in the codend. The behaviour of these fish was considered of minor interest in the assessment of FLEX efficiency and therefore the related branches were removed from the resulting trees. To further reduce the dimensions of the trees and therefore to improve their readability, information relative to fish body orientation was also removed (Figures 6 and 7). Raw trees for flatfish and roundfish containing the information of fish orientation and counts of fish outside FLEX active zone are found in Supplementary Figure S2 and S3.

Only 10 out of the 77 flatfish individuals swimming in the operative zone of FLEX ended in the codend. On the other hand, three quarters of the total flatfish observed (59 individuals) approached the device with no evident avoidance behaviour, contacted the device directly at the outlet, and escaped with no evident reaction after contact [MP = 74.7% (57.9–86.5%)] (Figure 6). Seven individuals that steadily approached and contacted the outlet, reacted to the contact actively, and, as a result, four of them ended in the codend. Six individuals that entered in the operative zone of FLEX approached the device swimming upwards [CP = 7.8 (0.0–19.4%)], but none of them avoided contacting the device; four out of the six contacted the net shield [CP = 66.7% (0.0–100.0%)], but such contact did not stimulate a downwards reaction; therefore, all ended up in the codend. The remaining two contacted the outlet [CP = 33.3% (0.0–83.3%)], and one of them escaped. Three flatfish within the active zone approached the device swimming sideways and one did it swimming downwards. These four fish were aggregated into the node "others" at the approach stage [MP = 5.2% (0.0–14.0%)]. All these four fish escaped through FLEX.

The behavioural tree for roundfish resulted leafier than the flatfish tree, indicating more behavioural variation in relation to the selection device. Three quarters of the observed roundfish (115 individuals) entered the field of view of the camera swimming in the operative zone of FLEX. Half of these fish approached FLEX swimming upwards [55 fish, CP = 47.8% (35.1–62.7%)] or other less frequent approaching paths categorized as "others" [3 fish, CP = 2.6% (0.0–6.3%)]. All of these fish ended in the codend, having contacted or not the device. The other 57 individuals steadily approached the device and 34 of them contacted the net shield. Such contact prompted an upwards reaction in 25 of them directing the fish towards the codend [MP = 16.7% (8.7–25.3%)]. Five out of the six observed roundfish escapees occurred when fish steadily approached and contacted the outlet, displaying infrequent reactions after contact categorized as "others" [MP = 1.3% (0.0–5.3%)] or no reacting at all [MP = 2.0% (0.0–4.7%)]. Of those 57 fish that approached FLEX steadily, 22 contacted the outlet and 17 of them avoided passing through it by performing upwards [MP = 7.3% (2.7–12.7%)] or forwards–upwards [MP = 4.0% (0.0–9.3%)] reactions.

Due to the impossibility to obtain escape efficiency indicators by species from the video observations, the comparison with the indicators calculated from the catch data only could be done relatively and by groups of species (Table 3). For flatfish, the average

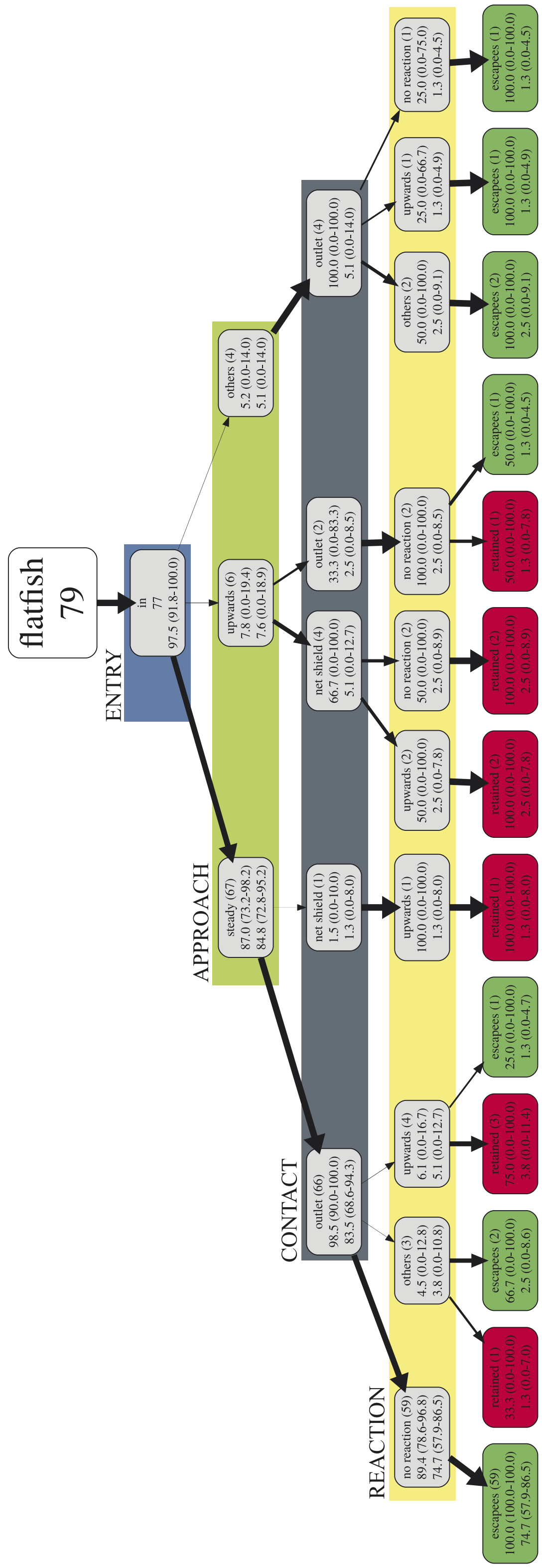

Figure 6. Behavioural trees resulting from the analysis of flatfish video observations. White box represents the root of the tree showing the total number of fish observed. Behavioural events are represented as grey nodes and organized in four different levels related to the behavioural stages. Red boxes represent leafs with counts of fish caught after following a specific sequence of behavioural events, while green boxes represent leafs with counts of fish that escaped through FLEX. The first text line within each node/leaf contains the label of the event plotted and the number of fish observed performing such event (in brackets). The second and third lines show the CP and MP with 95% confidence intervals (in brackets).

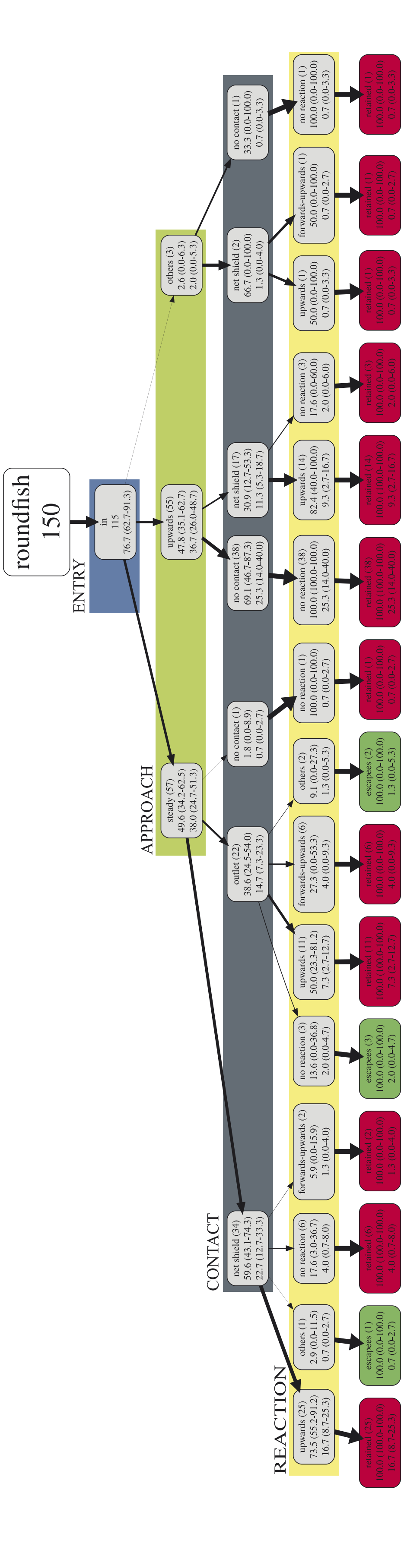

Figure 7. Behavioural trees resulting from the analysis of roundfish video observations. White box represents the root of the tree showing the total number of fish observed. Behavioural events are represented as grey nodes and organized in four different levels related to the behavioural stages. Red boxes represent leafs with counts of fish caught after following a specific sequence of behavioural events, while green boxes represent leafs with counts of fish that escaped through FLEX. The first text line within each node/leaf contains the label of the event plotted and the number of fish observed performing such event (in brackets). The second and third lines show the CP and MP with 95% confidence intervals (in brackets).

*nE** value obtained was very similar to the average *nE* value obtained for flounder (∼85 vs. ∼83%, respectively). Although the estimated percentile confidence intervals overlap each other, the average *nE** obtained for roundfish was considerably lower than the average *nE* values of cod and whiting (∼4% vs. ∼14% and ∼13%, respectively).

A selection of fish observations can be found in the Supplementary Material (Supplementary Footages S1–S3). In addition to the observations on fish behaviour in relation to FLEX, the videos also showed that the device consistently released benthic debris entering the trawl (Supplementary Video S4).

Discussion

This study demonstrates the applicability of a method for quantitative analysis of fish behaviour, which can be used to supplement catch-data analyses of performance of selection devices in trawl gears.

Results from this analysis are presented graphically by the so-called behavioural trees (Figures 5 and 6). Behavioural trees provide the researcher with several layers of information regarding fish behaviour in relation to the tested device; while an overview reveals general behavioural patterns and relationships between these patterns and the fate of the fish being selected, a detailed visualization provides information regarding the average probability of occurrence (marginal and conditional) of individual behavioural events. Furthermore, the method provides confidence intervals based on the same bootstrap resampling scheme applied in the catch comparison analysis, therefore properly accounting for different sources of variation potentially influencing fish behaviour in relation to the selection process. To the best of our knowledge, this is the first time the bootstrap scheme usually applied in selectivity analysis is adapted and incorporated into behavioural analysis based on video recordings.

The method has a broad scope of applicability to address questions regarding the functioning of selection devices currently in use. For example, the performance of square mesh panels or grids (Catchpole and Reville, 2008) is usually assessed using models able to quantify the probability that fish efficiently contact the device, and the size selection properties of the device (Zuur *et al.*, 2001; Alzorriz *et al.*, 2016; Santos *et al.*, 2016). However, these models do not provide further information regarding how fish contact the selection device, and which of the potential contact modes could be regarded as "efficient" in relation to the selection process. Our method could provide quantitative answers with uncertainties to such questions, providing guidance for further developing the intended selection.

In this study, we applied the proposed method to assess fish behaviour in relation to a flatfish excluder (FLEX), which was developed and tested in the cod-directed trawl fishery in the Baltic Sea. The potential of using fish behaviour to reduce bycatch remains largely unexploited in the Baltic Sea trawl fishery, and FLEX is probably one of the few selection devices developed in the region whose functioning fully relies upon species' behaviour. During the development phase, very limited quantitative behavioural information was available to guide the conceptual design of FLEX (Krag *et al.*, 2009a). The results from the behavioural analysis obtained in this study revealed that the assumptions regarding expected differences in the behaviour of flatfish and roundfish were valid. Moreover, the behavioural results obtained help to understand how fish interact with the device and provide quantitative information that can be used for future developments.

During the experimental sea trials, most flatfish catches occurred in hauls conducted on muddy or sandy fishing grounds. In these hauls, mud clouds entered the trawl reducing the visibility of the videos recorded, therefore limiting the possibilities to obtain sharp footage of fish behaviour. Attempting to maximize such possibilities, we adopted a systematic sampling scheme, whereby the behaviour of the first 30 flatfish and 30 roundfish observed per haul was evaluated. Due to the uneven presence of mud clouds, flatfish observations were drawn at different towing times. However, all roundfish observations were collected in the first 50 min of towing. Although the knowledge of the swimming capabilities of fatigued fish entering and escaping from a trawl is limited (Ingólfsson *et al.*, 2007), it could be argued that individuals approaching FLEX during the first half of the haul could be less fatigued than those observed during later stages, potentially influencing behavioural responses to the device and the final outcome of the selection process. We argue that such a potential effect would be of concern if observed fish tend to hold their position to avoid the device, maintaining a swimming speed equal to or greater than the towing speed (Krag *et al.*, 2009a). However, the short duration of the selection process observed for roundfish [$\Delta t = 1.97$ s (1.54–2.53)] indicates that the presence of FLEX induced, if any, low-demanding avoidance responses that might be affordable even for exhausted fish (Hannah and Jones, 2012). In any case, the presence of the device did not interrupt their travel towards the codend. An ad hoc inspection of roundfish behaviour during the later stages of towing showed no obvious difference between towing time and roundfish behaviour in relation to FLEX.

Based on catch comparison data from 33 experimental hauls, it was demonstrated that using FLEX greatly reduced the number of flatfish that otherwise would have entered the codend, providing a proof of efficiency required for the device before being considered for commercial adoption. The analysis of catch data from dab and flounder revealed an average escape efficiency of FLEX above 75%, independent of the fish size (Figure 4 and Table 3). Small catches of plaice were obtained during the experiment, resulting in an inaccurate estimate of escape efficiency for this species (Figure 4). However, having noted the low accuracy achieved, and considering the very similar results obtained for flounder and dab, there is no statistical evidence to reject the hypothesis that FLEX could perform for plaice as it did for the other two flatfish species.

Discrepancies between quantitative results from catch-data analysis and video observations can restrict the usability and interpretation of the latter source of information (Krag *et al.*, 2009a). In this study, the close average values and overlap of confidence intervals of the nE indicators estimated for dab and flounder based on the catch-data analysis ($nE = \sim78$ and $\sim83\%$, respectively), and those from the estimated flatfish indicator based on video observations ($nE^{*} = \sim85$) demonstrate the validity of the behavioural analysis to assess escape efficiency of FLEX visually.

The behaviour of flatfish in trawl gears has been mostly studied during initial phases of the catch process in the fore part of the gear (Bublitz, 1996; Ryer, 2008; Underwood *et al.*, 2015); however, less effort has been invested in assessing flatfish behaviour in the trawl body. Krag *et al.* (2009a) quantified vertical preferences and behavioural responses of flatfish in the extension piece of a trawl, using a rigid separator grid that divided the codend into three vertically stacked compartments. Because the part of the trawl investigated, the catches and the behavioural events recorded were similar, the results reported in Krag *et al.* (2009a) are comparable to those presented in the current study. In Krag *et al.* (2009a), 83% of the observed flatfish were retained in the lower compartment of the separator grid, which is nearly the same value as the nE^{*} value obtained in this study. Our behavioural analysis shows that flatfish are inclined to escape through FLEX without performing avoidance reaction before or after contacting the device. This is also consistent with the findings from Krag *et al.* (2009a), which reported that most flatfish approached the separator grid calmly, without showing evident avoidance reactions before contacting the grid, or panic after passing through it. Moreover, most of the flatfish observed in this study (78%) entered the field of view heading aft towards the codend, a value which is consistent with the 70% reported in Krag *et al.* (2009a) or the 55% reported in He *et al.* (2008). The results obtained in Krag *et al.* (2009a), He *et al.* (2008), and the current study demonstrate that flatfish tend to travel across the aft of the trawl swimming near to the bottom panel of the trawl and oriented towards the codend, without significantly altering their swimming behaviour even when interacting with selection devices placed in their way, at least if such devices do not substantially impede the passing through them. These findings can be useful for future developments of flatfish selection devices located in the trawl body.

Previous studies demonstrated that cod can also be found swimming low at the trawl mouth (Main and Sangster, 1985; Beutel *et al.*, 2008), trawl body (Ferro *et al.*, 2007), and even in the aft end of the trawl (Krag *et al.*, 2009a,b; Melli *et al.*, 2019). Therefore, the potential for overlapping in the vertical distribution of cod and flatfish challenged the development of FLEX. The behavioural analysis demonstrated the need to take such concern seriously, since three quarters of the observed roundfish entered the extension piece through the lower layer of the water column, becoming available for FLEX. Our strategy to avoid losses of marketable cod was to connect a simple deterrent device consisting of a rectangular net shield with small fluttering floats to the outlet (Figure 1). This device was inspired by the findings in Herrmann *et al.* (2015), who demonstrated that the efficiency of escape windows can be improved by provoking upwards swimming reactions of Baltic cod with similar stimulation techniques. The behavioural analysis showed that nearly half of the observed roundfish swimming in the operative zone of FLEX detected the device in advance and displayed upwards-avoidance reactions. This result indicates that the use of stimulation devices in the design of FLEX successfully contributed to reduce potential roundfish escapes. Upwards-avoidance reactions were also the most observed roundfish reaction after contacting FLEX.

Although FLEX's escape efficiency for roundfish was estimated to be low and not significantly different from 0.0%, the comparison among catch-based indicators and the analogous indicators based on video recordings revealed a discrepancy between the nE value calculated for cod and whiting, and the lower nE^{*} value calculated for roundfish. One explanation for this discrepancy could be a potential effect of device's visibility on the roundfish escape efficiency. It was observed that muddy waters resulting from trawling on soft grounds significantly reduced visibility of FLEX. Under low visibility conditions, it is plausible that the stimulating effect of the net shield and fluttering floats of FLEX could be lower than when those device's elements are highly visible for the approaching fish. Following this argumentation, a reduced stimulation effect due to low visibility could increase the probability for roundfish to contact the device and escape. The inability of the camera system used in this study to collect fish observations under low visibility could therefore bias the estimation of nE^* to lower values. Another explanation is related with roundfish escapees observed during the haul-back, which were not accounted in the behavioural analysis. When bringing the trawl to the vessel, it was observed that some roundfish swam from the codend to the front of FLEX, contacted the outlet near the surface and escaped. These events could be related to the complex manoeuvres conducted by the vessel to retrieve the experimental DBT used in this study. In particular, the vessel had to stop towing before initiating the haul-back, and the process itself took double the time required for a standard trawl, since the crew only could handle the catches of each side one after the other. We speculate that the losses of roundfish observed during the haul-back could be largely avoided by using standard trawls in twin-trawl configuration, a common set-up in Baltic Sea trawl fisheries. Twin trawls are brought on board simultaneously and at towing speed, drastically reducing the duration and complexity of the haul-back process. However, this option was not available due to the lack of twin-trawl facilities on board the research vessel. In any case, since the selection of FLEX occurs in a very specific location at the aft part of the trawl, we argue that the escape efficiency of the device quantified in this study during towing should not be affected by the type of trawl used, at least under same fishing conditions and towing speeds.

Although the difference was not significant, the test codend caught on average fewer small-sized roundfish than the control codend. This was reflected in the average escape efficiency curve, which was >0.0% for smaller length classes. Previous studies quantitatively demonstrated that smaller gadoids tend to swim lower in the trawl body (Melli *et al.*, 2019). Therefore, it could be speculated that the probability of encountering FLEX is higher for small individuals of these species, consequently increasing their chances to escape relative to larger individuals. Since it was not possible to accurately determine the size of the fish observed in the video, this hypothesis could not be investigated in the current study. However, fish size could be obtained in future experiments by using other camera technologies, such as stereo cameras. The resulting size information could be added to the behavioural trees enabling investigations regarding length-dependent behavioural patterns influencing the performance of selection devices like FLEX.

FLEX was conceived as an alternative to the industry-driven FRESWIND device (Santos *et al.*, 2016). FRESWIND exploits differences in fish morphology to largely avoid flatfish catches without compromising the catchability of marketable sizes of cod. However, the device is relatively complex and includes rigid grids that fishermen might be reluctant to use, especially on vessels not equipped with stern ramps (Graham *et al.*, 2004). Furthermore, disabling FRESWIND requires changing the trawl's complete extension piece, limiting the fishermen's flexibility in adapting their fishing strategies on short notice. Therefore, despite the positive results obtained with FRESWIND (Santos *et al.*, 2016), we identified the need for a simpler and more adaptive device without rigid parts, able to reduce flatfish bycatch in the Baltic Sea trawl fishery. Our results demonstrate that it is possible to release a significantly large fraction of flatfish entering a trawl gear by applying a simple and adaptive technical modification in front of the codend. The possibility to easily activate or deactivate FLEX on board allows a dynamic control of trawl-species selectivity, even between hauls. This feature could help fishers adapt their exploitation patterns to changing scenarios in the fishery, which could be an advantage in fisheries regulated by limiting catch quotas or as adaptation to market requirements. Although the study was conducted in the Baltic Sea, the FLEX concept could also be of interest to fishers in other regions with a similar need for adaptive reduction in flatfish bycatch.

Other simple and adaptive devices have been recently proposed to address specific bycatch problems in trawl fisheries. For example, Kynoch *et al.* (2015) demonstrated that the bycatch of skate and sharks can be reduced significantly by removing the tickler chain usually connected to the mouth of demersal trawls. Another adaptive species-selection device proposed recently is FLEXSELECT (Melli *et al.*, 2018), a removable counter-herding device to reduce the bycatch of fish in crustacean trawl fisheries. The effectiveness of these two devices and FLEX mostly depends on species-specific behavioural patterns. It is known, however, that fish behaviour can be largely influenced by intrinsic or environmental factors (Claireaux *et al.*, 1995). Therefore, it should be expected that the efficiency of behavioural devices varies according to variations in fish and/or fishing conditions (Winger *et al.*, 2010). The method for behavioural analysis presented here could be also helpful to quantify and understand variations in the effectiveness of behavioural devices due to such variations in fish and fishing conditions.

Supplementary data

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

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Data availability

The datasets generated and analysed during the current study are available from the corresponding author on request.

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