



Original research article

Size selectivity of flatfish in trawl codends

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ABSTRACT

Flatfish constitute a substantial proportion of the catch in several demersal trawl fisheries across the globe. Therefore, knowledge on how to discriminate between the individuals that are to be captured or released, by size, is important for the sustainability of exploited stocks. Using European plaice (*Pleuronectes platessa*), flounder (*Platichthys flesus*), and dab (*Limanda limanda*) as case-study species, here we investigate how flatfish are selected in trawl codends by experimentally testing the influence of mesh geometry, and its variability, on size selection. Both diamond-mesh and square-mesh codends were tested, as well as three codends where the mesh shape was fixed to minimize its variation during fishing. The most discriminating size selectivity was found with fixed mesh geometry, revealing that variability in mesh openness negatively affects the selectivity of flatfish. Our results further demonstrate that the risk of retaining undersized flatfish tends to increase with increasing mesh opening angle in diamond-mesh codends. Our results also confirm that when fishing with codends of the same nominal mesh size, the square-mesh codend retains significantly higher proportions of undersized flatfish than the traditional diamond-mesh.

1. Introduction

Flatfish species are widely distributed across the world's marine regions and can make up a substantial proportion of the catch in demersal trawl fisheries, both as target and bycatch species (Borges et al., 2005; Feekings et al., 2012; Gibson et al., 2015; Uhlmann et al., 2014). When flatfish species and/or sizes are unintentionally caught, they are often discarded due to variety of reasons, for example, low market value, high-grading, or legal restrictions (Feekings et al., 2012; Rochet & Trenkel, 2005). Unintended bycatch and discard provide unnecessary waste of natural resources and are a source of unaccounted fishing mortality that undermines science-based fisheries management (Catchpole et al., 2017; Ward et al., 2012).

In demersal trawl fisheries, gear modifications are among the most widely used strategies to avoid bycatch (Catchpole et al., 2005; Kennelly & Broadhurst, 2021; Madsen, 2007). However, a review of the available literature reveals that most of these gear modifications are developed to provide escape opportunities for roundfish species (Kennelly & Broadhurst, 2021; Suuronen & Sardà, 2007), while little or no consideration is

given to other groundfish species, such as flatfish species, which are caught alongside the species of concern, such as target or threatened species (Hilborn et al., 2021). Often, this can lead to unsatisfactory flatfish selection and consequently a major cause of bycatch of these species (Wienbeck et al., 2014). In recent decades, several marine regions of the world have adopted catch-restricting legislation to promote selective fishing and sustainable exploitation of fish stocks (Condie et al., 2014). Thus, in order to conduct economically viable demersal trawl fisheries under catch-restrictive legislation, it is important to understand how to achieve sustainable exploitation of flatfish species.

Research into the capture process and selectivity of flatfish species in trawl gears has traditionally focused on investigating how these species are herded at the trawl mouth (Bublitz, 1996; Ryer, 2008; Winger et al., 2004), how they enter the net (Bublitz, 1996; Underwood et al., 2015), or how they move towards the rear end of the trawl (Ferro et al., 2007; Karlsen et al., 2019; Santos et al., 2016). In contrast, no controlled experimental study has been carried out to investigate how flatfish are discriminated by size in the codend, the rear end of the trawl where the catch accumulates and most attempts to escape from capture occur

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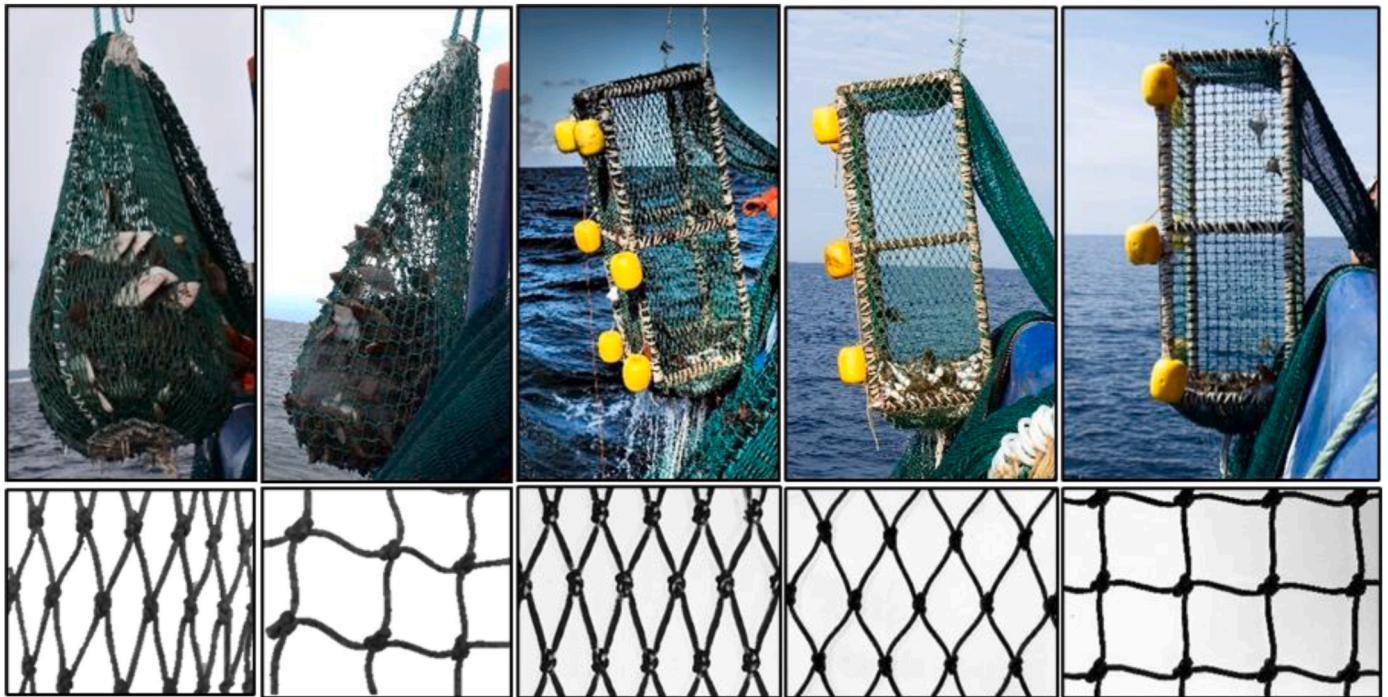


Fig. 1. First row: pictures of the five different codends tested. From left to right, SDC (Standard Diamond Codend), SSC (Standard Square Codend), FDC40 (Fixed Diamond Codend 40°), FDC60 (Fixed Diamond Codend 60°) and FSC (Fixed Square Codend). Bottom row: scans of the netting from each codend.

(Wileman et al., 1996). The ability of the codend to discriminate marine organisms by size is often referred to as size selection. This is usually expressed as the probability of an individual of a given size being retained once it enters the codend (Wileman et al., 1996). Understanding codend size selection for flatfish is essential for predicting how a given codend modification will affect the probability of catching these species by size. Such knowledge may be particularly important when endeavoring to optimize multi-species catch profiles.

The design of the codend is known to play a critical role in determining the size selection, especially the characteristics of the meshes, such as mesh size and shape (Bak-Jensen et al., 2023; Robertson & Stewart, 1988). Regarding the latter feature, codends with meshes in diamond configuration (diamond-mesh codends) are preferred by fishers and commonly used due to their simplicity, ease of handling on board and repair (Herrmann, Wienbeck, et al., 2013; Wileman et al., 1996). However, the use of standard diamond-mesh codends can result in unsatisfactory size selection for roundfish species. This is because the opening angle (OA) of the diamond meshes tends to close as a result of the drag forces, leaving only the meshes in the few rows immediately in front of the bulk of the catch widely open, and thus more suitable for the cross section of roundfish species (Herrmann, 2005). As a result of the change in the OA the width of the mesh will change accordingly. Specifically, a mesh with a narrow OA will have a wider mesh opening compared to a mesh with a wider OA. An alternative design often considered to improve escape possibilities for roundish species is square-mesh codends (Fonteyne & MRabet, 1992; Halliday et al., 1999; Robertson & Stewart, 1988). In these codends, the bars of the meshes are oriented parallel and perpendicular to the longitudinal towing force, thereby the drag forces do not tend to close the meshes and they remain more open along the length of the codend than in the case of diamond-mesh codends. However, the effect of using square-mesh codends is less evident for size selection of flatfish species, whose laterally compressed morphology might provide better escape opportunities through the diamond-shape opening of traditional codends (Guijarro & Massutí, 2006; Tokac et al., 2014). This suggests that a larger retention of smaller flatfish could be expected when using a square-mesh codend, while the opposite should be expected for

diamond-mesh codends.

However, experiments designed to demonstrate the selectivity characteristics of a traditional codend cannot properly evaluate the effect of mesh shape on the size selection of flatfish. Specifically, due to the forces acting on the codend during the fishing process the meshes tend to vary in openness both spatially and temporally (O'Neill & Herrmann, 2007). This lack of control over actual mesh shape makes it challenging to evaluate in detail the effect of mesh geometry on size selection of flatfish species. To overcome these limitations Bak-Jensen et al. (2022) introduced a novel experimental framework that specifically allows for the control of mesh geometry during fishing operations. The experiment was conducted using a steel frame which allowed the meshes to have a constant OA. Using such an experimental framework, Bak-Jensen et al. (2022) introduced a method to experimentally quantify the effect of both mesh shape and mesh shape variability on codend size selection. Using the same controlled experimental design, this study investigates the following five research questions related to flatfish size selectivity in trawl codends.

1. Does a standard square-mesh codend (flexible meshes) have a higher probability of retaining undersized flatfish than a standard diamond-mesh codend (flexible meshes)?
2. Does a diamond-mesh codend with a wide and stable OA (fixed meshes) have a higher probability of retaining undersized flatfish than one with a narrow and stable OA (fixed meshes)?
3. Does a diamond-mesh codend with a wide and stable OA (fixed meshes) have a higher probability of retaining undersized flatfish than a standard diamond-mesh codend with variable OAs (flexible meshes)?
4. Does a codend with stable square-meshes (fixed meshes) have a higher probability of retaining undersized flatfish than a standard square-mesh codend with variable OAs (flexible meshes)?
5. Does a codend with stable mesh geometry (fixed meshes) have a lower variability in size selection of flatfish than a codend with the same mesh shape but variable mesh geometry (flexible meshes)?

Table 1

Mean mesh size with std. deviation of the measurements (in brackets) and construction details of the tested codends. Information related to Standard Diamond Codend (SDC) is extracted from Bak-Jensen et al. (2022). Acronyms as follows: SDC (Standard Diamond Codend), SSC (Standard Square Codend), FDC40 (Fixed Diamond Codend 40°), FDC60 (Fixed Diamond Codend 60°) and FSC (Fixed Square Codend).

	SDC	SSC	FDC40	FDC60	FSC
Mesh size (mm)	112.4 (2.7)	110.4 (4.0)	111.5 (2.1)	113.9 (2.1)	111.9 (1.9)
Mesh orientation	T0	T45	T0	T0	T45
Opening Angle	variable	variable	40°	60°	90°
No. of panels	2	2	4	4	4
Panel length (No. of meshes)	49.5	95	15	16	30
Panel width (No. of open meshes)	44	24	17	11	10

The span of OAs (40°, 60°, 90°) chosen for the fixed codend designs (respectively: FC40, FC60, FSC) was expected to provide sufficient contrast in the size selection for flatfish.

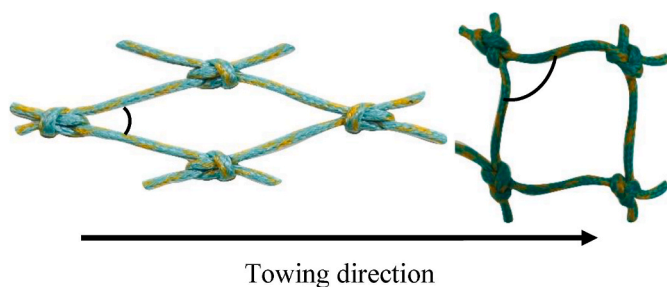


Fig. 2. Illustration of the knot where the OA was measured in the fixed frames. To the left a diamond-mesh and to the right a square-mesh.

Table 2

Mean OA of the meshes from the three tested rigid codends. The standard deviation of the OA measurements of the samples is given in brackets.

OA measures for rigid codends			
	FDC40	FDC60	FSC
OA (°)	39.1 (2.4)	63.3 (2.9)	86.3 (8.2)

2. Materials and methods

2.1. Fishing gears

Five codend designs were tested (Fig. 1 and Table 1): a standard diamond-mesh codend (Standard Diamond Codend; SDC), a standard square-mesh codend (Standard Square Codend; SSC) and three codends with mesh openness kept fixed: two fixed in a diamond-mesh orientation (Fig. 2) at 40° nominal OA (Fixed Diamond Codend 40; FDC40) and at 60° nominal OA (Fixed Diamond Codend 60; FDC60), respectively; and one fixed in a square-mesh orientation at 90° nominal OA (Fixed Square Codend; FSC). All codends were constructed using high tensile PE 5-mm single twine netting (Euroline®) with a nominal mesh size of 110 mm. The diamond-mesh codend (SDC) and the standard square-mesh codend (SSC) were made of two netting panels, with the netting of SSC turned 45° relative to the standard diamond netting configuration to obtain the square-mesh shape.

To achieve a fixed openness of the meshes for codends FDC40, FDC60, and FSC, we mounted the netting on steel frames forming a rectangular box, according to Bak-Jensen et al. (2022). The steel frames were made in the dimensions 2 x 0.75 x 0.75 m (length, width, and height, respectively; 1.125 m³). The netting, mounted with fixed

Table 3

Number of hauls used for each species in the analysis and the number of flatfish (PLE-plaice; FLE-flounder, DAB-dab) caught in the test codend or the cover for each of the codends and used in the analysis. SDC (Standard Diamond Codend), SSC (Standard Square Codend), FDC40 (Fixed Diamond Codend 40°), FDC60 (Fixed Diamond Codend 60°) and FSC (Fixed Square Codend). Additionally, mean catch weight and mean towing time is listed. The haul time varied between species for the same codend due to the different number of hauls that were used in the analysis. (For information on the individual hauls see Table S1 in Supplementary).

		Number of hauls and aggregated catches (No. fish)				
		SDC	SSC	FDC40	FDC60	FSC
PLE	No. hauls	22	16	22	6	28
	Fish in codend	2065	3655	1055	226	9310
	Fish in cover	3052	2132	1716	130	3657
	Mean Catch Weight	107.1	226.8	172.8	239.9	239.8
	Mean Towing Time	37.0	26.3	30.9	15.1	23.0
FLE	No. hauls	19	16	21	5	22
	Fish in codend	4277	1912	2882	144	4036
	Fish in cover	2386	242	1579	22	74
	Mean Catch Weight	117.6	226.8	68.2	244.5	190.2
	Mean Towing Time	40.8	26.3	33.3	15.0	23.9
DAB	No. hauls	8	15	9	5	19
	Fish in codend	129	456	345	52	1356
	Fish in cover	1235	1185	2064	109	1463
	Mean Catch Weight	83.4	226.8	21.0	244.5	182.2
	Mean Towing Time	23.1	27.0	17.8	15.0	26.8

opening angles, covered the four rectangular sides of the frame. To make sure that size selection only occurred through the meshes with the fixed opening angle (OA), PE netting with a nominal mesh size of 55 mm was used at the closing end of the rigid codends and in the extension piece ahead of the steel frames. This mesh size was considered non-selective for the species and sizes investigated. The codend mesh sizes were measured in dry conditions using an OMEGA-gauge with 125 N stretching force for 20 meshes. The mesh size of the fixed-mesh codends was measured at a section of loose meshes located between the aft end of the frame and the codline. The total length of the standard codends and the rigid codends, including the extension piece and rear ending, was ~6 m (measured as stretched length, except steel frames).

To determine the actual opening angle for the three rigid codends, 20 fixed meshes were randomly chosen per panel, and the OA was estimated photographically using scans of the netting after the fishing trials with the software FISHSELECT (Herrmann et al., 2009). The OAs were measured according to Fig. 2. To measure the exact OAs, individual meshes were digitized, the internal boundary of the bars in the mesh was marked, ignoring the knots, and a symmetric quadrilateral shaped model was fitted to the marks using image analysis facilities in FISHSELECT.

The covered codend method was used to investigate the size selection of each codend (Wileman et al., 1996). The cover was made of single 2.5 mm PE twine with a nominal mesh size of 55 mm. It had a stretched length of ~16 m (2.6 x the length of the extension piece and rigid codend combined) and a diameter of ~3 m. To prevent the cover from affecting the selectivity of the test codend, a total of seven kites were attached to the cover (Madsen et al., 2001). When testing a rigid codend, six EVA-foam floats, each with a buoyancy of 5000 g, were attached to the longitudinal upper bars of the codend frame to avoid interactions with the seabed and the codend cover (Fig. 1). Experimental fishing trials were conducted using a bottom trawl type TV300/60, made of 3 mm PE single-twine Euroline® netting with a nominal mesh size of 110 mm. The circumference of the trawl at the mouth was 34.6 m (288 meshes) and the length of the fishing line was 25.5 m. The trawl was spread using Thyboron Type 2 (1.78 m²) trawl doors and 100 m long sweeps.

Table 4

Parameter values and fit statistics obtained from the cover codend analysis, for the five codends and three flatfish species tested. Values in parentheses represent 95% CI's. The fit statistics, namely the p-value and deviance, and model degrees of freedom (DOF) are additionally noted. For the models containing either dual selection or contact parameter the L50 and SR values listed first in the table are the overall size selection parameters. Overall selection parameters are referred to as L50 and SR, while the contact parameters are referred to as L50₁ and SR₁ and L50₂ and SR₂ (see Eq. (1)).

Parameter values and fit statistics						
PLE		SDC	SSC	FDC40	FDC60	FSC
	Model	DLogistic	DLogistic	DLogistic	Richards	DLogistic
	L50 [cm]	24.51(23.91:25.03)	23.02(22.61:23.29)	24.97(24.10:25.74)	23.38(22.50:24.08)	20.69(20.23:21.08)
	SR [cm]	2.18(1.57:3.28)	3.03(2.59:3.48)	2.22(1.47:2.97)	3.50(2.27:5.28)	1.61(1.43:1.85)
	L50 ₁ [cm]	24.68 (24.12:25.13)	23.66(22.82:32.31)	25.20 (24.37:25.77)	–	20.73(20.31:21.28)
	SR ₁ [cm]	1.83 (1.28:2.53)	1.45(1.00:2.84)	1.77(1.06:2.57)	–	1.37(1.11:7.07)
	L50 ₂ [cm]	19.51 (2.51:23.82)	22.12(9.44:22.97)	21.18 (1.93:24.13)	–	19.38(14.09:20.98)
	SR ₂ [cm]	7.70 (0.78:41.86)	3.86(1.04:30.98)	5.47 (1.58:25.24)	–	7.31(1.54:15.14)
	D	–	–	–	0.01(0.01:0.12)	–
	C ₁	0.86 (0.6:0.95)	0.36(0.01: 0.95)	0.82 (0.53:0.95)	–	0.85(0.13:0.94)
	P-value	0.18	0.99	0.17	0.99	0.34
	Deviance	36.82	12.15	31.66	4.18	34.62
	DOF	30	25	25	19	32
FLE		SDC	SSC	FDC40	FDC60	FSC
	Model	CRichards	Logistic	CRichards	Probit	DLogistic
	L50 [cm]	23.68(23.02:24.05)	21.59(20.58:22.46)	24.28(23.67: 24.70)	23.30(21.85:24.23)	18.86(4.97:21.09)
	SR [cm]	4.54(3.65:6.00)	4.02(3.24:5.05)	3.85(2.96: 5.34)	3.55(1.46:5.85)	3.01(-1.31:20.66)
	L50 ₁ [cm]	24.03 (23.33:24.41)	–	24.54 (23.96: 24.93)	–	21.08(17.06:31.01)
	SR ₁ [cm]	3.62 (2.83:5.01)	–	3.20 (2.47: 4.44)	–	31.14(30.37:79.37)
	L50 ₂ [cm]	–	–	–	–	18.86(8.43:26.85)
	SR ₂ [cm]	–	–	–	–	2.98(-2.50:45.25)
	D	0.31 (0.14: 0.71)	–	0.32 (0.16:0.77)	–	–
	C ₁	0.90 (0.83:0.99)	–	0.92 (0.84:0.99)	–	0.01(0.01:0.99)
	P-value	0.05	0.99	0.63	0.99	0.60
	Deviance	40.58	11.49	26.00	5.28	16.88
	DOF	27	24	29	17	19
DAB		SDC	SSC	FDC40	FDC60	FSC
	Model	DLogistic	CProbit	CRichards	CProbit	DLogistic
	L50 [cm]	26.94(26.02:27.46)	25.09(24.80:25.37)	27.11 (26.78: 27.61)	25.14(24.52:25.75)	22.05(21.74:22.30)
	SR [cm]	1.94(1.18:4.15)	3.18(2.62:3.83)	2.01 (1.42: 3.05)	2.26(1.68:3.07)	2.16(1.66:2.97)
	L50 ₁ [cm]	27.11(26.14:29.09)	25.22(24.91:25.51)	27.17 (26.85: 27.74)	25.22(24.59:25.87)	24.19(23.06:28.73)
	SR ₁ [cm]	1.22(0.63:11.39)	3.00(2.45:3.69)	1.88 (1.31: 2.51)	2.15(1.61:2.82)	5.50(1.00:9.79)
	L50 ₂ [cm]	25.15(16.65:29.51)	–	–	–	21.79(21.42:22.17)
	SR ₂ [cm]	6.54 (3.89:11.41)	–	–	–	1.34(1.02:2.20)
	D	–	–	0.38 (0.02: 1.30)	–	–
	C ₁	0.66 (0.17:0.85)	0.95(0.92:0.98)	0.96(0.91: 0.98)	0.96(0.89:0.99)	0.34(0.12:0.53)
	P-value	0.99	>0.99	0.07	0.24	0.99
	Deviance	5.31	2.76	32.73	13.82	7.04
	DOF	20	17	22	11	18

2.2. Experimental fishing and data collection

Experimental fishing trials were conducted in the Baltic Sea onboard the German FRV *Solea* (42.40 m LOA, 950 kW) in 2021 (16th to the 27th of September) and 2022 (13th to 27th of June). The hauls were spatially distributed across German and Danish fishing grounds (ICES Subdivisions 22 and 24). The experimental codends were tested one at a time for a number of hauls. The catches obtained for each haul were treated separately for the two compartments: test codend and cover codend. The total lengths of all European plaice (*Pleuronectes platessa*), flounder (*Platichthys flesus*), and dab (*Limanda limanda*) were measured and rounded down to the nearest centimeter below. The three species were chosen because of their high abundance and commercial interest in the research area. In the case of catch making it impossible to measure all individuals of a given species, a random subsample was taken from the total, and the ratio of subsampled weight to the species' total catch weight was used as sampling fraction.

2.3. Ethics statement

The authors confirm that the ethical policies of the journal, as noted in the author guidelines page for Aquaculture and Fisheries, have been

adhered to. No ethical approval was required for this study as the dataset used for this article consisted of field samples that were collected following a fishing practice that did not expose the fish to any other harm than in commercial fishing in the region in accordance with the local legislation and institutional requirements. Therefore, no other authorization or ethics board approval was required to conduct this study. The captured animals were not exposed to any additional stress other than that involved in commercial fishing practices, and no further direct or indirect manipulation with the fish or other animals was conducted during the trials. Therefore, no information on animal welfare or on steps taken to mitigate fish suffering and methods of sacrifice is provided. This study did not involve endangered or protected species.

2.4. Estimation of codend selectivity

Codend size selection can be described as the binomial process resulting in a number of fish of length l being retained in the codend (ncd_{*l*}) and a number of fish of length l escaping (here collected in the cover codend, ncc_{*l*}). Based on the observed binomial data (ncd_{*l*} and ncc_{*l*}), a retention probability can be estimated for each length l , resulting in a retention curve, here denoted $r(l, \mathbf{v})$. The vector \mathbf{v} contains the parameters defining the retention curve, which are namely the L50, i.e.,

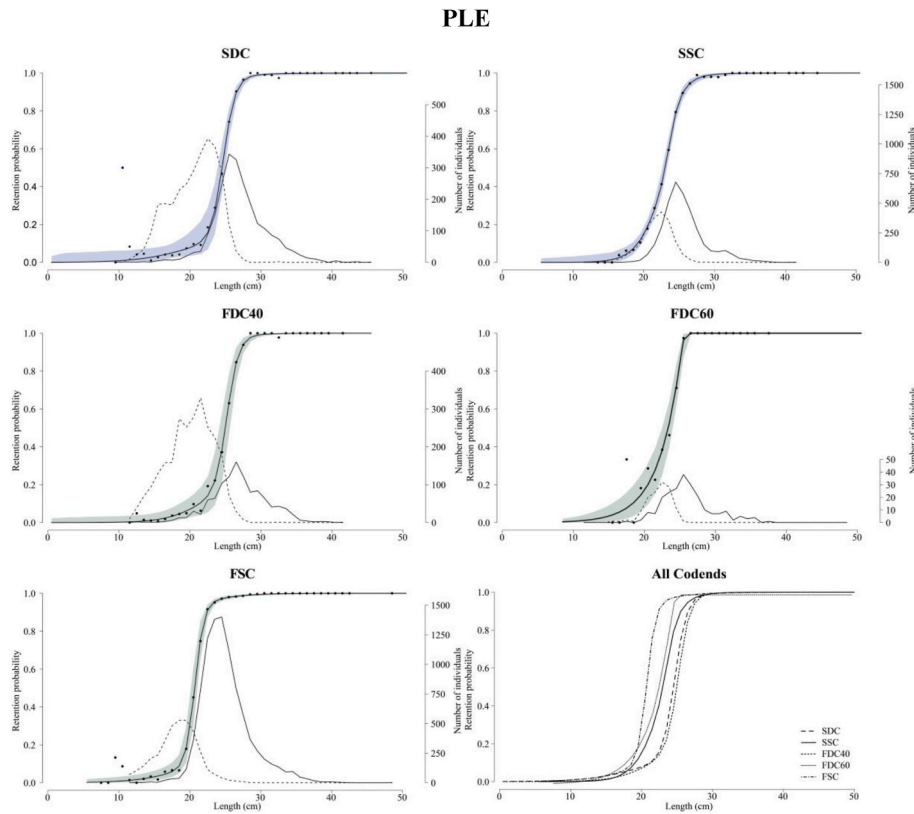


Fig. 3. Length-dependent retention probabilities of plaice estimated for the different codends tested. The solid curves represent the models fitted to the data (points) with the 95% CIs (shaded area). The solid and dashed lines at the bottom of each plot represent the number of fish at length caught in the test codend and the cover codend, respectively. Bottom right: average curves of all codends are presented together. SDC (Standard Diamond Codend), SSC (Standard Square Codend), FDC40 (Fixed Diamond Codend 40°), FDC60 (Fixed Diamond Codend 60°) and FSC (Fixed Square Codend).

the length at which retention probability is estimated to be 50%, and SR (Selection Range), i.e., the range of lengths between the 25% and 75% retention probabilities, respectively. The methodology described in [Wileman et al. \(1996\)](#) suggests using simple sigmoid functions to model $r(l, \mathbf{v})$, namely the *logistic*, *probit*, *gompertz*, and *Richards* functions. Note that in the case of *Richards*, the vector \mathbf{v} contains an additional parameter D , which adds a certain degree of asymmetry to the retention curve.

However, there are cases where the functions introduced above may not fit the experimental data very well. Therefore, for each of the four traditional models, an equivalent model where only a fraction (C) of the fish entering the codend was subjected to a length-dependent probability of escape through the meshes in the codend was considered ([Herrmann et al., 2013a, 2024](#); [Larsen et al., 2018](#); [Sistiaga et al., 2010](#)). These models are often described as CLogistic, CProbit, CGompertz, and CRichards (further detail on the models can be found in [Cuende et al., 2020](#)). In these models, if 15% of the fish would not contact the codend meshes, C acquired a value of 0.85. These models were considered relevant especially for the hauls with the rigid codends. Here distance from the center of the codend to the netting panels could have increased from what occurs in the SDC or SSC and affected the contact of fish with the codend meshes ([Herrmann et al., 2024](#)). In addition to the eight presented models including the DLogistic model ([Herrmann et al., 2016](#)) was also considered a model candidate. The DLogistic model can describe a dual selection process assuming that a fraction of the fish entering the codend is subjected to one logistic size selection process whereas the remaining fraction is subjected to another logistic size selection process ([Herrmann et al., 2024](#)). The nine model candidates can be described as follows:

$$r(l, \mathbf{v}) = \begin{cases} \text{Logistic}(l, L50, SR) \\ \text{Probit}(l, L50, SR) \\ \text{Gompertz}(l, L50, SR) \\ \text{Richard}(l, L50, SR, D) \\ \text{CLogistic}(l, C, L50, SR) \\ \text{CProbit}(l, C, L50, SR) \\ \text{CGompertz}(l, C, L50, SR) \\ \text{CRichard}(l, C, L50, SR, D) \\ \text{DLogistic}(l, C, L50_1, SR_1, L50_2, SR_2) \end{cases} \quad (1)$$

The selection curves and associated selectivity parameters \mathbf{v} were estimated by means of a maximum likelihood function for data pooled over hauls ([Bak-Jensen, 2022](#)). The parameters $L50_1$, SR_1 contained in are referred to as contact selection parameters. In the DLogistic the $L50_2$ and SR_2 are the selection parameters for the second size selection process. The overall selectivity parameters ($L50$ and SR) for $r(l, \mathbf{v})$ are obtained using the numerical technique described by [Sistiaga et al. \(2010\)](#).

The estimations were made separately for each species and codend for selectivity data pooled across hauls. This includes the effect of between-haul variations into a single selection curve, to make what [Millar \(1993\)](#) called a “fishery selection curve” ([Sala et al., 2015](#); [Sistiaga et al., 2010](#); [Herrmann et al., 2012](#)).

Hauls where $n_{cd_i} + n_{cc_i} < 20$ fish for the species of interest were excluded from analyses. Specifically, this means that only hauls containing more than 20 individuals of the species analyzed were used in the analysis. As the size selection process potentially can differ between species and codends ([Cuende et al., 2022](#); [Jacques et al., 2024](#)), model choice was conducted separately among the nine candidate models in Eq. (1) for each species and codend. Specifically, the fitted models were ranked according to their AIC values ([Akaike, 1974](#)), and the model with the lowest AIC was chosen for the specific species and codend. Diagnosis of the selected model was conducted by visual inspection of residuals

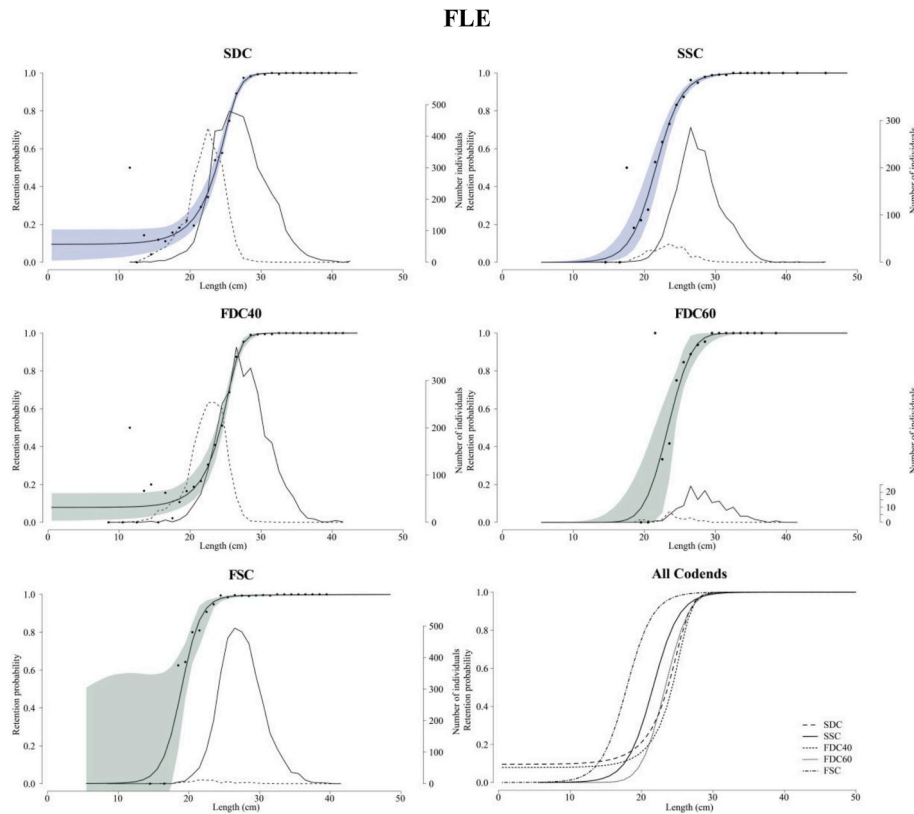


Fig. 4. Length-dependent retention probabilities of flounder estimated for the different codends tested. The solid curves represent the models fitted to the data (points) with the 95% CIs (shaded area). The solid and dashed lines at the bottom of each plot represent the number of fish at length caught in the test codend and the cover codend, respectively. Bottom right: average curves of all codends are presented together. SDC (Standard Diamond Codend), SSC (Standard Square Codend), FDC40 (Fixed Diamond Codend 40°), FDC60 (Fixed Diamond Codend 60°) and FSC (Fixed Square Codend).

distribution and Chi-square test (acceptable if p -value ≥ 0.05) according to [Wileman et al. \(1996\)](#). In the context of size selectivity modeling, the p -value quantifies the probability for by chance obtaining at least as big deviation between experimental size selectivity data collected and the modelled size selection curve. Therefore, as long as the obtained p -value is at least 0.05 corresponding to at least 5% probability for by chance obtaining the deviation between data and modelled size selection curve we cannot rule out that the model can describe the data. The uncertainties on the estimated size selection curves and associated parameters were quantified in terms of 95% Efron confidence intervals (CIs) that were estimated using the bootstrap method with 1000 repetitions according to [Bak-Jensen et al. \(2022\)](#).

2.5. Evaluation of differences in $L50$ and SR in size selection between tested codends

The selective properties of the codends were compared by estimating the difference in the values for $L50$ and SR between them (For more details see [Bak-Jensen et al. \(2022\)](#)):

$$\Delta L50 = L50_T - L50_B \quad (2)$$

$$\Delta SR = SR_T - SR_B$$

Where $L50_B$ and SR_B are the values for the codend used as baseline for the specific comparison, and $L50_T$ and SR_T are the values for the codend considered as treatment for the specific comparison. 95% Efron confidence intervals were estimated from a bootstrap distribution of $\Delta L50$ and ΔSR obtained from the previously estimated bootstrap distributions for baseline and treatment codend ([Efron, 1979](#); [Herrmann et al., 2018](#); [Larsen et al., 2018](#)). Thus, we consider differences between baseline and treatment as statistically significant when the 95% confidence intervals

around $\Delta L50$ or ΔSR do not encompass zero.

2.6. Supplementary analysis of potential effect of catch weight and towing time on size selection

To investigate whether differences in mean towing time and codend catch weight potentially could have affected the inference of difference in size selection between codend designs tested, an additional analysis was conducted for each codend and species separately. The procedure for this analysis, which is only an explorative supplement to the fishery mean selection analysis ([Millar et al., 2004](#)), as conducted for each codend and species in the main analysis of this study is identical to the one used by [Herrmann, Wienbeck, et al. \(2013\)](#), [Herrmann et al. \(2015\)](#), [Pol et al. \(2016\)](#), [Brčić et al. \(2018\)](#). In this analysis the size selectivity was analyzed in two steps using a random and fixed effect method proposed by Fryer (1991). Specifically, in the first step, the size selection in each haul separately was modelled by the logistic model with the $L50$ and SR values of each haul and their covariance matrix being estimated. In the second step, which took into account both the uncertainty in the individual hauls and between-haul variation in size selection, the results were combined over hauls to predict mean $L50$ and mean SR and the potential effect of catch weight (CW) and the towing time (TT) on the mean. A full model on the form was used:

$$\begin{aligned} L50 &= \alpha_0 + \alpha_1 \times CW + \alpha_2 \times TT \\ SR &= \beta_0 + \beta_1 \times CW + \beta_2 \times TT \end{aligned} \quad (3)$$

Based on the full model, all simpler models that could be obtained by ignoring one or more of the parameters ($\alpha_0, \alpha_1, \alpha_2, \beta_0, \beta_1, \beta_2$) were also considered as candidate models for predicting the size selection in the specific codend for the specific species. The model resulting in the lowest AIC values was then selected for the specific codend and species. In case

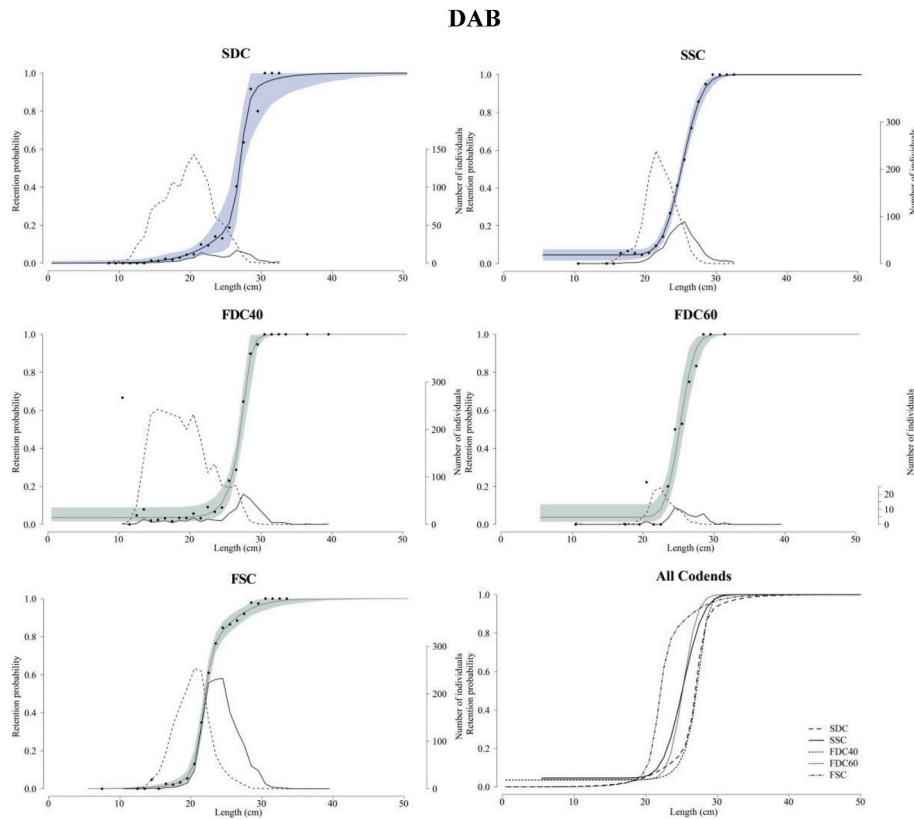


Fig. 5. Length-dependent retention probabilities of dab estimated for the different codends tested. The solid curves represent the models fitted to the data (points) with the 95% CIs (shaded area). The solid and dashed lines at the bottom of each plot represent the number of fish at length caught in the test codend and the cover codend, respectively. Bottom right: average curves of all codends are presented together. SDC (Standard Diamond Codend), SSC (Standard Square Codend), FDC40 (Fixed Diamond Codend 40°), FDC60 (Fixed Diamond Codend 60°) and FSC (Fixed Square Codend).

the selected model did not include any of the parameters ($\alpha_1, \alpha_2, \beta_1, \beta_2$), we concluded that neither codend catch weight nor towing time were found to affect the size selection for that specific species when being size selected in that specific codend. Conversely, in case CW or TT was in the selected model we used the model to predict the maximal effect on mean L50 and SR. In this case, the magnitude of influence of the CW and TT was investigated. The mean values for the CW and TT for each codend and the total mean were used as potential CW and TT. Then we estimated the corresponding maximal percentage change in the value due to differences in catch weights and towing durations.

3. Results

3.1. Measurements of OA in the fixed codends

The variability of the OAs in the rigid codends was generally low, and the mean was close to the intended value (Table 2).

3.2. Description of fishing operations and catches

In September 2021, a total of 55 hauls were conducted, of which 32 hauls were made with the Fixed Diamond 40° codend (FDC40) and 23 hauls with the Standard Diamond Codend (SDC). In June 2022, an additional 50 hauls were conducted: 18 hauls with the Standard Square Codend (SSC), 28 hauls with the Fixed Square Codend (FSC), and 6 hauls with the Fixed Diamond Codend 60° (FDC60). The mean haul time varied between 15.0 and 30.9 min. The haul time varied between species for the same codend due to the different number of hauls that were used in the analysis. The mean catch weights varied between 21.0 and 239.9 kg. Further operational information related to the hauls can be found in supplementary materials (Table S1). Fishing depths varied between 14

and 46 m, and the haul duration varied between 15 and 60 min. The total number of hauls included in the analyses for each species is listed in Table 3.

3.3. Codend selectivity analysis

The models in Eq. (1) were estimated for all species and codends. The best model for each combination was chosen according to the lowest AIC. The fit statistics for all the selected models (Table 4) showed that the deviation between the experimental data and the modelled curves is acceptable (p -value ≥ 0.05). In most cases, the best candidate model was one of the contact models considered or the Dlogistic model (Eq. (1)). This means that there is often a fraction of the individuals that either do not contact the meshes or are subjected to a second selection process. The primary selection (described by $L50_1$ and SR_1) was in most cases the dominating selection occurring (C_1 above 0.5). However, uncertainty in the estimation of C-values is relatively high for some models (for plaice SDC, FSC, for flounder FSC, and for dab SDC). The average L50s for plaice varied from 20.69 cm to 24.97 cm (Fig. 3). For flounder and dab, L50s varied from 18.86 cm to 24.28 cm (Fig. 4), and from 22.05 cm to 27.11 cm (Fig. 5), respectively. The CI for flounder is considerably higher for the FSC than for the two other species, both in terms of L50 and SR. The SR for all species and codend configurations were below 5 cm.

The difference between the L50s estimated using Eq. (2) was significant in the majority of the pairwise comparisons for all species (Table 5). The pattern for the difference in L50 between the codends is similar for all three species, with both square-mesh codends (SSC and FSC) having significantly lower L50s than the SDC and FDC40. When comparing FDC40 with FDC60 and FSC, the L50 was significantly higher for FDC40 in almost all cases except for flounder when comparing

Table 5

Differences in overall L50 values, estimated by the best candidate models ($\Delta L50$ (cm)) for the multiple pairwise comparisons between the five different codend configurations, and for all species. Values in parentheses represent 95% CIs. Numbers in bold denote significance.

		$\Delta L50$ (cm)			
		PLE			
		Baseline			
		SDC	SSC	FDC40	FDC60
Treatment	SDC				
	SSC	-1.49 (-2.06; 0.86)			
	FDC40	0.46 (-0.56;1.30)	1.95 (1.05;2.80)		
	FDC60	-1.13 (-2.15; 0.28)	0.36 (-0.59;1.16)	-1.59 (-2.69; 0.49)	
	FSC	-3.82 (-4.46; 3.10)	-2.33 (-2.87; 1.80)	-4.28 (-5.13; 3.34)	-2.69 (-3.51; 1.69)
		FLE			
		Baseline			
		SDC	SSC	FDC40	FDC60
Treatment	SDC				
	SSC	-2.09 (-3.26; 1.07)			
	FDC40	0.60 (-0.09;1.30)	2.69 (1.66;3.82)		
	FDC60	-0.38 (-2.35;0.83)	1.70 (-0.38;3.20)	-0.98 (-2.72;0.14)	
	FSC	-4.82 (-18.73; 2.44)	-2.73 (-16.71; 0.02)	-5.42 (-19.31; 2.99)	-4.44 (-18.24; 1.26)
		DAB			
		Baseline			
		SDC	SSC	FDC40	FDC60
Treatment	SDC				
	SSC	-1.85 (-2.46; 0.86)			
	FDC40	0.17 (-0.46;1.15)	2.02 (1.56;2.55)		
	FDC60	-1.80 (-2.66; 0.75)	0.04 (-0.68;0.73)	-1.97 (-2.73; 1.22)	
	FSC	-4.89 (-5.50; 3.89)	-3.04 (-3.47; 2.64)	-5.06 (-5.64; 4.64)	-3.09 (-3.78; 2.47)

FDC40 to FDC60. The L50 for FSC was significantly lower compared to SSC for all species (Table 5).

For comparison of SRs, the ΔSR was calculated according to Eq. 4. For all species, no significant differences were found for most of the codend comparisons in terms of SR (Table 6). However, there was a significant difference between the FSC and SSC for plaice and dab, as well as between FSC and FDC60 for plaice.

3.4. Potential effect of catch weight and towing time on size selection

Due to the differences between codends in mean CW and TT, the potential effect of this on size selection was investigated following the procedure described in section 2.5. The towing time varied between tows, which might affect the escape opportunities and thereby the size selectivity. Furthermore, the catch weight also vary between the hauls and mean between codends. In most cases, the CW and TT showed no effect on the L50 and SR (Table 7).

In the cases where CW or TT were included in the model, further analysis showed that either of these two parameters had less than a 2% difference in size selectivity estimated between the five tested codends for any of the three species (Table 8).

4. Discussion

Based on an experimental design that allows full control of the shape of the codend meshes, this study provides a comprehensive and systematic testing of five research questions about the size selectivity of flatfish species in relation to mesh geometry and its variability. To be able to generalize the results regarding the size selection of flatfish species, three flatfish species were included in this investigation. We haven't found previous proof-of-concept studies testing the selectivity properties of SDC and/or SSC with 110 mm mesh size on these three species. However, the meta-analysis in O'Neill et al. (2020) on size selection of plaice in SDC, enables placing our results in the context of previous research on codend selectivity for flatfish. The L50 was estimated to be between 23 cm and 25 cm (O'Neill et al., 2020), which is in line with the L50 we found in all cases for the diamond-mesh configurations.

The fixed codends raise questions about how the construction of the codend may challenge the size selectivity compared to a standard codend, for instance, the frame and the covered meshes in the rear end of the codends. The small meshes in the rear end of the codend are assumed not to have more influence than the catch buildup in a standard codend. In a standard codend, the catch will likewise mask the netting in the rear end of the codend as it builds up. During the fishing operation *GoPro* cameras were attached to the fixed codends. The video in Supplementary Material shows the cover in the background with free passage for the fish to escape the codend. One haul (Haul ID 13 in Table S1 in Supplementary Material) was eliminated based on video material due to doubt whether the cover had twisted and thereby masked part of the codend. Obviously, the metal frame being used in the fixed mesh codends is a construction not being part of the standard diamond and square mesh codends. Whether this frame could have a visual effect affecting the behavior of the flatfish making them less willing to seek escape through the meshes is unknown. However, given the fact that the size selectivity estimates do not show any sign of less contact for the fixed frame codends compared to the two traditional codends we find it unlikely that the frame itself should have had any negative effect on the size selectivity.

Since mean towing time varied between codends (Table 3), this could potentially have affected the difference in size selectivity estimated between them. This, as well as the mean towing time, could have affected the estimated difference in size selectivity between the codends. To gain more insight into whether differences in towing time and/or codend catch weight could have affected the difference size selectivity between codends we did an additional analysis exploring this. The analysis showed that it is unlikely that any of these two parameters had any notable effect on the differences in size selectivity estimated between the five tested codends for any of the three species (less than 2% in the most extreme cases; Table 8).

First, we inquired whether standard square-mesh codends have a higher probability of retaining undersized fish than standard diamond-mesh codends. Our results found that square-mesh codends risk retaining more undersized flatfish than diamond-mesh codends. For all three species significantly lower L50s were found for the square-mesh configurations compared to all diamond-mesh configurations (Table 9). This confirms the results found in earlier selectivity studies for scaldfish (*Arnoglossus laterna*) (Sala et al., 2008) and four-spot megrim (*Lepidorhombus boschii*) (Guijarro & Massutí, 2006). Furthermore, this confirms the need that when optimizing selectivity in mixed demersal fisheries, all species of interest should be considered to avoid negatively impacting some species when trying to improve others (Guijarro & Massutí, 2006; Bak-Jensen et al., 2023).

Table 6

Differences in overall SR values estimated by the best candidate models (Δ SR (cm)) for the multiple pairwise comparisons between the five different codend configurations, and for all species. Values in parentheses represent 95% CIs. Numbers in bold denote significance.

Δ SR (cm)					
PLE					
Baseline					
		SDC	SSC	FDC40	FDC60
Treatment	SDC				
	SSC	0.85(-0.37:1.55)			
	FDC40	0.04(-1.21:1.11)	-0.81(-1.68:0.15)		
	FDC60	1.32(-0.37:3.04)	0.47(-0.85:2.18)	1.28(-0.11:3.15)	
	FSC	-0.57(-1.71:0.04)	-1.42(-1.92: 0.93)	-0.61(-1.38:0.09)	-1.89(-3.59: 0.62)
FLE					
Baseline					
		SDC	SSC	FDC40	FDC60
Treatment	SDC				
	SSC	-0.52(-2.01:0.94)			
	FDC40	-0.69(-2.39:1.11)	-0.17(-1.56:1.57)		
	FDC60	-0.98(-3.67:1.29)	-0.47(-2.76:1.95)	-0.30(-2.87:2.11)	
	FSC	-1.53(-6.48:16.06)	-1.01(-5.79:16.62)	-0.84(-5.99:16.93)	-0.54(-6.44:17.19)
DAB					
Baseline					
		SDC	SSC	FDC40	FDC60
Treatment	SDC				
	SSC	1.24(-1.06:2.32)			
	FDC40	0.07(-2.15:1.44)	-1.17(-2.04:0.03)		
	FDC60	0.32(-2.02:1.53)	-0.93(-1.79:0.03)	0.25(-0.99:1.25)	
	FSC	0.22(-2.06:1.33)	-1.02(-1.93: 0.11)	0.15(-0.98:1.13)	-0.10(-1.05:0.81)

Table 7

Outcome of the chosen model parameter. "N" has no significant effect. "Y" is a significant effect. "-" notes where it was not possible to calculate an effect due to no variation in the parameter between hauls.

		SDC		SSC		FDC40		FDC60		FSC	
		CW	TT	CW	TT	CW	TT	CW	TT	CW	TT
		Plaice	L50	N	N	N	N	N	N	N	-
SR	N	Y	N	N	N	N	N	N	-	N	N
Flounder	L50	Y	N	N	N	Y	Y	N	-	Y	N
SR	Y	N	N	N	N	N	N	N	-	N	N
Dab	L50	N	N	N	N	N	N	N	-	N	N
SR	N	N	N	N	N	N	N	N	-	Y	Y

Table 8

The calculated effect on L50 or SR in percentage between changing the catch size or towing time from the average for the codend (found in Table 3) to the total average (Found in Table S1). The values are calculated for the significant parameters from Supplementary Material 4, Table S3.

	Different in mean L50 with significant difference (%)	Different in mean SR with significant difference (%)
Plaice SDC	-	<0.1
Flounder SDC	0.9	<0.1
Flounder FDC40	1.7	-
Dab FSC	-	<0.1

The second question was whether the probability of retention of undersized fish was greater with a wider OA in fixed diamond-mesh compared to a narrower one. The FDC60 was observed to retain significantly more undersized plaice and dab compared to the FDC40, but no difference was observed for flounder where CIs were wide (Table 9). For plaice and dab, the increase in OA led to significant

increases in the retention of undersized individuals. However, there was no significant difference for flounder when increasing the OA from 40° to 60°. One explanation for the different result obtained for flounder could be morphological differences of flounder compared to plaice and dab, such as width, spine placement, or skin roughness. For example, a 60° OA may result in the mesh being too narrow for broad-bodied flatfish such as turbot (*Scophthalmus maximus*), whereas slim-bodied flatfish like Dover Sole (*Solea solea*) could more easily escape. In addition, other species-specific characteristics, such as skin roughness and anal spines, may affect the likelihood of escape. Despite inter-species differences, our results imply that fixing the mesh with a wide OA is likely to result in reduced escape possibilities for flatfish compared to narrow OA.

The third question concerned whether using a codend with a wide fixed OA (60°) would have a higher probability of retaining undersized flatfish than the SDC. The FDC60 was observed to retain significantly more undersized plaice and dab compared to the SDC, but no difference was observed for flounder where the CIs were wide (Table 9). The SDC codend would probably have narrower OA than 60° during fishing, which would provide escape possibilities for larger sized flatfish. This can explain the larger L50 found for the SDC compared to FC60. The

Table 9

Overview of the answers to the research questions addressed in this study, using the three flatfish species considered. “Y” is a confirmation of the question. “ns” is not significant. And “N” is noted when the negative answer is significant. The evaluation is based on the numbers in Table 5 and delta-figures in Supplementary (Figure S1 to Figure S3).

Research Question 1			
Does a standard square-mesh codend (flexible meshes) have a higher probability of retaining undersized flatfish than a standard diamond-mesh codend (flexible meshes)?			
	PLE	FLE	DAB
SSC risk retaining more undersized flatfish than SDC	Y	Y	Y
Research Question 2			
Does a diamond-mesh codend with a wide and stable OA (fixed meshes) have a higher probability of retaining undersized flatfish than one with a narrow and stable OA (fixed meshes)?			
	PLE	FLE	DAB
FDC60 risk retaining more undersized flatfish than FDC40	Y	ns	Y
Research Question 3			
Does a diamond-mesh codend with a wide and stable OA (fixed meshes) have a higher probability of retaining undersized flatfish than a standard diamond-mesh codend with variable OAs (flexible meshes)?			
	PLE	FLE	DAB
FDC60 risk retaining more undersized flatfish than SDC	Y	ns	Y
Research Question 4			
Does a codend with stable square-meshes (fixed meshes) have a higher probability of retaining undersized flatfish than a standard square-mesh codend with variable OAs (flexible meshes)?			
	PLE	FLE	DAB
FSC risk retaining more undersized flatfish than SSC	Y	Y	Y
Research Question 5			
Does a codend with stable mesh geometry (fixed meshes) have a lower variability in size selection of flatfish than a codend with the same mesh shape but variable mesh geometry (flexible meshes)?			
	PLE	FLE	DAB
SDC have higher variability in size selection than FDC40	ns	ns	ns
SDC have higher variability in size selection than FDC60	ns	ns	ns
SSC have higher variability in size selection than FSC	Y	ns	Y

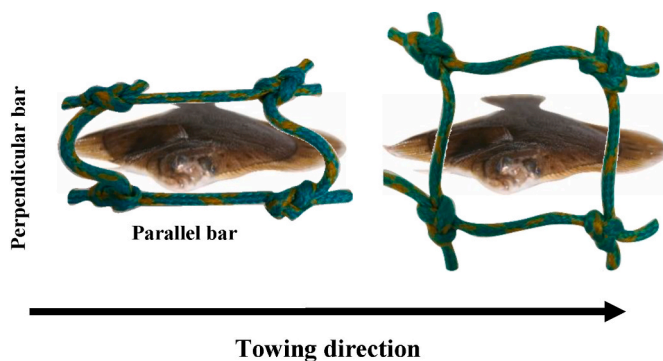


Fig. 6. Illustration of how the slack bars in a square-mesh codend can facilitate escape for flatfish.

results for flounder again differed partially from the other species.

The fourth question asked if the probability of retention of undersized fish was greater for a fixed square-mesh than for the standard square-mesh. The answer was significantly positive in all cases (Table 9). The significant difference between the FSC and SSC strongly supports the hypothesis that the SSC deforms toward a more rectangular shape, which is more suitable for flatfish escape. The slackness in the bars means that the meshes in the SSC are more suitable for flatfish penetration, allowing larger flatfish to escape (Fig. 6). The significant difference in SR between the FSC and the SSC for plaice and dab also indicates that the SSC is not as stable as Robertson and Stewart (1988) believed it to be (Table 6). As Robertson and Stewart (1988) believed the square-mesh would retain its shape under load and that the meshes

would not be stretched and constricted.

The last question asked if a fixed mesh would have sharper size selection compared to a standard mesh. In seven out of nine cases, the answer was not significant (Table 9). For plaice and dab there were no significant differences between the fixed diamond-meshes (FDC40 and FDC60) and the SDC. However, for the SSC compared to the FSC, the SR was found to be lower when the meshes were fixed, indicating that the meshes in the SSC must deform during fishing. Results obtained in experiments show that flatfish selection in codends is often related to narrow SR (Sala et al., 2018) thus the sharpness of their size selection is not a major issue.

The assumption that diamond-meshes are well-suited to flatfish escape based on their shape depends on the angle at which the fish approach the mesh opening (contact angle) and orientation of the fish relative to the mesh. Cuende et al. (2020) and Krag et al. (2014) found evidence that rotation and contact angle influence the ability of blue whiting (*Micromesistius poutassou*) and Antarctic krill (*Euphausia superba*) to penetrate mesh openings and escape. Making optimal contact with the mesh appears to be highly dependent on the fish's ability to maneuver. For example, if fish are assumed to be swimming either against or with the towing direction, for an individual to escape from a diamond-mesh codends in the top or bottom panels, it would have to perform a 90° yaw rotation followed by a 90° pitch rotation (Fig. 7b). Therefore, the orientation of the mesh might have influenced the selectivity to a larger degree, as the rigid construction with diamond-meshes had the acute angle parallel to the length of the codend and the bottom part, depending on where in the codend and the catch volume, is likely to be larger than in a standard diamond-mesh codend. In contrast, escaping through square-meshes in the top or bottom panels requires a 45° body roll in addition to the 90° pitching movement (Fig. 7b). Very little is known about flatfish's ability to maneuver in the water flow, as these species typically rely on maintaining proximity to the seabed (Fox et al., 2018); some of these rotations may be unnatural for these species or greatly destabilize them by exposing their body surface to the flow. This may ultimately affect which panel or panels most escapes occur, and thus it should be taken into consideration in future studies.

When considering meshes in the side panels, only a 90° yaw would be needed in the case of diamond-meshes, while an additional 45° body roll is required for the square-meshes (Fig. 7c). If the side panels were to offer the most suitable option for escapement, this may reflect negatively on the overall selectivity, as according to Ryer (2008), flatfish tend to keep close proximity to the bottom netting and seek escape downwards. These mechanics might also be responsible for why the models including the contact parameter C (Eq. (1)) were chosen by AIC in most cases (Table 4). However, processes described by the Dlogistic model could also be caused by a different selection process occurring during haul-back.

Our results show that fixing meshes to a square shape (FSC) provides a more well-defined size selection compared to a standard square-mesh. From a practical point of view, a well-defined size selection means that adjusting mesh size would result in more predictable changes in size selection. Fixing the mesh openings to square-meshes in flatfish fisheries would enable more precise control over catches of commercial and undersized individuals. This is desirable from a fisheries management point of view (better control on exploitation patterns), and for the economical sustainability of the fishing activities (especially in fisheries subjected to catch-restrictive rules). However, dealing with multiple species with different minimum conservation reference sizes (MCRSs) or commercially rentable sizes inevitably results in some losses of commercial catch and retention of undersized individuals. Increasing the mesh size in a square-mesh configuration could potentially contribute to reducing bycatch of unwanted roundfish species and maybe also invertebrates. A square-mesh codend with a mesh size aligned with the MCRS for flatfish could provide escape possibilities that could reduce the number of unwanted individuals caught while maintaining high

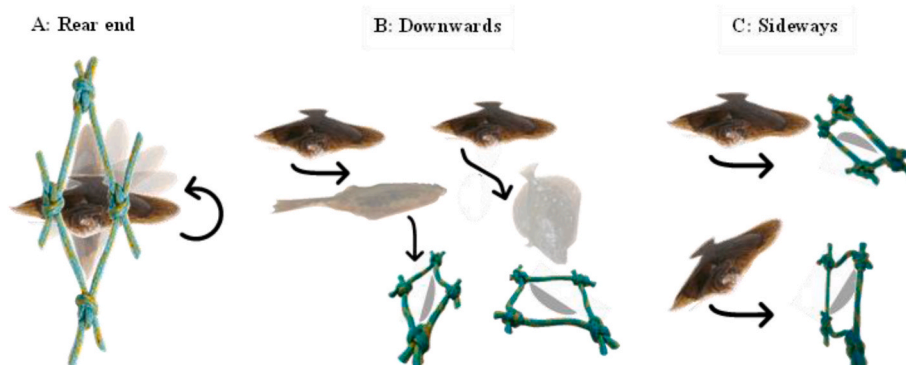


Fig. 7. A: Illustration of the possible need for rotation for escapement through a diamond-mesh with 40° OA. B: Sketching of the movement a flatfish needs to make to escape downwards through a diamond-mesh and square-mesh respectively in the codend. C: Sketching of the movement a flatfish needs to make to escape sideways in the codend.

catch efficiency for commercially sized individuals. As the L50 for dab was significantly higher than for the other two species, there might be a loss of commercially size dab in case with a square-mesh is fixed to fit MCRS for plaice or flounder. In fisheries where there is a need to reduce the capture of flatfish, either undersized individuals or in general, fixed meshes could be a solution to improve escape probabilities. For example, fixing diamond-meshes in a narrow OA and turning the orientation of the meshes in the upper and lower panels 90° so the widest part of the mesh opening is perpendicular to the towing direction would be optimal for bottom and top escape for flatfish but would retain larger roundfish.

To investigate the effect of mesh shape and OA on the selectivity of flatfish species, in this study we applied an experiment specifically designed to control the mesh shape during fishing operations. However, it needs to be noted that the tested fixed-mesh codends (FDC40, FDC60, and FSC) have been designed only for experimental purposes and they are not directly applicable to commercial fisheries. To apply the knowledge obtained in this study into commercial fisheries, several technological challenges need to be addressed. For instance, fixed meshes require some kind of rigidness, but rigidness is often associated with handling, clogging, and storing issues. Rigidness has been previously pursued by coating the netting materials (e.g. Ultracross netting; Madsen et al., 2002) but perhaps it is time for a more dramatic rethinking of the codend design, moving away from standard netting materials in favor of, for example, non-mesh codends (e.g. Millar et al., 2023). The gain of a knife-edge size selection has high value, as this could improve the catch efficiency and reduce unwanted bycatch of undersized flatfish while improving escape possibilities of other non-targeted marine organisms.

CRedit authorship contribution statement

Zita Bak-Jensen: Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Data curation, Conceptualization. **Bent Herrmann:** Writing – review & editing, Writing – original draft, Validation, Supervision, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Juan Santos:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Project administration, Methodology, Formal analysis, Data curation, Conceptualization. **Daniel Stepputtis:** Writing – review & editing, Writing – original draft, Project administration, Methodology. **Valentina Melli:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Conceptualization. **Jordan P. Feekings:** Writing – review & editing, Writing – original draft, Project administration, Methodology, Funding acquisition, Conceptualization.

Data availability

Derived data supporting the findings of this study are available from the corresponding author zitba@aqu.dtu.dk on request.

Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.aaf.2024.10.001>.

References

- Akaike, H. (1974). A new look at the statistical model identification. *IEEE Trans. Automat. Contr.*, 19(6), 716–723.
- Bak-Jensen, Z., Herrmann, B., Santos, J., Jacques, N., Melli, V., & Feekings, J. P. (2022). Fixed mesh shape reduces variability in codend size selection. *Canadian Journal of Fisheries and Aquatic Sciences*, 79(11), 1820–1829.
- Bak-Jensen, Z., Herrmann, B., Santos, J., Jacques, N., Melli, V., & Feekings, J. P. (2023). The capability of square-meshes and fixed-shape meshes to control codend size selection. *Fisheries Research*, 264, Article 106704.
- Borges, L., Rogan, E., & Officer, R. (2005). Discarding by the demersal fishery in the waters around Ireland. *Fisheries Research*, 76(1), 1–13.
- Brić, J., Herrmann, B., & Sala, A. (2018). Predictive models for codend size selectivity for four commercially important species in the Mediterranean bottom trawl fishery in spring and summer: Effects of codend type and catch size. *PLoS One*, 13(10), Article e0206044. <https://doi.org/10.1371/journal.pone.0206044>, 2018 Oct 22 PMID: 30346961; PMCID: PMC6197670.
- Blublitz, C. G. (1996). Quantitative evaluation of flatfish behavior during capture by trawl gear. *Fisheries Research*, 25, 293–304.
- Catchpole, T. L., Frid, C. L. J., & Gray, T. S. (2005). Discards in north sea fisheries: Causes, consequences and solutions. *Marine Policy*, 29(5), 421–430.

- Catchpole, T. L., Ribeiro-Santos, A., Mangi, S. C., Hedley, C., & Gray, T. S. (2017). The challenges of the landing obligation in EU fisheries. *Marine Policy*, *82*, 76–86.
- Condie, H. M., Grant, A., & Catchpole, T. L. (2014). Incentivising selective fishing under a policy to ban discards; lessons from European and global fisheries. *Marine Policy*, *45*, 287–292.
- Cuende, E., Arregi, L., Herrmann, B., Sistiaga, M., & Aboitiz, X. (2020). Prediction of square mesh panel and codend size selectivity of blue whiting based on fish morphology. *ICES Journal of Marine Science*, *77*(7–8), 2857–2869 (2020).
- Cuende, E., Sistiaga, M., Herrmann, B., & Arregi, L. (2022). Optimizing size selectivity and catch patterns for hake (*Merluccius merluccius*) and blue whiting (*Micromesistius pouassou*) by combining square mesh panel and codend designs. *PLoS One*, *17*(1), Article e0262602. <https://doi.org/10.1371/journal.pone.0262602>. PMID: 35051211.
- Efron, B. (1979). Bootstrap methods: Another look at the jackknife. *Annals of Statistics*, *7*, 1–26.
- Feekings, J., Bartolino, V., Madsen, N., & Catchpole, T. (2012). Fishery discards: Factors affecting their variability within a demersal trawl fishery. *PLoS One*, *7*(4), Article e36409.
- Ferro, R., Jones, E., Kynoch, R., Fryer, R., & Buckett, B. (2007). Separating species using a horizontal panel in the Scottish North Sea whitefish trawl fishery. *ICES Journal of Marine Science*, *64*, 1543–1550.
- Fonteyne, R., & Mrabet, R. (1992). Selectivity experiments on sole with diamond and square mesh codends in the belgian coastal beam trawl fishery. *Fisheries Research*, *13*, 221–233.
- Fox, C. H., Gibb, A. C., Summers, A. P., & Bemis, W. E. (2018). Benthic walking, bounding, and maneuvering in flatfishes (pleuronectiformes: Pleuronectidae): New vertebrate gaits. *Zoology*, *130*, 19–29.
- Gibson, R. N., Nash, R. D. M., Geffen, A. J., & van der Veer, H. W. (2015). *Flatfishes: Biology and exploitation* (2nd ed.). John Wiley & Sons, Ltd.. Published 2015 by John Wiley & Sons, Ltd.
- Guijarro, B., & Massutí, E. (2006). Selectivity of diamond- and square-mesh codends in the deepwater crustacean trawl fishery off the Balearic Islands (western Mediterranean). *ICES Journal of Marine Science*, *63*(1), 52–67.
- Halliday, R. G., Cooper, C. G., Fanning, P., Hickey, W. M., & Gagnon, P. (1999). Size selection of Atlantic cod, haddock and pollock (saithe) by otter trawls with square and diamond mesh codends of 130–155mm mesh size. *Fisheries Research*, *41*, 255–271.
- Herrmann, B. (2005). Effect of catch size and shape on the selectivity of diamond mesh cod-ends. II. Theoretical study of haddock selection. *Fisheries Research*, *71*, 15–26.
- Herrmann, B., Bak-Jensen, Z., Sistiaga, M., Brinkhof, J., Larsen, R. B., Grimaldo, E., Cerbule, K., Kostak, E. N., & Eighani, M. (2024). Are rigid sorting devices necessary to control size selectivity in demersal trawl fisheries? *Regional Studies in Marine Science*, *72*(2024), Article 103445.
- Herrmann, B., Krag, L. A., Frandsen, R. P., Madsen, N., Lundgren, B., & Stæhr, K. J. (2009). Prediction of selectivity from morphological conditions: Methodology and a case study on cod (*Gadus morhua*). *Fisheries Research*, *97*, 59–71.
- Herrmann, B., Krag, L. A., & Krafft, B. A. (2018). Size selection of Antarctic krill (*Euphausia superba*) in a commercial codend and trawl body. *Fisheries Research*, *207*, 49–54.
- Herrmann, B., Sistiaga, M., Larsen, R. B., & Nielsen, K. N. (2013). Size selectivity of redfish (*Sebastes* spp.) in the Northeast Atlantic using grid-based selection systems for trawls. *Aquatic Living Resources*, *26*, 109–120. <https://doi.org/10.1051/alr/2013051>
- Herrmann, B., Wienbeck, H., Moderhak, H., Stepputtis, D., & Krag, L. A. (2013). The influence of twine thickness, twine number and netting orientation on codend selectivity. *Fisheries Research*, *145*, 22–36.
- Herrmann, B., Wienbeck, H., Stepputtis, D., Krag, L. A., Feekings, J. P., & Moderhak, W. (2015). Size selection in codends made of thin-twined dyneema netting compared to standard codends: A case study with cod, plaice and flounder. *Fisheries Research*, *167*, 82–91. <https://doi.org/10.1016/j.fishres.2015.01.014>
- Hilborn, R., Hively, D. J., Loke, N. B., de Moor, C. L., Kurota, H., Kathena, J. N., Mace, P. M., Minto, C., Parma, A. M., Quiroz, J. C., & Melnychuk, M. C. (2021). Global status of groundfish stocks. *Fish and Fisheries*, *22*(5), 911–928.
- Jacques, N., Herrmann, B., Brinkhof, J., & Sistiaga, M. (2024). Understanding size selectivity of trawls using structural models: Methodology and a case study on fish sorting grids. *Aquaculture and Fisheries*. <https://doi.org/10.1016/j.aaf.2024.03.003>
- Karlsen, J. D., Krag, L. A., Herrmann, B., & Lund, H. S. (2019). Using vertical distribution to separate fish from crustaceans in a mixed species trawl fishery. *Canadian Journal of Fisheries and Aquatic Sciences*, *76*, 1781–1794.
- Kennelly, S. J., & Broadhurst, M. K. (2021). A review of bycatch reduction in demersal fish trawls. *Reviews in Fish Biology and Fisheries*, *31*(2), 289–318.
- Krag, L. A., Herrmann, B., Iversen, S. A., Enga's, A., Nordrum, S., & Krafft, B. A. (2014). Size selection of Antarctic krill (*Euphausia superba*) in trawls. *PLoS One*, *9*, Article e102168.
- Larsen, R. B., Herrmann, B., Sistiaga, M., Brinkhof, J., & Grimaldo, E. (2018). Bycatch reduction in the Norwegian Deep-water Shrimp (*Pandalus borealis*) fishery with a double grid selection system. *Fisheries Research*, *208*, 267–273.
- Madsen, N. (2007). Selectivity of fishing gears used in Baltic Sea cod fishery. *Reviews in Fish Biology and Fisheries*, *17*, 517–544.
- Madsen, N., Hansen, K.-E., & Moth-Poulsen, T. (2001). The kite cover : A new concept for covered codend selectivity studies. *Fisheries Research*, *49*(3), 219–226.
- Madsen, N., Holst, R., & Foldager, L. (2002). Escape windows to improve the size selectivity in the Baltic cod trawl fishery. *Fisheries Research*, *57*(3), 223–235, 2002.
- Millar, R. B. (1993). Incorporation of between-haul variation using bootstrapping and nonparametric estimation of selection curves. *Fish. Bull.*, *91*, 564–572.
- Millar, R. B., Broadhurst, M. K., & Macbeth, W. G. (2004). Modelling between-haul variability in the size selectivity of trawls. *Fisheries Research*, *67*(2), 171–181. <https://doi.org/10.1016/j.fishres.2003.09.040>, 2004 ISSN 0165-7836.
- Millar, R. B., O'Driscoll, R. L., Black, S., Janssen, G., Hamill, J., Woods, D., & Moran, D. (2023). Size selectivity of a novel non-mesh codend (the Modular Harvesting System) in a New Zealand deepwater fishery. *Fisheries Research*, *264*, Article 106705.
- O'Neill, F. G., Fryer, R. J., Frandsen, R. P., Herrmann, B., Madsen, N., & Mieske, B. (2020). A meta-analysis of plaice size-selection data in otter trawl codends. *Fisheries Research*, *227*, Article 105558.
- O'Neill, F. G., & Herrmann, B. (2007). PRESEMO—a predictive model of codend variability—a tool for fishery managers. *ICES Journal of Marine Science*, *64*, 1558–1568.
- Pol, M. V., Herrmann, B., Rillahan, C., & He, P. (2016). Impact of codend mesh sizes on selectivity and retention of Acadian redfish *Sebastes fasciatus* in the Gulf of Maine trawl fishery. *Fisheries Research*, *184*(2016), 54–63. <https://doi.org/10.1016/j.fishres.2016.06.013>. ISSN 0165-7836.
- Robertson, J. H. B., & Stewart, P. A. M. (1988). A comparison of size selection of haddock and 529 whiting by square and diamond-mesh codends. *J. Cons. Int. Explor. Mer.*, *44*, 148–161.
- Rochet, M., & Trenkel, V. M. (2005). Factors for the variability of discards: Assumptions and field evidence. *Canadian Journal of Fisheries and Aquatic Sciences*, *62*(1), 224–235.
- Ryer, C. H. (2008). A review of flatfish behavior relative to trawls. *Fisheries Research*, *90* (1–3), 138–146.
- Sala, A., Lucchetti, A., Perdichizzi, A., Herrmann, B., & Rinelli, P. (2015). Is square-mesh better selective than larger mesh? A perspective on the management for mediterranean trawl fisheries. *Fisheries Research*, *161*, 182–190 (2015).
- Sala, A., Lucchetti, A., Piccinetti, C., & Ferreti, M. (2008). Size selection by diamond and square-mesh codends in multi-species Mediterranean demersal trawls fisheries. *Fisheries Research*, *93*, 8–21.
- Santos, J., Herrmann, B., Mieske, B., Stepputtis, D., Krumme, U., & Nilsson, H. (2016). Reducing flatfish bycatch in roundfish fisheries. *Fisheries Research*, *184*, 64–73.
- Sistiaga, M., Herrmann, B., Grimaldo, E., & Larsen, R. B. (2010). Assessment of dual selection in grid based selectivity systems. *Fisheries Research*, *105*, 187–199.
- Suuronen, P., & Sardá, F. (2007). The role of technical measures in European fisheries management and how to make them work better. *ICES Journal of Marine Science*, *64* (4), 751–756.
- Tokac, A., Herrmann, B., Aydın, C., Kaykac, H., Ünlüer, A., & Gökce, G. (2014). Predictive models and comparison of the selectivity of standard (T0) and turned mesh (T90) codends for three species in the Eastern Mediterranean. *Fisheries Research*, *150*, 76–88.
- Uhlmann, S. S., Helmond, A. T. M.v., Stefánsdóttir, E. K., Sigurðardóttir, S., Haralabous, J., Bellido, J. M., Carbonell, A., Catchpole, T., Damalas, D., Fauconnet, L., Feekings, J., Garcia, T., Madsen, N., Mallold, S., Margeirsson, S., Palialexis, A., Readdy, L., Valeiras, J., Vassilopoulou, V., & Rochet, M. (2014). Discarded fish in European waters: General patterns and contrasts. *ICES Journal of Marine Science*, *71*(5), 1235–1245.
- Underwood, M., Winger, P. D., Ferno, A., & Engås, A. (2015). Behavior-dependent selectivity of yellowtail flounder (*Limanda ferruginea*) in the mouth of a commercial bottom trawl. *Fishery Bulletin*, *113*(4), 430–441.
- Ward, J. M., Benaka, L. R., Moore, C. M., & Meyers, S. (2012). Bycatch in marine fisheries. *Marine Fisheries Review*, *74*(2), 13–25, 2012.
- Wienbeck, H., Herrmann, B., Feekings, J. P., Stepputtis, D., & Moderhak, W. (2014). A comparative analysis of legislated and modified Baltic Sea trawl codends for simultaneously improving the size selection of cod (*Gadus morhua*) and plaice (*Pleuronectes platessa*). *Fisheries Research*, *150*, 28–37.
- Wileman, D. A., Ferro, R. S. T., Fonteyne, R., & Millar, R. B. (Eds.). (1996). *Manual of methods of measuring the selectivity of towed fishing gears*, 215 p. 126). ICES Cooperative Research Report.
- Winger, P. D., Walsh, S. J., He, P., & Brown, J. A. (2004). Simulating trawl herding in flatfish: The role of fish length in behaviour and swimming characteristics. *ICES Journal of Marine Science*, *61*, 1179–1185.