

Escape panels in trawls: does placement matter when every individual contacting the panel can escape?

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Abstract

Escape panels are one of the bycatch reduction devices most used in trawl fisheries but their efficiency rely on fish actively contacting the panel to escape. To investigate if contact behaviour changes at different panel placements, we tested a 300 mm square mesh panel placed in the upper panel of the codend at 3, 4 and 7 m from the codline. Seven competing models of contact probability were fitted to the empirical data. Based on the results, we inferred that panel placement significantly affects escape efficiency due to a change in type of contact behaviour. Cod (*Gadus morhua*) showed a contact increasing with length when the panel was closest to the codline, while contact probability decreased with length at the other placements. Similarly, contact probability for plaice (*Pleuronectes platessa*) was found to increase with length at 3 and 4 m, whereas a length-independent contact best represented the data at 7 m. Finally, *Nephrops (Nephrops norvegicus*) had in general low contact probability. The results provide new knowledge regarding species and placement-dependent panel escape.

Key words: escape panel, escape window, panel placement, contact probability, fish behaviour

1. Introduction

Escape panels, otherwise known as escape windows, are one of the most used bycatch reduction devices in mixedspecies trawl fisheries (Catchpole and Revill 2008; Kennelly and Broadhurst 2021). They are typically made of larger mesh sizes than the adjacent netting, either in the standard mesh orientation (diamond) or turned 45 degrees (square) to increase mesh openness (Kennelly and Broadhurst 2021). These panels have been inserted in several sections of the trawl, that is, the codend (e.g., Broadhurst and Kennelly 1997; O'Neill et al. 2006; Madsen et al. 2021), extension (e.g., Krag et al. 2008; Fraser and Angus 2019) or tapered section (e.g., Briggs 2010; Bayse et al. 2016), as well as in different positions within the netting geometry, for example, in the top, side or bottom panel (e.g., Madsen et al. 2012; Santos et al. 2016; Fraser and Angus 2019). Their popularity derives from altering only a small section of conventional trawls, thus maintaining many existing operational characteristics, and having a generally low cost and impact on commercial catches (Brčić et al. 2018; Kennelly and Broadhurst 2021). Escape panels are frequently adopted when codend size-selection is not sufficient to reduce unwanted species and sizes without causing the loss of one or more target species (Kennelly and Broadhurst 2021). For example, escape panels have been made mandatory in many crustacean fisheries (e.g., Broadhurst 2000; Catchpole and Revill 2008) as well as mixed finfish fisheries (e.g., Herrmann et al. 2015; Cuende et al. 2020). Depending on the multi-species catch goals within a fishery, escape panels can be designed to improve the size-selection of commercial species (i.e., only undersized individuals contacting the panel can escape; hereafter referred to as type I) or to minimize overall catches of unwanted species (i.e., every individual contacting the panel can escape; hereafter referred to as type II).

A panel that is designed to reduce catches of undersized individuals (type I), while retaining commercial sizes, has typically a mesh size close to what is used to target that species in the area, but with a different orientation to maintain mesh openness. For example, Brčić et al. (2018) documented that a 50 mm square mesh panel (SMP) partially improves the sizeselection of the target species in the Mediterranean mixed bottom trawl fishery, which uses a 50 mm diamond mesh codend. Madsen et al. (2002) demonstrated that a 120 mm SMP inserted on the top netting within the codend catch accumulation zone reduces undersized catches of cod (Gadus morhua) in the demersal Baltic fishery targeting flatfish and cod with a 105 mm diamond mesh codend. Similarly, Cuende et al. (2022) showed that combining a 80 mm SMP inserted in the bottom netting of the codend extension with a 80 mm diamond mesh codend improves the gear size-selectivity for the target species, hake (Merluccius merluccius).

In contrast, an escape panel designed to minimize catches of an unwanted species (type II), regardless of size, adopts much larger mesh sizes than the adjacent netting. For example, Fraser and Angus (2019) developed a 300 mm SMP inserted in the bottom netting of the 120 mm diamond mesh codend and substantially reduced cod catches from the mixed whitefish fishery in the North Sea. Bayse et al. (2016) demonstrated that a 330 mm diamond mesh panel inserted in the bottom panel of a 50 mm diamond mesh trawl body can be used to effectively target silver hake (*Merluccius bilinearis*) while keeping catches of regulated groundfish species below 5%. Furthermore, Madsen et al. (2010, 2012) developed a four-panels codend (i.e., SELTRA box) with a 370 mm SMP inserted in the top, and substantially reduced catches of cod in the Kattegat *Nephrops* (*Nephrops norvegicus*) directed fishery, with only minimal losses of target catch.

Although several studies have investigated which design parameters affect the efficiency of escape panels, most of these tested type I panels (i.e., size-selective). In particular, panel placement with respect to the codline is one of the parameters specified in the legislation of escape panels (Krag et al. 2016). It is generally accepted that the escape efficiency of a panel will increase the closer it is to a catch accumulation zone (Graham and Kynoch 2001; Herrmann et al. 2015). Indeed, regardless of their position, escape panels rely on fish altering their general swimming path inside the trawl, which is typically parallel to the towing direction (Glass 2000) and actively contacting the panel to escape. This is more likely to happen in areas where fish hold stationary (e.g., junction between tapered section and codend) or when they do not have the option of drifting deeper into the trawl (e.g., codend; Graham and Kynoch 2001; Winger et al. 2010; Herrmann et al. 2015). However, panel position was not found to have a significant effect for all species (e.g., whiting; O'Neill et al. 2006) nor was the effect consistent at different positions (e.g., between 6 and 12 m from codline; Drewery et al. 2010). Some studies have concluded that the difference in efficiency is due to panel positions being within and outside the catch accumulation zone (Herrmann et al. 2015). It is possible that panel placement plays a more important role for type I panels, where multiple attempts and optimal contact angles may be necessary for a fish to escape (Cuende et al. 2020). In contrast, type II panels should release individuals at first contact and almost irrespective of contact angle, thus being potentially less affected by their distance from a catch accumulation zone.

To investigate this hypothesis, we tested three different positions of a 380 mm SMP in a SELTRA codend, hereafter referred to as SELTRA 300 according to the regulations for the Nephrops-directed fishery in the Kattegat and Skagerrak. This fishery uses demersal trawls designed to catch various roundfish and flatfish species along with Nephrops (Frandsen et al. 2011). However, the critically low level of the cod stock in these areas has led to the implementation of the SELTRA 300, a 3 m long SMP located at 3-6 m from the codline, aimed at minimizing catches of cod (BEK No. 1249, 24 August 2020). However, due to concerns regarding the loss of commercial catches of Nephrops and valuable fish bycatch (e.g., plaice, Pleuronectes platessa), the panel was subsequently moved at 4-7 m from the codline (BEK No. 2513, 13 December 2021). To determine if panel placement has an effect on the efficiency of this type II SMP, we collected selectivity data with the panel inserted at 3-6, 4-7 and 7-10 m from the codline, for the three

main species of interest: the target crustacean (Nephrops), the unwanted roundfish (cod) and the wanted flatfish (plaice). Moreover, by using models that assume a given contact type, we tested hypothetical scenarios of contact probability (i.e., no contact, length-independent contact and increasing and decreasing contact with length) and investigated if an eventual difference in the efficiency of the panel can be explained by a change in the type of contact at different panel placements. A number of previous studies investigating type II panels have assumed or approximated the contact probability to be length-independent (Zuur et al. 2001; O'Neill et al. 2006; Sistiaga et al. 2018) and only recently-developed models have allowed for the contact parameter to vary with size (Krag et al. 2014; Herrmann et al. 2018). Nonetheless, lengthdependent contact has been assumed to be species-specific and no studies, to the best of our knowledge, have investigated its relation to panel placement.

2. Materials and methods

2.1. Gear description

The experimental trials were conducted using a Combi trawl with a 40 m long footrope, 10 m long wings, 420 meshes in circumference at the trawl mouth and a trawl body with a stretched length of approximately 26 m (excluding codend) made of two panels in 80 mm (nominal mesh) netting. The two panel tapered section of the trawl was directly joined with a four panel SELTRA 300 codend by connecting a circumference of 140 meshes in the body to 100 meshes in the codend, as it is common practice in the fishery. The codend was made of double 3 mm polyethylene (PE) 90 mm diamond netting and had 25 meshes in each of the four panels, with one mesh on each side used to create the selvedge between panels. Thus, the codend had a circumference of 92 open meshes (Table 1). The codend included a 3 m long panel with a nominal mesh size of 300 mm square mesh (380 mm actual size) made of green PE 4 mm single twine. In all experiments, the forward end of the panel was placed at 2.5 m from the end of the tapered area (Fig. 1). This was done to minimize the risk of having differences in panel height (i.e., distance between the panel and bottom netting), which is determined by the attachment of the codend to the tapered section (Krag et al. 2016). To achieve the desired differences in panel placement with respect to the codline, a section of codend was either added or removed after the panel. Specifically, the panel was first placed at 4-7 m from the codline. In the second experiment, the distance from the panel to the codline was increased by adding a 3 m long section after the panel to achieve the 7–10 m position from the codline and, in experiment three, the codline was moved forward by removing the 4 m section after the panel to obtain the 3-6 m position (Table 1). This resulted in a difference in codend length across experiments but, to the best of our knowledge, no literature has identified codend length as a factor affecting selectivity.

We constructed the SELTRA codend according to the regulations in Kattegat (BEK nr 1249 af 24 August 2020); therefore, no floats and weights were added to increase the height of the section and no stopnet was inserted after the panel.

Table 1. Summary of codend and panel parameters.

| | Characteristic | First cruise | Second cruise |
|--------|------------------------------------------------|--------------------------------|--------------------------------|
| Codend | Mesh type | Diamond | Diamond |
| | Nominal mesh size (mm) | 90 | 90 |
| | Measured mesh size \pm SD (mm) | 98.1 ± 2.5 | 96.1 ± 1.9 |
| | Codend circumference (no. of open meshes) | 92 | 92 |
| | Twine thickness (mm) and no. of twines | 3, double | 3, double |
| | Material | Polyethylene (PE) | PE |
| | Codend stretched length (m) | 6.3/9.3 | 5.3 |
| | No. of selvedges | 4 | 4 |
| | Number of meshes in selvedge | 2 | 2 |
| Panel | Mesh type | Square | Square |
| | Actual mesh size (mm) | 380 | 380 |
| | Number of meshes across (length $	imes$ width) | 16×3 | 16×3 |
| | Panel stretched length (m) | 2.9 | 2.9 |
| | Twine thickness (mm) and no. of twines | 4, single | 4, single |
| | Material | Polyethylene (PE) | PE |
| | Distance from the codline to the panel (m) | 4, 7 | 3 |
| Cover | Material | Dyneema and PE | Dyneema and PE |
| | Mesh type | Square (Dyneema), diamond (PE) | Square (Dyneema), diamond (PE) |
| | Measured Dyneema mesh size \pm SD (mm) | 34.2 ± 0.6 | 34.2 ± 0.6 |
| | Measured PE mesh size \pm SD (mm) | 41.2 ± 1.3 | 41.2 ± 1.3 |
| | Total length (m) | 25 | 25 |
| | Length of Dyneema section (m) | 11 | 11 |
| | Maximum circumference (m) | 8 | 8 |
| | Distance from panel | 5 | 5 |
| | Spreading mechanism | Kites, floats and weights | Kites, floats and weights |

Fig. 1. Schematic representation of the SELTRA 300 codend design tested in this study. The three different panel placements were achieved by changing the length of the codend extension piece. PE, polyethylene.



A small-meshed cover made of knotted PE diamond netting (41.2 \pm 1.3 mm, n = 50) was used to capture individuals that escaped from the codend or panel (Table 1). Although no cover can be considered fully non-selective, a cover mesh size halved with respect to the codend mesh size should ensure full retention in the selective range of the codend (Wileman et al. 1996). To limit the visibility of the cover from inside the codend, the cover netting in the region around the SMP and codend was made of thin (1.2 mm) grey Dyneema[®] netting oriented to form square meshes ($34.2 \pm 0.6 \text{ mm}$, n = 50; Table 1). A long zipper was inserted in the lower panel at the aft end of the Dyneema[®] netting to enable collecting the catch in the test codend. The cover had a total length of 25.0 m and a widest circumference of 8 m (Table 1). A conical section of large meshes (100 mm nominal mesh) was used to connect the cover to trawl body, 5 m ahead of the SMP. According to the design described by Madsen et al. (2001), a combination of kites, lead weights and floats were used to prevent the cover from masking the SMP or codend meshes.

The mesh size of the codend were measured in wet conditions after each trial while the cover mesh sizes (Dyneema and PE; n = 50 for each) were measured dry after the last trial. Five rows of 10 meshes were selected randomly from different areas of the codend and cover and measured using an OMEGA mesh gauge (Fonteyne et al. 2007).

2.2. Sea trials

Two trials were carried out on board R/V Havfisken (17 m, 373 kW), one in May/June and one in September 2020. Both trials took place in ICES Division IIIa, under similar weather conditions and in the same fishing area (Table 2). Fishing was conducted following full commercial conditions in terms of towing speed but, due to the use of the small mesh cover, hauls durations were shorter (average 2.3 h; Table 2) than what is typically observed in the *Nephrops* fishery (5–6 h; Feekings et al. 2016). Cameras (Paralenz DC+) were placed ahead of the panel pointing backwards to observe codend geometry and escapement through the panel. No artificial light was added to prevent affecting species behavioural responses, thus escape observations were limited to the haul-back process.

Handling of the catch was kept standard across experiments and cruises, with the catch of the codend collected and processed first, followed by the catch of the cover. For each compartment, the total catch weight was recorded prior to sorting. Catches of the species of interest (Nephrops, cod, and plaice) were length-measured. Nephrops were measured in carapace length (CL) using digital calipers and fish were measured in total length (TL), rounding down to the nearest millimeter and centimeter, respectively. Other commercial fish species, like haddock (Melanogrammus aeglefinus), saithe (Pollachius virens) and witch flounder (Glyptocephalus cynoglossus), were also length-measured but excluded from analyses due to the low number of individuals in each haul and across experiments. When subsampling was required due to high catches of one species, the weight of the total catch of the species and length-measured subsample were recorded and used to estimate the sampling ratio. The catch of the species was mixed prior to subsampling to prevent a biased sample

$$(3) \quad C_{SMP}(l, \mathbf{v}_{SMP}) = \begin{cases} 0.0 : Model1 (m1) \\ 1.0 : Model2 (m2) \\ A_{SMP} : Model3 (m3) \\ \frac{\exp\left(\frac{\ln(9.0)}{SR_{SMP}} \times (l - L50_{SMP})\right)}{1.0 + \exp\left(\frac{\ln(9.0)}{SR_{SMP}} \times (l - L50_{SMP})\right)} : Model4 (m4) \\ 1.0 - \frac{A_{SMP}}{1.0 + \exp\left(\frac{\ln(9.0)}{SR_{SMP}} \times (l - L50_{SMP})\right)} : Model5 (m5) \\ \frac{1.0}{1.0 + \exp\left(\frac{\ln(9.0)}{SR_{SMP}} \times (l - L50_{SMP})\right)} : Model5 (m5) \\ \frac{A_{SMP}}{1.0 + \exp\left(\frac{\ln(9.0)}{SR_{SMP}} \times (l - L50_{SMP})\right)} : Model6 (m6) \\ \frac{A_{SMP}}{1.0 + \exp\left(\frac{\ln(9.0)}{SR_{SMP}} \times (l - L50_{SMP})\right)} : Model7 (m7) \end{cases}$$

2.3. Statistical analysis

The aim of the study was to determine if and how the selectivity of the SELTRA 300 codend changes when the panel is moved further away from the codline. Given that all individuals contacting the panel are in theory able to escape, and that the codend used was the same across experiments, the only parameter potentially changing with panel placement was the contact probability (C_{SMP}).

We used the covered codend method, which implies that all individuals that entered the trawl were caught in either the codend or the cover (Wileman et al. 1996). However, individuals in the cover could have escaped from either the panel, given that they had made contact with it, or the codend. Therefore, for each species and position of the panel, we tested different parametric models to estimate the combined retention rate at length of the panel and codend, $r_{\text{combined}}(l, v_{SMP}, v_{\text{codend}})$, where v_{SMP} and v_{codend} are vectors consisting of the parameters of the model (1).

(1) $r_{combined} (l, v_{SMP}, v_{codend}) = (1.0 - C_{SMP} (l, v_{SMP}))$

 $\times r_{codend} (l, \boldsymbol{v_{codend}})$

where $C_{SMP}(l, v_{SMP})$ is the probability of an individual of length *l* contacting the panel to escape and, $r_{codend}(l, v_{codend})$ is the size-selection process in the codend. For the codend size selection, we assumed it could be sufficiently well modelled by a logistic model that is often used for codends with a single mesh size and type (Wileman et al. 1996):

(2)
$$r_{codend}(l, \boldsymbol{v}_{codend}) = \frac{\exp\left(\frac{ln(9.0)}{SR_{codend}} \times (l - L50_{codend})\right)}{1.0 + \exp\left(\frac{ln(9.0)}{SR_{codend}} \times (l - L50_{codend})\right)}$$

where the L50_{codend} is the length of an individual that has 50% probability for retention in the codend, conditioned it entered the codend. SR_{codend} (=L75_{codend}-L25_{codend}) is the codend selection range defined as the difference in length of individuals with respectively 75% and 25% probability for codend retention conditioned codend entry.

For the probability of contacting the panel, we considered seven different models:

| arometric pressure (bars) | Total catch codend (kg) | Total catch cover (kg) | |
|---------------------------------|-------------------------------|---------------------------|--|
| 1.0297 | 19 | 47 | |
| 1.0285 | 19 | 250 | |
| 1.0287 | 32 | 454 | |
| 1.0290 | 37 | 479 | |
| 1.0299 | 29 | 190 | |
| 1.0298 | 41 | 386 | |
| 1.0278 | 55 | 199 | |
| 1.0282 | 79 | 479 | |
| 1.0282 | 55 | 436 | |
| 1.0199 | 44 | 175 | |
| 1.0187 | 45 | 312 | |
| 1.0175 | 62 | 438 | |
| 1 0075 | 00 | 202 | |

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Table 2. Summary of experimental hauls.

| Cruise | Day | Haul | Panel placement | Lat. (start) | Long. (start) | Lat. (end) | Long. (end) | Fishing time (min) | Towing speed (kt) | Depth (m) | Bottom tempera- ture (°C) | Wind speed (m/s) | Barometric pressure (bars) | Total catch codend (kg) | Total catch cover (kg) |
|--------|------------------|------|--------------------|--------------|---------------|-------------|-------------|--------------------------|-------------------------|--------------|------------------------------------|------------------------|----------------------------------|-------------------------------|---------------------------|
| 1 | 29 May 2020 | 1 | 4–7 m | 57.51.069 N | 10.32.061 E | 57.54.914 N | 10.24.911 E | 120 | 2.8 | 105 | 7.9 | 3 | 1.0297 | 19 | 47 |
| 1 | 29 May 2020 | 2 | 4–7 m | 57.56.812 N | 10.23.779 E | 57.56.488 N | 10.16.694 E | 90 | 2.5 | 96 | 7.7 | 5 | 1.0285 | 19 | 250 |
| 1 | 30 May 2020 | 3 | 4–7 m | 57.49.304 N | 9.50.867 E | 57.50.961 N | 9.41.961 E | 121 | 2.8 | 44 | 8.4 | 2 | 1.0287 | 32 | 454 |
| 1 | 30 May 2020 | 4 | 4–7 m | 57.50.636 N | 9.43.736 E | 57.49.987 N | 9.54.950 E | 210 | 2.7 | 50 | 8.8 | 5 | 1.0290 | 37 | 479 |
| 1 | 31 May 2020 | 5 | 4–7 m | 57.52.504 N | 9.57.373 E | 57.53.848 N | 9.50.093 E | 92 | 2.7 | 58 | 8.3 | 7 | 1.0299 | 29 | 190 |
| 1 | 31 May 2020 | 6 | 4–7 m | 57.55.592 N | 9.51.671 E | 58.01.515 N | 9.59.550 E | 166 | 2.9 | 71 | 7.6 | 7 | 1.0298 | 41 | 386 |
| 1 | 1 June 2020 | 7 | 4–7 m | 57.48.992 N | 9.58.432 E | 57.51.163 N | 9.59.062 E | 49 | 2.8 | 52 | 8.3 | 3 | 1.0278 | 55 | 199 |
| 1 | 1 June 2020 | 8 | 4–7 m | 57.50.047 N | 9.57.321 E | 57.49.063 N | 9.46.926 E | 138 | 2.7 | 54 | 9.1 | 3 | 1.0282 | 79 | 479 |
| 1 | 1 June 2020 | 9 | 4–7 m | 57.49.466 N | 9.45.692 E | 57.46.782 N | 9.57.134 E | 150 | 2.7 | 42 | 9.4 | 1 | 1.0282 | 55 | 436 |
| 1 | 2 June 2020 | 10 | 7–10 m | 57.46.367 N | 9.56.659 E | 57.48.821 N | 9.57.199 E | 57 | 2.6 | 50 | 9.3 | 6 | 1.0199 | 44 | 175 |
| 1 | 2 June 2020 | 11 | 7–10 m | 57.49.485 N | 9.55.700 E | 57.50.165 N | 9.40.821 E | 180 | 2.6 | 50 | 8.9 | 7 | 1.0187 | 45 | 312 |
| 1 | 2 June 2020 | 12 | 7–10 m | 57.53.787 N | 9.35.378 E | 57.57.386 N | 9.48.499 E | 166 | 2.9 | 99 | 7.6 | 6 | 1.0175 | 62 | 438 |
| 1 | 3 June 2020 | 13 | 7–10 m | 57.46.276 N | 9.56.641 E | 57.47.753 N | 10.05.572 E | 126 | 2.6 | 51 | 8.3 | 7 | 1.0075 | 86 | 292 |
| 1 | 3 June 2020 | 14 | 7–10 m | 57.45.482 N | 10.13.704 E | 57.45.528 N | 10.25.270 E | 131 | 2.7 | 82 | 7.8 | 3 | 1.0073 | 50 | 220 |
| 1 | 3 June 2020 | 15 | 7–10 m | 57.41.713 N | 10.19.675 E | 57.39.885 N | 10.12.449 E | 96 | 2.8 | 25 | 8.5 | 4 | 1.0067 | 120 | 630 |
| 1 | 4 June 2020 | 16 | 7–10 m | 57.46.058 N | 10.00.670 E | 57.48.975 N | 10.21.918 E | 259 | 2.7 | 63 | 7.9 | 7 | 0.9992 | 85 | 330 |
| 1 | 4 June 2020 | 17 | 7–10 m | 57.49.697 N | 10.23.680 E | 57.50.962 N | 10.38.720 E | 174 | 2.7 | 84 | NA | 9 | 0.9977 | 39 | 40 |
| 1 | 5 June 2020 | 18 | 7–10 m | 57.45.177 N | 10.57.356 E | 57.47.546 N | 11.01.803 E | 76 | 2.5 | 35 | 9.3 | 6 | 0.9871 | 51 | 67 |
| 1 | 5 June 2020 | 19 | 7–10 m | 57.48.987 N | 11.01.485 E | 57.50.737 N | 10.52.836 E | 115 | 2.8 | 45 | 8.2 | 7 | 0.9879 | 62 | 221 |
| 1 | 5 June 2020 | 20 | 7–10 m | 57.50.521 N | 10.53.031 E | 57.48.280 N | 10.58.629 E | 116 | 2.8 | 47 | 8.2 | 1 | 0.9895 | 100 | 260 |
| 2 | 1 September 2020 | 1 | 3 - 6 m | 57.45.001 N | 10.59.625 E | 57.48.931 N | 11.02.388 E | 120 | 2.7 | 36 | 13.6 | 2 | 1.0221 | 52 | 575 |
| 2 | 1 September 2020 | 2 | 3 - 6 m | 57.50.281 N | 10.58.566 E | 57.51.445 N | 10.44.394 E | 180 | 2.6 | 57 | 7.9 | 5 | 1.0213 | 152 | 521 |
| 2 | 2 September 2020 | 3 | 3 - 6 m | 57.48.705 N | 9.58.096 E | 57.50.432 N | 9.49.282 E | 120 | 2.6 | 50 | 11.7 | 3 | 1.0199 | 155 | 560 |
| 2 | 2 September 2020 | 4 | 3 - 6 m | 57.59.143 N | 9.40.552 E | 58.02.271 N | 9.54.284 E | 189 | 2.7 | 171 | 7.6 | 6 | 1.0199 | 152 | 489 |
| 2 | 3 September 2020 | 5 | 3 - 6 m | 57.52.309 N | 9.37.800 E | 57.50.670 N | 9.31.360 E | 90 | 2.4 | 75 | 7.9 | 3 | 1.0131 | 48 | 242 |
| 2 | 3 September 2020 | 6 | 3 - 6 m | 57.50.384 N | 9.28.073 E | 57.49.239 N | 9.20.951 E | 90 | 2.5 | 84 | 7.6 | 4 | 1.0124 | 28 | 295 |
| 2 | 3 September 2020 | 7 | 3 - 6 m | 57.46.349 N | 9.23.562 E | 57.44.163 N | 9.35.813 E | 155 | 2.6 | 41 | 15.5 | 6 | 1.0116 | 62 | 510 |
| 2 | 4 September 2020 | 8 | 3 - 6 m | 57.53.124 N | 9.45.458 E | 57.57.470 N | 9.58.207 E | 180 | 2.8 | 65 | 9.7 | 13 | 1.0067 | 30 | 610 |
| 2 | 4 September 2020 | 9 | 3 - 6 m | 57.56.300 N | 9.58.951 E | 57.48.609 N | 10.01.553 E | 180 | 2.4 | 68 | 11.4 | 13 | 1.0084 | 25 | 733 |

- Model 1: no individuals, independent of their length, contacts the panel.
- Model 2: all individuals, independent of their length, contact the panel.
- Model 3: a fraction A_{SMP} of the individuals, independent of their length, entering the section with the panel contact the panel.
- Model 4: the probability of contacting the panel increases with length following a logistic curve with parameters L50_{SMP} and SR_{SMP}.
- Model 5: similar to Model 4 (i.e., increase in probability of contacting the panel with length, based on a logistic curve with parameters $L50_{SMP}$ and SR_{SMP}) but constrained by the parameter A_{SMP} not being able to assume a value lower than $1.0 A_{SMP}$.
- Model 6: the probability of contacting the panel decreases with length following a logistic curve with parameters L50_{SMP} and SR_{SMP}.
- Model 7: similar to Model 6 (i.e., decrease in probability of contacting the panel with length based on a logistic curve with parameters L50_{SMP} and SR_{SMP}) but constrained by the parameter A_{SMP} not being able to assume a value higher than A_{SMP}.

For each species and panel position separately, we tested the ability of each of the Models 1–7 for panel contact and escape (eq. 3) and the logistic model for the codend selection (eq. 2) combined as in eq. 1 to describe the experimentally obtained combined size selection. The estimation was conducted maximizing the probability for the observed experimental data under the assumption of each of the panel contact models (1–7) to find the values of the parameters v_{SMP} and v_{codend} that makes the experimental data most likely to be observed. The estimation was conducted summed over hauls for each species and panel placement by minimizing the following expression which corresponds to maximize the likelihood for the observed experimental data:

(4)
$$-\sum_{j=1}^{m} \sum_{l} \left\{ \frac{nCD_{lj}}{qCD_{j}} \times \ln\left(r_{combined}\left(l, \boldsymbol{v_{SMP}}, \boldsymbol{v_{codend}}\right)\right) + \frac{nCV_{lj}}{qCV_{j}} \times \ln\left(1.0 - r_{combined}\left(l, \boldsymbol{v_{SMP}}, \boldsymbol{v_{codend}}\right)\right) \right\}$$

The outer summation in expression (4) comprises the hauls conducted with the specific panel position and the inner summation over length classes l in the data. nCD_{lj} is the number of individuals of length class l length-measured in the codend in haul j. nCV_{lj} is the number of individuals of length class l length-measured in the cover in haul j. qCD_j and qCV_j represent the sampling fractions (i.e., proportion of individuals length-measured with respect to the total caught) in the codend and cover, respectively. For each species and panel placement, we included only hauls with at least ten individuals in total $(nCD_{lj} + nCV_{lj})$ (20 for cod, due to the wider length range; Krag et al. 2014; Bak-Jensen et al. 2022). Among the models for C_{SMP} (l, v_{SMP}), we chose for each species and panel placement the one leading to the lowest individual Akaike information criterion (AIC) value (Akaike 1974) based on minimizing (4) with respect to parameters v_{SMP} and v_{codend} . Furthermore, based on Wagenmakers and Farrell (2004), we estimated the relative likelihood L_i for each of the other *i* models compared to the model with the lowest AIC value (AIC_{min}). Let L_i be the relative probability for a model to be the model of choice. Relative to the one with lowest AIC with that probability set at 1.0.

(5)
$$L_i = exp\left(-\frac{AIC_i - AIC_{min}}{2.0}\right)$$

We found delta AIC (\triangle AIC) where relative probability was at least 5%.

(6)
$$\triangle AIC = AIC_i - AIC_{min} = -2.0 \times ln (0.05) = 5.99 \approx 6.0$$

Therefore, we considered as candidate models all those with an AIC value up to 6.0 points higher.

Once the best model was selected, for each species and panel placement, its ability to describe the experimental data was assessed based on the p-value, which expresses the likelihood to obtain by coincidence a discrepancy between the fitted model and the experimental data at least as big as the one observed. If the model selected did not produce acceptable fit statistics (p value < 0.05; deviance >> DOF), it had to be determined whether the failure was caused by the model's inability to describe the data, or caused by overdispersion in the data. We plotted the predicted curve against the experimental rates to visually check for patterns in the deviations between the model and data. In case of a clear pattern, the model would be discarded, otherwise we would assume that poor fit statistics would be due to overdispersion in the data (Wileman et al. 1996; Santos et al. 2016). 95% Efron confidence intervals (CI; Efron 1982) were estimated to account for between and within hauls variation, using a double bootstrapping method with 1000 iterations (Millar 1993). Subsampling was accounted for in the bootstrapping by resampling prior to raising data according to subsampling factor (Eigaard et al. 2012). The analyses were performed using the software SELNET (Herrmann et al. 2009).

3. Results

A total of 29 valid hauls were carried out during the sea trials to collect selectivity data on the three panel placements, 20 and 9 hauls in May/June and September, respectively (Table 2). During the first cruise, data were collected for the 4–7 and 7–10 m panel positions, while the 3–6 m position was tested in September.

3.1. Observations of gear geometry and escapement through the panel

Video observations were collected for six hauls (three, one and two at the 4–7, 7–10 m and 3–6 m placements, respectively). The observations revealed that, at all panel placements, the panel section is open during towing, yet slack is observed in both the escape panel and in the side panels of **Fig. 2.** Still images extracted from underwater footage. (A) View of panel section during fishing in shallow waters. (B) Collapse of panel section at the end of the tow. (C) Cod swimming forward from the codend by exploiting the inversion in flow direction at the end of the tow. (D) Cod escaping through the panel during the haul-back process. (E) Flatfish (plaice and dab) escaping through the panel during the haul-back process. (F) *Nephrops* under the panel during the haul-back process. The letter C, N and F indicate individuals of cod, *Nephrops* and flatfish, respectively.



the codend, at least in shallow waters (Fig. 2A). Using as reference the mesh size of the panel, we can estimate that the height of the section was approximately 45–50 cm. Regardless of panel placement, it was also noted that the section collapses (i.e., the top and bottom netting panel contact each others) when towing speed decreases, such as at the beginning of the haul-back process (Fig. 2B).

For each panel placement, the haul with clearest video footage was fully processed to assess escapement of the species of interest. Observations of escape during fishing were mostly impaired by the sediment cloud. In contrast, visibility improved during the haul-back process and quantitative observations of all three species of interest could be collected for this phase (i.e., from the collapse of the section at the end of towing, Fig. 2B, to surface). Specifically, a total of 141 cod and 129 flatfish (plaice and dab, *Limanda limanda*) were observed escaping through the panel during the haulback process. To estimate the escape rate during haul-back, we counted the number of escapes vs the number of individuals observed in the panel area. It should be noted that an individual could be counted in the panel area multiple times, if it exited and re-entered the field of view; thus, the escape rate refers to successful escape attempts rather than absolute number of escapees. For cod, the escape rate was estimated

| | Panel placement | No. of hauls | No. of individuals $(nCD + nCV)$ | Length range |
|----------|-----------------|--------------|----------------------------------|--------------|
| Cod | 3–6 m | 9 | 2812 | 7–112 |
| | 4–7 m | 9 | 3579 | 11-72 |
| | 7–10 m | 11 | 3074 | 12-68 |
| Plaice | 3–6 m | 8 | 1227 | 13–49 |
| | 4–7 m | 9 | 1290 | 12-55 |
| | 7–10 m | 8 | 956 | 10-43 |
| Nephrops | 3–6 m | 7 | 7365 | 21-64 |
| | 4–7 m | 8 | 2423 | 22-60 |
| | 7–10 m | 9 | 5630 (4893) | 17–64 |
| | | | | |

 Table 3. Summary of selectivity data included in the analyses for each species and panel placement.

Note: in case of subsampling, the number of individuals length-measured is shown in parentheses. The length range refers to the total length in centimetre for fish species and the carapace length in millimetre for *Nephrops*.

Table 4. Summary of fit statistics for each model fitted.

| | | 3–6 m | | 4–7 | m | 7–10 m | | |
|----------|-------|------------|---------|-----------|---------|------------|---------|--|
| | Model | ΔAIC | P value | ΔΑΙΟ | P value | ΔAIC | P value | |
| Cod | m1 | 2096.11 | <0.01 | 351.33 | <0.01 | 376.23 | <0.01 | |
| | m2 | 72019.95 | < 0.01 | 159415.82 | < 0.01 | 138940.28 | <0.01 | |
| | m3 | 16.18 | 0.77 | 1.65 | 0.15 | 2.43 | 0.09 | |
| | m4 | 6.61 | 0.98 | 10.10 | 0.04 | 14.32 | 0.01 | |
| | m5 | 0.00 | >0.99 | 10.89 | 0.04 | 12.69 | 0.02 | |
| | m6 | 29.17 | 0.31 | 0.00 | 0.17 | 0.69 | 0.14 | |
| | m7 | 20.18 | 0.70 | 1.58 | 0.20 | 0.00 | 0.18 | |
| Plaice | m1 | 174.31 | < 0.01 | 167.93 | <0.01 | 36.07 | <0.01 | |
| | m2 | 153489.63 | <0.01 | 186742.59 | < 0.01 | 120315.30 | <0.01 | |
| | m3 | 7.84 | 0.35 | 16.45 | < 0.01 | 0.00 | 0.50 | |
| | m4 | 1.87 | 0.74 | 3.95 | 0.07 | 5.10 | 0.30 | |
| | m5 | 0.00 | 0.87 | 0.00 | 0.16 | 6.78 | 0.26 | |
| | m6 | 12.03 | 0.21 | 38.85 | < 0.01 | 1.05 | 0.50 | |
| | m7 | 11.84 | 0.25 | 20.45 | <0.01 | 0.05 | 0.62 | |
| Nephrops | m1 | 9.43 | < 0.01 | 6.48 | 0.60 | 0.00 | 0.38 | |
| | m2 | 2497788.50 | <0.01 | 936581.10 | < 0.01 | 2007616.63 | < 0.01 | |
| | m3 | 6.07 | 0.01 | 0.00 | 0.90 | 0.52 | 0.39 | |
| | m4 | 10.49 | <0.01 | 6.37 | 0.71 | 6.94 | 0.20 | |
| | m5 | 10.07 | <0.01 | 6.67 | 0.74 | 8.97 | 0.17 | |
| | m6 | 0.00 | 0.04 | 2.11 | 0.87 | 1.95 | 0.37 | |
| | m7 | 1.89 | 0.03 | 2.10 | 0.91 | 0.12 | 0.48 | |

to be 0.39 at the 3–6 m placement (n = 148), 0.32 at the 4– 7 m placement (n = 153) and 0.52 at the 7–10 m placement (n = 66). All cod escaped at the first attempt by actively seeking contact with the panel; this was favored by the collapse of the section at the end of the tow (Fig. 2C–2D). For flatfish an escape rate of 0.47 (n = 49), 0.47 (n = 34) and 0.54 (n = 168) was estimated during the haul-back at the 3–6, 4–7 and 7–10 m positions, respectively. In most cases, escape occurred at first active contact with the panel and at a later stage than cod (Fig. 2E); few individuals (n = 22) were observed attempting escape several times before succeeding. A total of 12 *Nephrops* were observed, none of which contacted the panel despite showing a certain degree of active behaviour and being directly below the panel when the section collapsed (Fig. 2F).

3.2. Selectivity data

Selectivity data were collected for cod, plaice and *Nephrops*. All individuals of cod and plaice were length-measured, while subsampling was necessary in one haul for *Nephrops* (Table 3). For each species and panel placement, we fitted seven models to the pooled data (i.e., summed over hauls) and assessed their fit based on AIC and *p* values (Table 4; all model fits are illustrated in Appendix A). The model with the lowest AIC was selected as the best model and used to estimate absolute selectivity and panel escape probability considering within and between hauls variation.

For both fish species, the scenario that described the data best when the panel was placed at 3–6 m from the codline was the one where contact probability increases with **Fig. 3.** Candidate models (i.e., models within six \triangle AIC points; black lines) and best models (red lines) fitted to the pooled experimental data (points) for each species and panel placement. Length refer to the total length in centimetre for fish species and the carapace length in millimetre for *Nephrops*. \triangle AIC, delta Akaike information criterion.

length, even when considering alternative candidate models for plaice (i.e., within six points of \triangle AIC; Fig. 3, left column). In contrast, the results for *Nephrops* for the same panel placement fitted the scenario of decreasing contact probability for larger length classes, with m6 resulting as the best model and m7 as a candidate model (Figs. 3 and 4, left column).

When the panel was moved to 4–7 m from the codline, the scenario that best fitted the data differed among species. The best scenario for cod was a decreasing contact with length, however a length-independent contact scenario also scored as candidate, with the model fit differing only for the larger and less represented length classes (Fig. 3, central column). The same occurred for *Nephrops*, but in this case the best scenario was length-independent contact (m3) while the scenario of decreasing contact at length scored as candidate (both m6 and m7; Figs. 3 and 4, central column). The results for plaice continued to support an increased contact at length (Figs. 3 and 4, central column), as only models within that sce-

nario were found to describe sufficiently well the experimental data.

At the farthest position from the codline, 7–10 m, data for cod continued to be best represented by the scenario of contact probability decreasing with length, with the only competitive scenario being the length-independent one (m3). For plaice, the results became unclear, with the best scenario being length-independent contact, but scenarios with both increasing (m4) and decreasing contact with length (m6 and m7) scoring as candidates. Even more so, most models had more than 5% probability of representing well the experimental data for *Nephrops*, with changes to the fit limited to length classes poorly represented in the data (Figs. 3 and 4, right column).

For each species and panel placement we chose the best models as the model with lowest AIC, albeit candidates were considered when discussing the results. The p values of the best models for all species and panel placements were not significant, implying that the models were able to describe

Fig. 4. Panel escape rate for the candidate models (i.e., models within six \triangle AIC points; black lines) and best models (red lines) for each species and panel placement. Length refer to the total length in centimetre for fish species and the carapace length in millimetre for *Nephrops*. \triangle AIC, delta Akaike information criterion.

the experimental data sufficiently well. The only exception was Nephrops at the 3-6 m placement, where none of the models tested resulted in a non-significant p value (Table 4). However, after inspection of the residuals, which did not show any structure in the deviations between the data and the modelled curves, we concluded that the low p value is due to overdispersion in the data (Wileman et al. 1996). The best models reflected well the trends in the experimental data for all species and panel placements (Fig. 5). The combined selectivity of the codend and panel selection processes differed significantly for all species at different placements of the panel (Fig. 5). A bell shape curve was observed for cod, at the 3-6 m panel position, and plaice, at both the 3-6 and 4-7 positions, due to the length-dependent increase in contact probability with the panel (Fig. 5). For all three species, the combined selectivity when the panel was placed closer to the codline differed significantly from the 7-10 m placement, as shown by the lack of overlapping of the CIs (Fig. 5). Such differences were found for all length classes above 36 and 29 cm for cod

and plaice, respectively, and 44 mm for *Nephrops*. No difference in combined selectivity was found between the 4–7 and 7–10 m placements for neither cod nor *Nephrops*. In contrast, the selection for plaice above 41 cm differed significantly between these positions, albeit very few plaice above 35 cm were caught during the trials (Fig. 5, right panel).

As illustrated by both the combined selectivity curves (Fig. 5) and the estimated selection parameters (Table 5), the panel escape probability changed significantly when changing the position of the panel due to the change in type of contact (Fig. 6). For cod, a major difference was found between the 3–6 m placement and the other two positions. At the first, individuals above 36 cm had 100% probability of contacting and escaping through the panel whereas at the latter, large individuals had lower probability of contacting the panel and escape than the smaller ones. For plaice, contact probability was found to increase with length at both the 3–6 m and 4–7 m placements, and to reach 99% escape probability at 45 and 49 cm, respectively (Fig. 6). However, a difference in panel escape

Fig. 5. Combined selection curves (plots on the left) and structures of the populations encountered during each panel placement experiment (plots on the right) for the three species analyzed. The modelled combined retention rate (solid line) is shown fitted to the experimental points and the shaded ribbons represent the 95% Efron confidence intervals. Length refer to the total length in centimetre for fish species and the carapace length in millimetre for *Nephrops*.

probability was found between 24 and 30 cm, implying that medium sized plaice are less likely to contact and escape through the panel when placed at 4–7 m from the codline (Fig. 6). When the panel was moved even further away from the codline, the length-dependency in contact probability was not supported anymore, and all plaice ap-

peared to have a 37% (CI: 20%–50%) probability of contacting the panel, regardless of size (Fig. 6). Finally, the escape probability through the panel for *Nephrops* was highest when the panel was placed at 3-6 m from the codline (Fig. 6). This position resulted in significantly higher escape probabilities at all length classes encountered, with

| | | 3–6 m | 4–7 m | 7–10 m |
|----------|-----------------------|---------------------|------------------------|---------------------|
| Cod | Model | m5 | m6 | m7 |
| | L50 _{codend} | 12.35 (-1.79-27.21) | 17.21 (15.11 –; 26.57) | 13.94 (4.65–28.93) |
| | SR _{codend} | 5.28 (2.89-24.32) | 3.32 (1.18–17.41) | 5.28 (1.89-50.86) |
| | L50 _{SMP} | 35.51 (3.11-38.48) | 157.91 (93.74–231.75) | 64.79 (51.06–94.73) |
| | SR _{SMP} | 0.01 (-2.08-19.79) | 156.30 (60.50- 220.07) | 15.75 (8.67–42.92) |
| | A _{SMP} | 0.06 (-0.02-0.95) | - | 0.89 (0.76–0.96) |
| Plaice | Model | m5 | m5 | m3 |
| | L50 _{codend} | 21.41 (20.79–22.46) | 22.66 (21.69–23.96) | 22.83 (21.93-25.00) |
| | SR _{codend} | 1.20 (1.04-2.17) | 3.37 (2.38-4.60) | 3.27 (2.24-5.23) |
| | L50 _{SMP} | 35.69 (23.57–38.54) | 36.08 (31.06-41.59) | - |
| | SR _{SMP} | 6.02 (2.02-22.90) | 6.95 (1.88–14.75) | - |
| | A _{SMP} | 0.40 (0.22–0.93) | 0.78 (0.60–0.93) | 0.37 (0.20-0.50) |
| Nephrops | Model | m6 | m3 | m1 |
| | L50 _{codend} | 24.33 (21.68-30.05) | 25.74 (22.35-28.31) | 22.03 (17.26-25.40) |
| | SR _{codend} | 3.13 (0.48-12.36) | 10.87 (6.51-18.10) | 26.27 (19.21-32.03) |
| | L50 _{SMP} | 9.50 (6.52-25.98) | - | - |
| | SR _{SMP} | 58.04 (33.48-82.60) | - | - |
| | A _{SMP} | - | 0.05 (0.02-0.09) | - |

Table 5. Summary of estimated models parameters for each species and panel placement.

a negative length-dependency meaning that larger length classes had lower probability of escaping through the panel. At the other panel placements, *Nephrops* had a rather low contact probability with the panel, 5% (CI: 2%–9%) and 0% for the 4–7 and 7–10 m placements, respectively (Fig. 6).

4. Discussion

In this study, we provided empirical evidence that panel placement with respect to the catch accumulation zone has a significant effect on the escape efficiency of a type II panel, for all species investigated. Moreover, the results revealed that the difference in efficiency can be the consequence of lengthdependent contact behaviours, leading to higher escape rates for large cod and plaice at placements closer to the codline. This effect was detected as a result of the structural modelling approach adopted here. The approach allowed made it possible to test specific hypotheses of contact type without requiring the addition of a second cover (i.e., collecting escapees from the panel), which is difficult to deploy and can affect the escape behaviour through the panel (Madsen and Holst 2002). This approach was possible because the panel tested, type II, could be assumed to have full escape probability for all individuals contacting it. Although all mesh sizes will eventually become size-selective if large enough individuals are encountered, this was not the case in this study, where the predicted L50s for the species considered are above the maximum length class caught during the trials (112 cm, 55 cm and 64 mm for cod, plaice and Nephrops, respectively), thus supporting our assumption. Moreover, in most cases, at least one of the models considered was able to explain reasonably well the experimental data; the only exception was for *Nephrops* when the panel was placed at 3–6 m from the codline, which we attributed to the overdispersion in the data for the higher length classes as no pattern was evident in the residuals. Considering the close proximity between the catch accumulation zone and the escape panel when placed at 3–6 m from the codline, it is possible that there was a confounding effect of catch size and/or catch composition in this dataset (Broadhurst et al. 2002; Frandsen et al. 2010). Such confounding effects and their relevance for the efficiency of SELTRA codends in *Nephrops*-directed fisheries should be further investigated.

The results of this study show that the contact probability with an escape panel cannot be assumed to be lengthindependent and that the contact behaviour of each species can change depending on the distance from the catch accumulation zone. The strongest evidence of length-dependent contact was found at the 3-6 m placement for all species, and at the 4–7 m placement for plaice. For both cod and plaice, the data strongly supported an increase in contact at length, while the results for Nephrops implied a decrease in contact at length. In contrast, at the other two forward placements, the ability of the structural modelling approach to identify the best fitting contact scenario became less unequivocal, with multiple scenarios qualifying as candidate models. Interestingly, a trend can be noticed in terms of the number of candidate models: at the 4-7 m placement, the lengthindependent contact scenario becomes a competing explanation for cod and Nephrops, and at the 7-10 m placement multiple scenarios compete to explain the data. Nonetheless, it was possible to exclude some contact scenarios. For example, cod's increase in contact at length when the panel was placed at 3-6 m was not supported at all for the two placements further away from the codline. On the contrary, the data supported a decrease in contact at length at these two

Fig. 6. Panel escape probabilities (solid lines) and 95% Efron confidence intervals (ribbons) for each species and panel placements. Length refers to the total length in centimetre for fish species and the carapace length in millimetre for *Nephrops*.

placements. For both cod and plaice, this difference in contact behaviour is the critical factor that changes the release efficiency of the panel, resulting in a bell-shaped combined

selection curve, which is rarely achieved in trawl selectivity without including multiple selective devices (Stepputtis et al. 2016). Interestingly, a simple one meter difference in distance

Fig. 7. Schematic representation of the two competing explanations of the behavioural mechanisms leading to the differences in escape efficiency at different panel placements. (A) Length-dependent change in vertical distribution, with higher numbers of large individuals swimming upwards while approaching the codline. (B) Length-dependent escape during haul-back, where larger individuals can swim forward and escape at the end of the tow.

(A) length-dependent vertical distribution
(B) length-dependent escape during haul-back

of the SMP from the codline was sufficient to lose this bellshaped selection for cod but not for plaice. This could be related to the more passive and station-holding behaviour previously observed for cod (Briggs 1992; Grimaldo et al. 2007) or to differential behavioural mechanisms leading to the escape through the panel.

When it comes to understanding the behavioural mechanisms that led to the observed differences in panel escape and type of contact, there are two competing explanations (Fig. 7). On the one hand, it was previously demonstrated that the height of the panel section affects the escape efficiency (Krag et al. 2016) and that cod's vertical distribution changes throughout the trawl, with more cod moving upwards the closer it gets to the codline (Thomsen 1993; Fryer et al. 2017). Previous studies on the vertical distribution of species inside the trawl have also shown that small cod tend to stay in closer proximity to the bottom netting, which could result in a length-dependent contact probability with a panel placed in the top netting panel (Karlsen et al. 2019). Therefore, the differences in performance among panel placements could be related to a length-dependent vertical distribution, increasing the probability for large cod to contact the panel the closer this is placed to the codline (Fig. 7A). However, considering the low height of the panel section in this study (approximately 50 cm during towing), a closer proximity of large cod to the SMP could require a more dramatic change in swimming orientation for them to contact and escape through the large meshes (Cuende et al. 2020). Moreover, there is no evidence supporting a differential vertical distribution for plaicein relation to distance from codline (Fryer et al. 2017) or size (Karlsen et al. 2019). Therefore, this justification seems unlikely for plaice.

On the other hand, the alternative explanation is that the significant differences in contact probability are caused by a second wave of escape, during the haul-back process (Fig. 7B). Considering that swimming capacity increases with size (Webb 1975), larger fish could be able to swim forward after reaching the catch accumulation zone and escape through

the panel at a second stage, especially when towing is interrupted and the catch is displaced forward by its momentum (Engås et al. 1999). Considering that the haul-back process is relatively brief at the fishing depths of this study (approx. 80 m on average), the differences in escapement between panel placements may have derived from the distance the fish had to swim from the catch accumulation zone to reach the panel. Escapement during haul-back has been experimentally investigated and determined to contribute partially to the selection process (10%–20% of the escapees; Madsen et al. 2008; Grimaldo et al. 2009; Herrmann et al. 2013). However, only simple codends and codends with type I escape panels were investigated, and therefore these estimates may underestimate the contribution of the haul-back process for type II panels, where the lack of size-selectivity in the panel may result in high escape rates despite of the short time period of this phase of the fishing process. This explanation is supported by the video footage collected in this study, which revealed high numbers of escapees during haul-back, possibly accentuated by the collapse of the section when towing is interrupted. Albeit, escape during haul-back may not be desirable if it occurs at surface due to exposing the fish to barometric trauma and physical injuries (Madsen et al. 2008). The footage obtained in this study suggests that most individuals escape when the catch is displaced forward when towing is abruptly interrupted, for example to retrieve the doors. Depending on depth and length of the sweeps, this may occur in proximity of the seabed or in the water column. Hypothetically, haul-back escape of actively swimming fish could be accentuated if skippers were to accelerate briefly before the end of the tow, causing more momentum and opportunity for the fish to reach the escape panel even if this was placed further away from the codline. Future research could clarify the importance of haul-back selection by testing the effect of different haul-back procedures (e.g., full stop vs continuous towing) on the escape efficiency through the panel. Nonetheless, it could be critical for the survival and fitness of the escapees that the panel is used when the individuals first encounter it,

before they further interact with gear components and the rest of the catch.

Distinguishing between these two mechanisms can have critical consequences on the design and regulation of escape panels, and requires a change in the way we think about escape panels, where not only the outcome (escape rate) is considered but also the dynamic selective processes (when and how escapement occurs) are taken into consideration. Indeed, each of these mechanisms imply that the efficiency of the escape panel may vary substantially depending on environmental conditions and fishing dynamics. For example, if fish escape through the panel when they first encounter it during towing, escape rates may change depending on factors that affect species vertical distribution and perception of the panel. This includes environmental factors such as light level and sediment resuspension (e.g., Olla et al. 2000; Karlsen et al. 2019), as well as catch rates, where higher rates could lead to crowding and avoidance behaviour (e.g., Herrmann et al. 2015). As a consequence, selectivity studies may under or overestimate panel efficiency depending on season, depth and fishing area. In contrast, if fish escape at a second stage, only after first reaching the catch accumulation zone and mostly at the end of the tow, panel efficiency could be susceptible to towing time and catch size, as these would determine the level of exhaustion and the distance fish have to swim to reach the panel and escape. This implies that absolute selectivity studies, like ours, may overestimate panel escape due to the reduced towing time required to operate with a non-selective cover or control trawl and underestimate losses of target catch due to limited catch sizes in the test codend. Moreover, panel escape could be affected, regardless of escape mechanism, by bottom temperature as this would influence fish swimming endurance and speed (He 1993; Payne et al. 2016). This would cause seasonality in the performance of escape panels and could limit comparability across studies. The effect of all these parameters on trawl selectivity and escape panel performance have been rarely investigated, and research efforts are needed to address this knowledge gap.

The challenge of reducing bycatch in trawl fisheries is still far from resolved, and increasingly more bycatch reduction devices have come to include a behavioural component, exploiting inter-specific differences in swimming capacity, distribution and response to stimuli (Kennelly and Broadhurst 2021). However, the efficiency of behavioural-based devices is arguably less consistent, as it can be affected not only by gear design parameters but also environmental conditions, fishing dynamics, catch rates, and intra- and inter-species interactions. Since these factors can confound the interpretation of selectivity results and prevent the correct identification of critical design elements, the legislation and control of behavioural-based bycatch reduction devices can be complex and ineffective. For example, under commercial practice, floats would typically be mounted along the sides of escape panels, and in some cases stopnets are used to prevent the catch from coming forward during the haul-back process. These design elements are not typically specified in the technical regulations of fishing gears, and according to the results of this and previous study, could possibly result in

intra-fleet differences in performance of escape panels (Krag et al. 2016). Moreover, even though environmental parameters are known to effect fish behaviour and swimming capacity, it is rare to collect sufficient data to include them as covariates when modelling selectivity, nor feasible to keep them constant across hauls and experiments. For example, the performance of the gear may vary across seasons due to differences in temperature and light level, and fishing area, as sediment resuspension increases when fishing on muddy grounds (e.g., Oberle et al. 2016). Until we acquire a more systematic understanding of species behaviour inside the trawl, and how this is affected by the abovementioned factors, it will be difficult for behavioural-based bycatch reduction devices to be an efficient management tool to ensure the sustainable exploitation of stocks. Considering the recent developments in underwater observation technologies (e.g., Williams et al. 2010; Sokolova et al. 2022), future research should focus on facilitating quantitative behavioural analysis by, for example, increasing the range of observation, suppress sediment clouds, and limit the behavioural bias of the observation platform. This would allow to investigate the escapement process through bycatch reduction devices at the individual level, rather than between hauls, improving our ability to identify the factors and mechanisms that lead to the desired outcome (Robert et al. 2020; Santos et al. 2020).

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Data availability statement

Data generated or analyzed during this study are subject to an embargo of 12 months from the publication date of the article. Once the embargo expires the data will be available at doi: https://data.dtu.dk/account/home and upon request to the corresponding author.

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Appendix A

In this Appendix A, we present the fit of all the seven models considered in this study, for each species and panel placement, respectively.

In each figure, the plot in the first row shows the scenario of zero contact with the panel (m1). The second row includes the full contact (m2) and length-independent contact (m3) scenarios. The fourth and fifth rows shows the two models used for increasing contact with length (m4 and m5) and decreasing contact with length (m6 and m7), respectively.

All models were fitted to the pooled data for model selection. The \triangle AIC values are included in each plot to illustrate model ranking with respect to the best model (\triangle AIC = 0.0). All models with values up to 6.0 \triangle AIC were considered as candidate models to explain the experimental data.

Fig. A1. Fit of each model considered in this study (red lines) fitted to the pooled experimental data (points) for cod (*Gadus morhua*) when the panel was placed at 3-6 m from the codline. \triangle AIC, delta Akaike information criterion.

Cod: 3-6 m panel placement

Fig. A2. Fit of each model considered in this study (red lines) fitted to the pooled experimental data (points) for cod when the panel was placed at 4–7 m from the codline. \triangle AIC, delta Akaike information criterion.

Cod: 4-7 m panel placement

Fig. A3. Fit of each model considered in this study (red lines) fitted to the pooled experimental data (points) for cod when the panel was placed at 7–10 m from the codline. \triangle AIC, delta Akaike information criterion.

Cod: 7-10 m panel placement

Fig. A4. Fit of each model considered in this study (red lines) fitted to the pooled experimental data (points) for *Nephrops* (*Nephrops norvegicus*) when the panel was placed at 3–6 m from the codline. \triangle AIC, delta Akaike information criterion.

Nephrops: 3-6 m panel placement

Fig. A5. Fit of each model considered in this study (red lines) fitted to the pooled experimental data (points) for *Nephrops* when the panel was placed at 3–6 m from the codline. \triangle AIC, delta Akaike information criterion.

Nephrops: 4-7 m panel placement

Fig. A6. Fit of each model considered in this study (red lines) fitted to the pooled experimental data (points) for *Nephrops* when the panel was placed at 7–10 m from the codline. \triangle AIC, delta Akaike information criterion.

Nephrops: 7-10 m panel placement

Fig. A7. Fit of each model considered in this study (red lines) fitted to the pooled experimental data (points) for plaice (*Pleuronectes platessa*) when the panel was placed at 3–6 m from the codline. \triangle AIC, delta Akaike information criterion.

Plaice: 3-6 m panel placement

Fig. A8. Fit of each model considered in this study (red lines) fitted to the pooled experimental data (points) for plaice when the panel was placed at 4–7 m from the codline. \triangle AIC, delta Akaike information criterion.

Fig. A9. Fit of each model considered in this study (red lines) fitted to the pooled experimental data (points) for plaice when the panel was placed at 7–10 m from the codline. \triangle AIC, delta Akaike information criterion.

Plaice: 7-10 m panel placement