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Modelling towing and haul-back escape patterns during the fishing process: a case study for cod, plaice, and flounder in the demersal Baltic Sea cod fishery

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The survival likelihood of fish escaping through trawl codends may depend on when they escape. It is therefore relevant to investigate when during the fishing process fish actually attempt to escape and do escape from trawl codends. This subject is addressed by modelling data collected during a specially designed experiment. Results demonstrate that the escape process during towing cannot be described sufficiently by a traditional logistic model or something similar. Instead, a model is required that explicitly considers that not all fish necessarily contact the codend netting to attempt escape during the towing phase. A model that accounts for such behaviour is applied and it is demonstrated that this model can adequately describe the size selection process during towing. The overall escape process, which consists of the attempt probability, partial escape during towing, and partial escape during the haul-back phase, is also modelled. This proposed model sufficiently described the observed escape pattern for cod (*Gadus morhua*), plaice (*Pleuronectes platessa*), and flounder (*Platichtys flesus*). For all three species, a significant percentage of the individuals entering the codends during fishing first attempt to escape during the haul-back operation.

Keywords: BACOMA, cod (Gadus morhua), codend, escape pattern, flounder (Platichthys flesus), haul-back, plaice (Pleuronectes platessa), size selectivity, T90.

Introduction

Trawling involves a relatively long towing phase at the desired depth when the trawlnet herds and catches fish. This is followed by a short haul-back phase, during which the gear and the catch are hauled from the seabed, pass through the water column, and are brought on board the vessel. Usually, fish only enter the gear during the towing period, which can last for several hours. Fish can, however, escape throughout both towing and haul-back phases of the fishing process. The quicker a fish escapes after entering the fishing gear, the less physical stress it will experience. Thus, it is likely that the survival of fish escaping through the meshes of a demersal trawl codend will depend on when during the fishing

process escape occurs (Madsen *et al.*, 2008). In demersal trawl fishing, it is important that escape of unwanted fish occurs when the gear is still at towing depth rather than during haul-back (Madsen *et al.*, 2008). Physoclistous fishes, such as cod, experience considerable problems during the haul-back phase because their swim bladder cannot adapt instantaneously to changes in hydrostatic pressure. Consequently, the survival rate is expected to be reduced if the fish escapes during the later stages of fishing.

Experimental trawl fishing using traditional diamond-mesh codends has shown that a considerable number of fish escape through the codend meshes after haul-back has begun. Grimaldo *et al.* (2009) found that about 38% of the cod (*Gadus morhua*)

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escaping from the codend did so during the haul-back phase, and Madsen *et al.* (2008) reported 33% for haddock (*Melanogrammus aeglefinus*). Furthermore, Grimaldo *et al.* (2009) found differences in the escape patterns between the towing phase at the seabed and the haul-back phase for cod and haddock for different selection systems. Therefore, the temporal escape pattern and the overall escape for a given trawl fishery may depend on the different types of selectivity devices and/or codends being used.

Why such a large percentage of fish escape during the short haul-back period is an ongoing research question. Two conditions must be met for fish to escape through a mesh in a codend during a specific phase of the fishing process. First, the fish needs to contact the codend meshes to attempt to escape during that phase. Second, the fish needs to be able to squeeze itself through one of the codend meshes. The first condition is related to the behavior of the fish in the fishing gear, whereas the second is related to the cross-sectional morphology of the fish compared to the shape of the codend meshes (Herrmann et al., 2009). Based on these preconditions, the question becomes more specific: is the limited escape during the towing phase related to behavioral aspects of the fish in the fishing gear, since a considerable proportion of the fish do not contact the codend meshes during the towing process? Or is escape related to changes in the mechanical properties of the codend meshes that occur between the two phases of the fishing process, making it easier for fish to squeeze through the codend meshes during the haul-back phase?

Unfortunately, neither Madsen et al. (2008) nor Grimaldo et al. (2009) were able to quantitatively distinguish between the contributions of these two factors. Both studies applied a step-wise analysis of the available size selection during the different phases of the fishing process by separately fitting a logistic curve (Wileman et al., 1996) to the data, describing the retention probability for each phase of the fishing process separately. This type of analysis does not permit assessment of whether the lack of escape in one phase of the catching process is caused by lack of fish making contact with the codend meshes or by inability of the codend to release fish of that size during that phase of the fishing process. Moreover, such detailed assessment of the selectivity process requires a model that explicitly and separately accounts for both the behavioral aspects quantified by the mesh contact probability and the size-dependent selective potential of the codend for the fish contacting the meshes during the different phases of the fishing process. The latter is what Millar and Fryer (1999) describe as contact selectivity, meaning the size selection of the fish that actually come into contact with the selective device and therefore have a sizedependent probability of escaping.

There are several potential explanations for why some fish do not come into contact with the codend meshes during the towing phase. Some species are herded by the front part of the fishing gear and swim in front of the footrope for some time (reviewed in Wardle, 1993; He, 2010). After becoming exhausted, they begin to fall back through the trawl towards the codend, and in so doing they avoid the netting (Wardle, 1993; Glass *et al.* 1995). Additionally, some fish enter the codend very late in the towing process and therefore miss their escape opportunity; others may first arrive in the codend during the haul-back phase after the towing process has finished. In the codend, fish can also swim for some time without attempting to escape (Wardle, 1993).

The justification for implementing fishing gears with improved size-selective properties is based on the premise that most of the

fish being selected out during the fishing process actually survive. Thus, it is important that a high fraction of these fish escape while the gear is still at fishing depth, where the survival rate of escapees is assumed to be higher than during the haul-back phase. The type of fishing gear used, however, will affect escapement and survival. It is possible that different fishing gears with apparently similar overall selectivity can result in very different unaccounted mortality due to different temporal escape patterns. Therefore, when comparing the size-selective properties of two or more codends, it is important to compare their ability to release unwanted fish while the gear is still at fishing depth. To enable development of trawls with better survivability, it is necessary to assess the extent to which limited release during towing is caused by limited release potential for the fish that actually contact the device or by limited contact of fish with the device during towing.

In the Baltic Sea trawl fishery that targets cod, it is legal to use two different codend types. The first is a BACOMA codend with 105-mm mesh-size diamond mesh netting in the normal T0 orientation, with a 120-mm square mesh netting in the upper panel (Madsen et al., 2002); the second is a 120-mm T90 codend, in which the mesh orientation is turned by 90° (Wienbeck et al., 2011). From a management point of view, it is relevant to investigate whether these two legal codends differ in their temporal escape patterns and therefore differ in their risk of unaccounted mortality of cod (Gadus morhua), plaice (Pleuronectes platessa), and flounder (Platichtys flesus). The objectives of this study were to compare the timing of escape (i.e. during towing or haul-back) of cod, plaice, and flounder from the T90 and BACOMA codends, and to determine the extent to which escape during the towing process is restricted by the size-selective properties of the codends and/or by limited contact with the codend meshes. A new modelling approach was developed to address these objectives.

Material and Methods

Experimental design and data collection

Experimental fishing was conducted on board the German Fishery Research Vessel (FRV) "Solea" (total length 42 m, 1780 kW). The "Codhopper" trawl was used. Its fishing circle circumference was 530 meshes with a vertical net opening of \sim 4.5 m. The trawl was spread by two 3.3 m² Bison doors, resulting in a wingspread of 20–25 m.

The two legal codend designs for the Baltic Sea (120 mm BACOMA and 120 mm T90) (Table 1) were alternately attached to the same trawl. The actual codend used was the only change in gear between the individual tows. The covered codend method (Wileman *et al.*, 1996) was applied in conjunction with a dual-sampler (Madsen *et al.*, 2012) to enable the separate collection of fish escaping through the meshes in the test codend during towing at fishing depth and during the haul-back operation (Figure 1). In contrast to Madsen *et al.* (2012), the dual-sampler was controlled using a modified Scanmar-tension shackle in combination with several magnetic switches. Supporting hoops were applied to keep the cover netting clear of the test codends (Wileman *et al.*, 1996).

The nominal mesh size in the cover was 80 mm (Table 1). The mesh size was larger than that recommended by Wileman *et al.* (1996). We used this large mesh size for the cover because previous research indicated that any smaller mesh size cover would result in

Table 1. Measurements of the mesh sizes with the OMEGA mesh gauge.

	Mesh size	
Netting type	(mm)	Description
BACOMA codend: lower panel	104.5 (1.85)	5 mm single twine Alfa compact netting T0° aligned (diamond mesh)
BACOMA codend: escape window	125.7 (0.95)	5 mm single twine knotless Ultra cross netting T45° aligned (square mesh)
T90 codend	124.1 (1.32)	5 mm single twine Alfa compact netting T90 $^{\circ}$ aligned (diamond mesh).
		Two panel construction with 50 open meshes in codend circumference
Front part of the cover	76.2 (1.48)	2.3 mm single twine braided Nylon netting T0° aligned (diamond mesh)
Rear part of the covers (codend)	73.2 (1.40)	3 mm single Euroline netting T0° aligned (diamond mesh)

Standard deviations are shown in parentheses.

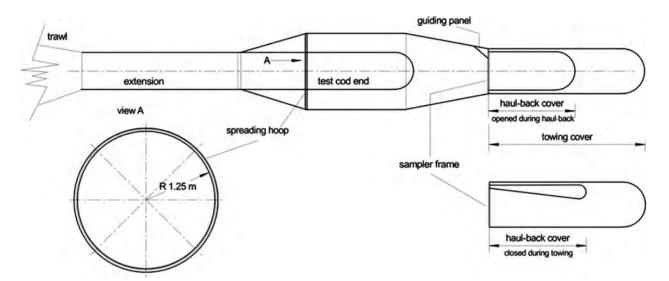


Figure 1. Schematic drawing of the experimental setup with the dual sampler to separately collect the escaped fish from the towing phase at fishing depth and the haul-back phase.

a large amount of herring in the cover and make operations difficult if not impossible (Wienbeck *et al.*, 2011). Consequently, special attention was given in the analysis to remove length classes where the size selection in the covers could bias results. Thus, for cod, length classes below 33 cm were removed prior to the analysis following the procedure described in Wienbeck *et al.* (2011). In contrast, a test using the same procedure as for cod (Wienbeck *et al.*, 2011) revealed that it is unlikely that any of the sizes of plaice and flounder caught (>14 cm) could have passed through the cover meshes. Therefore no length classes for plaice and flounder were excluded from the data prior to analysis.

Two phases of the fishing process were distinguished during experimental fishing and data analysis. The towing phase included the time spent fishing at the desired depth and the haul-back phase started when the winches began to retrieve the gear. At the beginning of the haul-back phase, the first codend cover was closed and the second codend cover was opened using the dual-sampler.

The three-compartment experimental design (Figure 1) meant that for each haul (i) and each length class (l), information about the number of fish in the tow cover (nct_{li}) , in the haul-back cover (nch_{li}) , and in the test codend (nt_{li}) was collected. The length of every cod, plaice, and flounder found in the three compartments (test codend, tow cover, haul-back cover) was measured to the nearest centimetre. No subsampling was applied in any of the hauls conducted.

The experimental fishing trials were conducted from 21–29 November 2010 in the Arkona Sea, western Baltic Sea (ICES SD

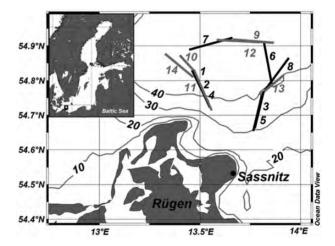


Figure 2. Area of investigation and tracks for the hauls conducted. The black tracks were conducted with the BACOMA codend while the grey were conducted with the T90 codend.

24, Figure 2). Water temperature at fishing depth, as measured on a stationary platform nearby, was 9.5°C. Water depth varied between 32 and 49 m. Average towing speed (GPS speed over ground) was 3.6 knots (range, 3.4–3.8 knots). The average haul duration was 131 min (range, 72–165 min). The average duration of the towing phase was 120 min (range, 62–155 min), while

the average duration of the haul-back phase was 11 min (range, 8-14 min). On average, the haul-back phase accounted for only 8.7% of the total fishing time (towing time plus haul-back time), whereas towing at the seabed accounted for >90%.

Estimation of the average relative escape during towing and haul-back

To estimate the average percentage of the number of fish that escaped prior to the beginning of the haul-back phase (pe_{tow}), the following fomula was applied for each species and for each codend type separately:

$$pe_{tow} = 100 \times \frac{\sum_{i} \sum_{l} [nct_{li}]}{\sum_{i} \sum_{l} [nct_{li} + nch_{li}]}.$$
 (1)

The average percentage escape during haul-back ($pe_{haul-back}$) was calculated as $100 - pe_{tow}$. To calculate the 95% confidence limits for petow and pehaul-back, a double bootstrap technique (Efron, 1982; Manly, 1997) was applied, in which within-haul variation and between-haul variation of the escape processes were taken into consideration. The hauls for each codend were used to define a group of hauls. To account for between-haul variation for each codend type, an outer bootstrap resample with replacement was included in the procedure. Within each resampled haul, the data for each length class were bootstrapped in an inner bootstrap with replacement to account for within-haul variation. Each bootstrap resulted in a "pooled" set of data, which was then analysed using equation (1). Thus, each bootstrap run resulted in a value for petow and for pehaul-back. We ran 10 000 bootstrap repetitions for each codend type and for each species, which enabled us to estimate the "Efron percentile" 95% confidence limits for the average values of pe_{tow} and $pe_{haul-back}$ (Efron, 1982; Chernick, 2007). The analysis was conducted using the analysis tool SELNET (developed by the first author of this study; Sistiaga et al., 2010; Eigaard et al., 2011; Frandsen et al., 2011; Wienbeck et al., 2011; Herrmann et al., 2012).

Modelling the size selection for the towing phase at fishing depth

When the haul-back of the fishing gear towards the surface begins, the number of fish in haul i in length class l that later end up being collected in the haul-back cover nch_{li} have not yet escaped through the test codend meshes. Thus, the fish retained after the towing phase has just been completed can be considered to be the sum of nt_{li} and nch_{li} . Therefore, when modelling size-selection during the towing process, nct_{li} represents the number of escaped fish and $(nt_{li} + nch_{li})$ represents the number of retained fish. The average size selection for the towing process $r_{tow}(l)$ for each codend type was modelled by minimizing the negative log likelihood function for the observed data (2) with respect to the parameters describing $r_{tow}(l)$:

$$-\sum_{i}\sum_{l}\left[\left(nt_{li}+nch_{li}\right)\times\ln\left(r_{tow}(l)\right)+nct_{li}\times\ln\left(1.0-r_{tow}(l)\right)\right] \tag{2}$$

Formula (2) is derived based on expressing the likelihood for the observed experimental data under the assumption that the selected model for $r_{tow}(l)$ is a sufficient approximation of the average size-selection in the towing process. Because a fish is either retained $(nt_{li} + nch_{li})$ or released (nct_{li}) during the towing process,

expressing the likelihood for the observed data is based on a binominal distribution. The selectivity analysis was carried out using the software tool SELNET (see previous section).

Data for all hauls conducted using the same codend type were pooled. According to Millar (1993), if between-haul variation is not of primary interest, then fitting the model to the pooled data should be a reasonable approach to estimating the "average" selectivity for the fishery. Therefore, the sample of experimental hauls for each case study must be a representative sample from that fishery (Millar, 1993). On the other hand, Fryer (1991) reported that the use of pooled data in parameter estimation would lead to an underestimation of the uncertainty for the estimated parameters. To circumvent the problem of underestimating the confidence limits for the average parameter values, we used a double bootstrapping method with 10 000 bootstrap repetitions for each species and each codend type separately. Our approach was similar to that described in Millar (1993) and applied in Sistiaga et al. (2010), Eigaard et al. (2011), and Herrmann et al. (2012), which took into account within-haul and between-haul variation of the size-selection process. The confidence limits for the average size-selection curve for the towing process were also estimated using this bootstrapping technique (Herrmann et al., 2012).

Madsen et al. (2008) and Grimaldo et al. (2009) used a standard logistic curve (see Wileman et al., 1996) with parameters L50_{tow} and SR_{tow} to describe size selection for the towing process $r_{tow}(l)$. However, this type of model does not distinguish between the behavioral aspects and the size-selective potential of the codend. In the current study, for the fish that actually contact the meshes during the towing process, it is assumed that the probability of being retained can be described sufficiently well by a logistic model with parameters $L50_{tow}$ and SR_{tow} . The likelihood of coming into contact with the codend meshes during towing is then modelled by the function c_{tow} which is constrained to values between 0.0 and 1.0. At $c_{tow} = 1.0$, every fish would contact the codend meshes during the towing phase and consequently have a length-dependent chance of escaping through the codend meshes. A value of 0.3 would indicate that only 30% of the fish entering the codend during the fishing process would contact the codend meshes at least once during the towing process and thereby have a length-dependent chance of escaping through the codend meshes during towing. However, fish swimming speed and endurance increase with fish length (Videler and Wardle, 1991), thus bigger fish most likely can swim for a longer time ahead of the footrope and, after entry into the trawl, would fall back into the codend more slowly compared to smaller fish of the same species. Consequently, c_{tow} should be modelled as a function of fish length if late arrival to the codend during the towing process contributes to a value of $c_{tow} < 1.0$. Additional factors such as towing speed, water temperature, and fish condition could also potentially affect $c_{tow}(l)$ (Wardle, 1993; Winger et al., 1999; He, 2010).

Based on the above considerations, we propose the following model $r_{clogit}(l)$ [(formula (3)] to model $r_{tow}(l)$ (size selection for the towing phase). In terms of the length-dependent contact function $c_{tow}(l)$, this model explicitly accounts for the fact that some fish might not contact the codend meshes during towing due to

late arrival or passive behavior in the codend:

$$r_{tow}(l) = r_{clogit}(1, c_{tow}, L50_{tow}, SR_{tow})$$

= 1.0 - c_{tow}(l) \times [1.0 - r_{logit}(l, L50_{tow}, SR_{tow})] (3)

where

$$r_{\log it}(l, L50_{tow}, SR_{tow}) = \frac{\exp\left((l - L50_{tow}) \times \frac{\ln(9)}{SR_{tow}}\right)}{1.0 + \exp\left((l - L50_{tow}) \times \frac{\ln(9)}{SR_{tow}}\right)}$$
(4)

Parameter $L50_{tow}$ is the 50% retention length for fish actually contacting the codend meshes during towing to attempt to escape, and parameter SR_{tow} (= $L75_{tow}$ - $L25_{tow}$) is the selection range for the fish contacting the codend meshes during towing to attempt to escape. Formula (4) is the traditional logistic function often applied to model size-selection trawls and further information on it can be found in Wileman *et al.* (1996). If $c_{tow}(l)$ is fixed at 1.0 for all length classes $l_i r_{clogit}(l)$ in formula (3) simplifies to the traditional logistic model [formula (4)]. However, for length classes at a species-dependent length l_{lim} where the retention probability is \sim 1.0, the exact value for $c_{tow(l)}$ will have a negligible influence on $r_{clogit}(l)$, as the retention probability will be \sim 1.0.

In contrast, for very small fish, individuals that contact the codend meshes during towing could easily pass through the meshes. For these fish, the value of $r_{clogit}(l)$ is approximately defined by the value of $c_{tow}(l)$. To avoid potential bias due to possible cover selection of small fish, we restricted the assessment and analysis to fish with a length above the species-dependent l_{cut} (see *Experimental design and data collection*). Therefore, the size interval for which the length dependency of $c_{tow}(l)$ has any influence on the assessment is restricted to the species-dependent length interval $[l_{cut}, l_{lim}]$. Before considering more complicated formulas for $c_{tow}(l)$, we tested a simplified version that was approximated

by a length-independent constant $c_{tow}(l) \approx c_{tow}$; however, in this case the estimated value for c_{tow} must be considered as an average value for the contact probability for fish of the species with length between l_{cut} and l_{lim} . A considerably different length interval of $[l_{cut}; l_{lim}]$ could potentially result in a different value for c_{tow} for the same species. Therefore, the estimated value for c_{tow} should not be applied to assess fish outside the length interval $[l_{cut}; l_{lim}]$.

The value for l_{cut} is set based on the assessed upper limit for cover selection or by the smallest sizes of fish in the experimental data. We also need to assess the upper length limit for length of fish for which the estimated average value for c_{tow} can be applied. For this length, l_{lim} , we will use the estimated length of fish that have a 95% probability of being retained in the codend during towing given that they contact the codend meshes during the towing process. Because we assumed a logistic model with parameters $L50_{tow}$ and SR_{tow} for the retention probability for the fraction of fish contacting the codend meshes during towing [equation (4)], l_{lim} is given by:

$$l_{\text{lim}} = L50_{tow} + \frac{\ln(19)}{\ln(9)} \times SR_{tow}$$
 (5)

Equation (5) is derived from equation (4) by setting $r_{tow} = 0.95$ and $l = l_{lim}$.

If the application of a constant value for c_{tow} in equations (3) and (2) leads to unacceptable fit statistics (see Wileman *et al.*, 1996 for use of the standard fit statistics in such an evaluation), a more complicated expression for $c_{tow}(l)$ will be needed. In addition to using equations (3) and (2) to model the size selection for the towing process, we will compare the ability of a standard logistic model (Madsen *et al.*, 2008, Grimaldo *et al.*, 2009) to describe the size selection for the towing phase for our data.

Modelling the escape pattern during the fishing process

The three-compartment experimental design (Figure 1) gives simultaneous information about the number of fish collected in the

Table 2. Number of individuals caught in the different compartments in individual hauls.

Cod				Plaice			Flounder		
Haul no.	Codend	Cover towing	Cover haul-back	Codend	Cover towing	Cover haul-back	Codend	Cover towing	Cover haul-back
3	73	422	43	107	477	20	1136	100	5
4	221	276	169	61	69	28	432	22	17
5	84	121	110	108	265	176	1329	87	57
6	167	975	400	137	78	42	714	11	7
7	283	669	430	186	31	23	394	2	5
8	211	393	173	96	86	63	1348	11	7
9	160	398	88	176	41	15	380	3	1
10	158	137	161	89	52	12	515	5	1
11	254	287	385	61	267	96	445	57	19
12	139	429	137	102	38	7	198	3	3
13	153	300	311	28	34	21	178	2	4
14	97	242	108	_	_	_	178	2	2
BACOMA pe _{tow}	6	68.31 (60.61 – 7	76.89)	7	4.08 (56.33 – 8	39.92)	70.	39 (43.22 – 9	92.18)
BACOMA pe _{haul-back}	3	31.69 (23.11 – 3	39.39)	2	5.92 (10.08 – 4	i 3.67)	29	.61 (7.82 – 5	6.78)
T90 pe _{tow}	6	60.11 (47.79 – 7	73.91)	7	4.10 (63.84 – 8	34.17)	70.	59 (32.26 – 8	39.66)
T90 pe _{haul-back}	3	39.89 (26.09 – 5	52.21)	2	5.90 (15.83 – 3	36.43)	29.	41 (10.34 – 6	57.74)

Data for cod are given for length classes >33cm, which were included in the analysis. Haul numbers 3–8 were conducted with the BACOMA codend, while hauls 9–14 were conducted with the T90 codend. The last four rows are average percentage escape during the towing phase (pe_{tow}) and during the haul-back phase ($pe_{haul-back}$). The 95% confidence limits are given in brackets.

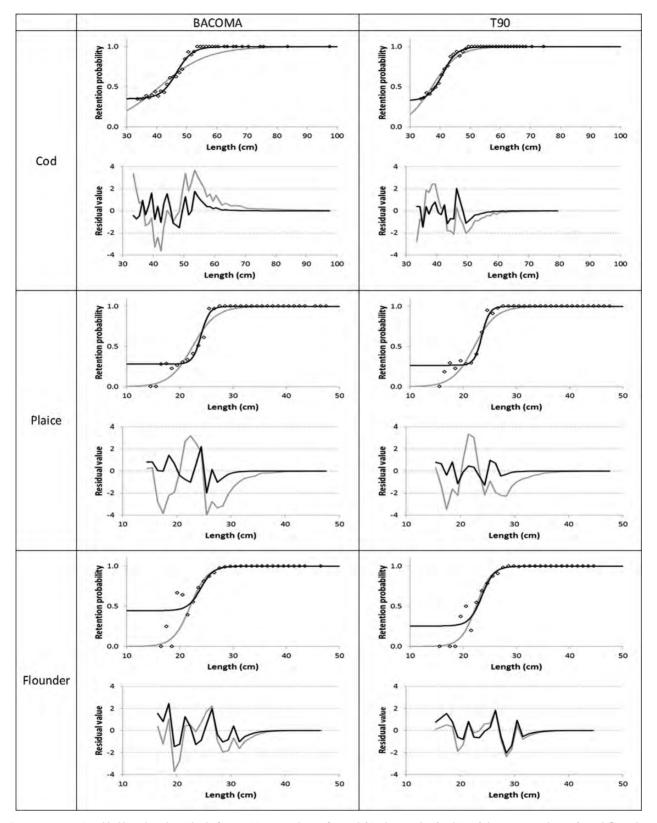


Figure 3. Retention likelihood and residuals for BACOMA and T90 for cod (*Gadus morhua*), plaice (*Pleuronectes platessa*), and flounder (*Platichthys flesus*). The diamonds represent the experimental data points. The black curve represents the $r_{clogit}(l)$ model and the grey curve the traditional $r_{logit}(l)$ model. See *Material and Methods* for interpretation or Wileman *et al.* (1996) regarding calculation of residual values.

tow cover (nct_1) , in the haul-back cover (nch_1) , and in the test codend (nt_l) , separated by haul, species, and length class l. Assuming that the fate of each fish is independent of that of other fish, the number of individuals of a specific length class l present in the three compartments can be modelled by a multinomial distribution with length-dependent probabilities for escape during the towing phase $[e_{tow}(l)]$ and during the haul-back phase $[e_{haul-back}(l)]$ and for being retained in the test codend during the entire haul $[r_{total}(l)]$. In this study, for the towing phase we assumed that the length-dependent retention probability can be described by the $r_{clogit}(l)$ model with the parameters c_{tow} , $L50_{tow}$, and SR_{tow} as described in the previous section. For the fish that did not escape during the towing phase, the probability of still being in the codend after completion of the haul-back phase can be described by a logistic model with parameters $L50_{haul-back}$ and $SR_{haul-back}$. For each codend type and species, the parameters c_{tow} , $L50_{tow}$, SR_{tow} , $L50_{haul-back}$, and $SR_{haul-back}$ are estimated simultaneously by maximizing the corresponding log likelihood function for the assumed model. Thus, function (6) can be minimized, which is equivalent to maximizing the likelihood for the observed data:

$$-\sum_{l}\sum_{l}\left[nt_{l}\times\ln(r_{total}(l))+nct_{l}\times\ln(e_{tow}(l))+nch_{l}\times\ln(e_{haul-back}(l))\right] \tag{6}$$

The log likelihood function (6) is derived following the procedure described for formula (2) (see *Modelling the size selection for the towing phase at fishing depth*) with the exception that (6) is based on a multinominal distribution because three outcomes (retained, escape during towing and escape during haul-back) are considered. The length-dependent probability functions in (6) are given by:

$$e_{tow}(l) = 1.0 - r_{clogit}(l, c_{tow}, L50_{tow}, SR_{tow})$$

$$e_{haul-back}(l) = (1.0 - r_{logit}(l, L50_{haul-back}, SR_{haul-back})$$

$$\times r_{c\log it}(l, c_{tow}, L50_{tow}, SR_{tow})$$

$$r_{total}(l) = 1.0 - e_{tow}(l) - e_{haul-back}(l)$$
(7)

The data were analysed using the computer software SELNET, which enables the analysis of data from experimental designs involving multiple compartments by means of complex selection models that include those represented by equations (3), (6), and (7). To estimate the overall selectivity parameters of the total fishing process [i.e. the towing phase followed by the haul-back phase ($L50_{total}$ and SR_{total})], a numerical method implemented in SELNET was applied. The values for c_{tow} , $L50_{tow}$, SR_{tow} $L50_{haul-back}$ and $SR_{haul-back}$ estimated using equations (3), (6), and (7) were used to solve $r_{total}(l) = 0.5$ numerically. The length l fulfilling this condition was then (according to the definition in Wileman et al., 1996) used as L50_{total}. Given the selection range of the total fishing process $SR_{total} = L75_{total} - L25_{total}$, we estimated SRtotal using the same approach as for L50total. Confidence limits for the model parameters, the escape curves, and the total retention curve were estimated using the double bootstrap method described in the previous section.

Results

Data from experimental fishing

Size selectivity data for cod, plaice, and flounder were collected from six valid hauls for each codend type.

Table 2 lists the number of individual fish in each compartment (test codend, towing cover, haul-back cover) summed over length classes. Besides cod, plaice, and flounder, the most abundant species were whiting (Merlangius merlangius), herring (Clupea harengus), and sprat (Sprattus sprattus). The length of all cod, plaice, and flounder caught was measured to the nearest centimetre. In total, 5220 and 3944 cod >33 cm long were measured when testing the BACOMA (hauls 3-8) and T90 (hauls 9-14) codends, respectively, and were used in the analyses. For plaice, the length span was 14-48 cm, with a total of 2053 and 1039 measured when testing the BACOMA codend and T90 codend. For flounder, 5684 and 1996 were measured when testing the BACOMA codend and the T90 codend. The length span for flounder was 15-47 cm. Given the numbers of specimens collected in the three compartments for each haul (Table 2), the data for cod were strong, whereas they were much weaker for flounder due to the lower sample size.

Average relative escape during towing and haul-back

Of the cod escaping during the fishing process, about 68% and 60% escaped during the towing phase from the BACOMA codend and the T90 codend, respectively (Table 2). Therefore, about 32% and 40% of the cod escape occurred during the haulback phase for the two codends, respectively. The difference in the escape values between the two codends was not statistically significant, as the confidence intervals of the data overlapped for the two codends. However, the escape rates during haul-back of the trawl were significantly higher than those during towing, which means that a large percentage of the escape occurred during the short (only about 9% of the total time) haul-back process (see Table 2).

For the two flatfish species investigated (plaice and flounder), a considerable and significant part of the escape occurred during the haul-back period (Table 2), with 26% for plaice and 29% for flounder. Due to relatively wide confidence limits, no significant difference between these species or between their escape rates from the two codend types was found.

Table 3. Fit statistics for the applied size selection models.

			$r_{clogit}(I)$	$r_{logit}(I)$
	BACOMA	p-value	0.930 0	< 0.000 1
		Deviance	23.35	120.37
		DOF	35	36
Cod		AIC	6 571.12	6 666.14
	T90	<i>p-</i> value	0.999 6	0.033 7
		Deviance	14.22	54.21
		DOF	36	37
		AIC	4 584.83	4 622.81
	BACOMA	<i>p-</i> value	0.979 9	< 0.000 1
		Deviance	16.32	111.58
		DOF	30	31
Plaice		AIC	1 940.54	2 033.8
	T90	<i>p-</i> value	>0.9999	0.000 2
		Deviance	7.14	66.21
		DOF	30	31
		AIC	809.16	866.23
	BACOMA	<i>p-</i> value	0.540 6	0.014
		Deviance	24.62	45.6
		DOF	26	27
Flounder		AIC	1 274.87	1 293.85
	T90	<i>p-</i> value	0.903 0	0.797 7
		Deviance	17.2	20.75
		DOF	26	27
		AIC	343.18	344.74

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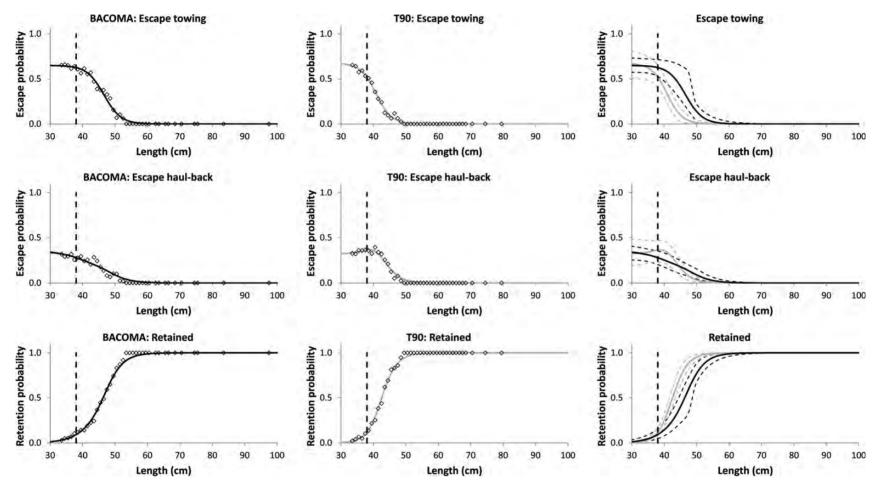


Figure 4. Escape likelihood for cod (Gadus morhua) during towing (top) and during haul-back (middle), and retention likelihood (bottom) for the BACOMA codend (left column) and the T90 codend (middle column). The diamonds represent the experimental datapoints. The right column compares the model curves for the BACOMA codend (black line) and the T90 codend (grey line) with the 95% confidence intervals for the models indicated by the stippled broken curves. The minimum landing size of 38 cm is indicated by the vertical broken line.

Analysis and modelling of size selection during towing

We modelled the size selection for the towing phase at fishing depth for the three species investigated (Figure 3). In addition to the $r_{clogit}(l)$ model [formula (3)], which accounts explicitly for the behavioral aspect that not every fish will actually attempt to escape during the towing phase, the traditional $r_{logit}(l)$ model [formula (4); Wileman *et al.*, 1996] was also tested. This model was previously applied to model the partial selection process during towing at the seabed (Madsen *et al.*, 2008; Grimaldo *et al.*, 2009) to describe the probability that a fish would still be retained after the towing process has been completed.

The $r_{clogit}(l)$ model (Figure 3, top row, black curve) clearly described the size selection for cod during the towing phase much better than the traditional $r_{logit}(l)$ model (grey curve). This result was also supported by the fit statistics (Table 3) and residuals (Figure 3): the residual values of the $r_{clogit}(l)$ model were much less extreme and showed considerably less structure in the deviations compared to the $r_{logit}(l)$ model. For cod, the p-values of the fit statistic for the $r_{clogit}(l)$ model were 0.9300 (BACOMA) and 0.9996 (T90), making it very likely that the observed discrepancy between the data and the model could well be a coincidence (consult Wileman et al., 1996 for interpretation of these basic fit statistics). Moreover, the deviance values did not exceed the degrees of freedom (DOF) values. In contrast, the deviance values for the results of the $r_{logit}(l)$ model for both codends exceeded the DOF values, implying that the model was not able to describe the experimental data sufficiently well. Additionally, the p-values for the fit of the $r_{logit}(l)$ model for both codends were < 0.05, thus it is very unlikely that the observed discrepancy between the data and the model could be a coincidence. Together with the clear structure in the residuals for the $r_{logit}(l)$ model (Figure 3, top), we can further rule out that the poor p-value was caused by overdispersion in the data. In summary, for cod, the traditional $r_{logit}(l)$ model could not describe the experimental data for the towing phase sufficiently well, whereas the $r_{clogit}(l)$ model could. The choice of the $r_{clogit}(l)$ model over the $r_{logit}(l)$ model was further supported by a lower AIC value (Akaike, 1974) for both codend types (Table 3).

We came to a similar conclusion for plaice (Figure 3 center row, Table 3), but the data for flounder were much weaker (see Table 2) and thus the results were not as clear. For the BACOMA codend, the results for flounder suggested ruling out the $r_{logit}(l)$ model and supported use of the $r_{clogit}(l)$ model to describe size selection during the towing phase. However, for the T90 codend, the $r_{logit}(l)$ and the $r_{clogit}(l)$ models both provided acceptable p-values (0.7977 and 0.9030, respectively), and residual plots did not clearly show the benefit of one model over the other. Based on AIC-values (Table 3), however, the $r_{clogit}(l)$ model was the model of choice for size selection during the towing phase for flounder in the T90 codend.

Based on these results, we concluded that the $r_{clogit}(l)$ model with a constant value for c_{tow} was the model of choice for size selection and the escape process during towing for all three species and for both codends. Therefore, this model was used to describe the escape pattern during the towing for all three species and both codends.

Analysis of escape patterns throughout the fishing process

The escape pattern throughout the fishing process was modelled for the all three species in both codends. Formulas (5) and (6)

were applied for all species to model the length-class data, which consisted of information about the number of fish collected in the test codend, the towing cover, and the haul-back cover.

Cod

The model describing the escape pattern for cod (Figure 4) reflects the datapoints well for both codends and phases of the fishing process. This was also confirmed by the *p*-values, which far exceeded 0.05, and was further supported by the deviance versus DOF relationship. The third column in Figure 4 shows that the BACOMA codend had a significantly higher escape likelihood during the towing phase at the seabed for cod from 41–50 cm long (i.e. for fish above the minimum landing size of 38 cm for the Baltic Sea, as indicated by the broken vertical line in the plots in Figure 4). This high escape probability of legal-sized cod results in economic losses for the fishermen.

In contrast, none of the length classes exhibited significantly different escape probability during the haul-back phase of the fishing process for either codend type, as indicated by the overlap in the confidence intervals for all length classes modelled.

The size selectivity of cod for the total fishing process differed between codends (Figure 4, lower right plot). The retention probability for cod was significantly lower for the BACOMA codend compared to the T90 codend for sizes from 41–50 cm long. This difference was clearly caused by the higher escape probability for these size classes during the towing phase at fishing depth.

For a cod of minimum landing size in the BACOMA codend (the vertical broken line in the plots in the first column of Figure 4), the overall probability of being retained throughout the entire fishing process was approximately 9% (third row of Figure 4). However, the first two rows in Figure 4 illustrate that of the 91% probability of escape, approximately 63% was during the towing phase and the remaining 28% was during haul-back of the fishing gear. This relatively low escape probability during the towing phase was to a large extent caused by a considerable proportion of the cod within the selective range of the codend not coming into contact with the codend meshes. This is evident from the value estimated for c_{tow} which was significantly < 1.0 (Table 4). The estimated $c_{tow} = 0.65$ for the BACOMA codend (confidence limit 0.58-0.75) implies that only 58-75% of the fish entering the codend during the fishing process contacted the codend meshes during the towing phase. This value for c_{tow} is considered to be the average value over

Table 4. Estimated model parameter and fit statistics for the temporal pattern of size selectivity of cod in the BACOMA and T90 codends.

	BACOMA	T90
L50 _{total} (cm)	46.29 (44.42 – 48.58)	42.55 (41.60 – 43.42)
SR_{total} (cm)	7.05 (3.89 – 8.98)	5.15 (4.06 – 6.09)
c_{tow}	0.65 (0.58 – 0.75)	0.67 (0.51-0.83)
$L50_{tow}$ (cm)	46.55 (43.39 – 48.87)	40.84 (39.18 – 42.46)
SR_{tow} (cm)	5.76 (1.06 – 10.47)	5.19 (2.87 – 7.47)
L_{cut} (cm)	33.00	33.00
L _{lim} (cm)	54.27	47.79
L50 _{haul-back} (cm)	42.07 (40.03 – 44.02)	40.99 (39.46 - 42.17)
SR _{haul-back} (cm)	8.10 (6.39 – 10.59)	5.91 (4.80 – 7.04)
<i>p-</i> value	0.95	>0.99
deviance	52.75	36.00
DOF	71.00	73.00

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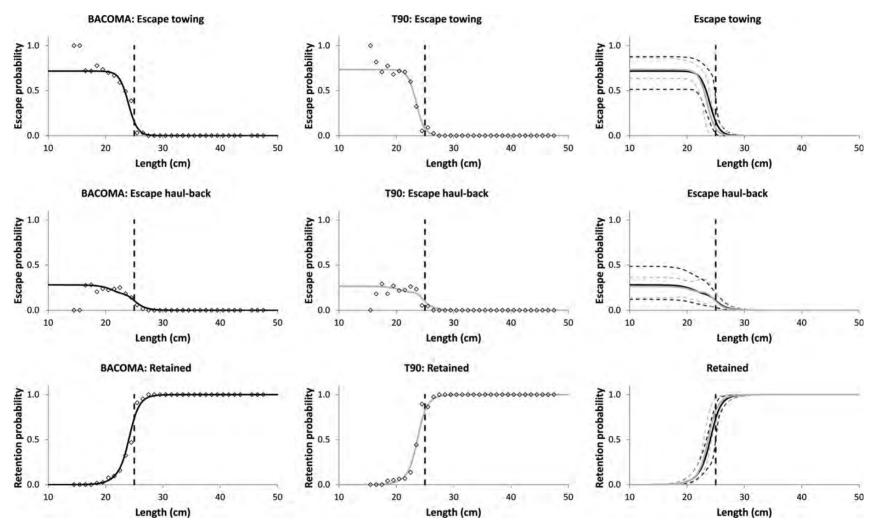


Figure 5. Escape likelihood for plaice (*Pleuronectes platessa*) during towing (top) and during haul-back (middle), and retention likelihood (bottom) for the BACOMA codend (left column) and the T90 codend (middle column). The diamonds represent the experimental datapoints. The right column compares the model curves for the BACOMA codend (black line) and the T90 codend (grey line) with the 95% confidence intervals for the models indicated by the stippled broken curves. The minimum landing size of 25 cm is indicated by the vertical broken line.

sizes in the interval 33-54 cm (l_{cut} to l_{lim} in Table 4) and cannot necessarily be extrapolated to other size ranges of cod (see Modelling the size selection for the towing phase at fishing depth). The selectivity parameters describing the escape potential of cod contacting the BACOMA codend meshes during towing and during haul-back respectively $[(L50_{tow}, SR_{tow})]$ and $(L50_{haul-back})$ SR_{haul-back})] were not significantly different, as indicated by the pair-wise overlapping of their confidence intervals (Table 4). The contact probability with the meshes during the towing phase was 67% for the T90 codend and therefore nearly the same as that estimated for the BACOMA codend. Based on the overlapping confidence limits, there was no significant difference in the mesh contact probability for cod during the towing phase between the two legal codends (Table 4). There was also no significant difference for the T90 codend in the selective properties between the towing phase and the haul-back phase for the cod that came into contact with the meshes.

Overall, the results show that for both codends, the limited escape probability during the towing phase was caused by limited contact with the meshes during towing and not by changes in the selective potential of each codend from one phase of the fishing process to the other. However, the BACOMA codend had a significantly higher selective potential than the T90 codend, as the $L50_{tow}$ was significantly higher for the BACOMA codend compared with the T90 codend. This explains why the escape likelihood for cod of length 41–50 cm during towing was significantly higher for the BACOMA codend (Figure 4, first row, third column).

Plaice

The model used to describe the escape pattern of plaice during the fishing process was able to describe the experimental data for plaice sufficiently (Figure 5, Table 5). This result was supported by the *p*-values of 0.9972 for the BACOMA codend and 0.9999 for the T90 codend (Table 5). Compared to cod, the confidence intervals were much wider (compare Figure 4 with Figure 5, right columns). This result is related to the relatively low number of plaice in the experimental data (Table 2). Overlapping confidence intervals for both codend types (Figure 5, right column) revealed no significant differences in the performance of the two codends for the escape probabilities during towing or haul-back for any of the length classes modelled. Even the mean curves were very similar for the two codends. The

Table 5. Estimated model parameter and fit statistics for the temporal pattern of size selectivity of plaice in the BACOMA and T90 codends.

	BACOMA	T90
L50 _{total} (cm)	24.04 (23.38 - 24.92)	23.67 (22.92 – 24.28)
SR _{total} (cm)	2.12 (0.24 – 2.77)	1.93 (0.28 – 2.66)
c_{tow}	0.72 (0.52 - 0.88)	0.73 (0.64 – 0.86)
$L50_{tow}$ (cm)	23.98 (22.98 – 24.98)	23.48 (22.50 - 24.31)
SR_{tow} (cm)	1.74 (0.1 – 2.67)	1.59 (0.1 – 2.89)
L_{cut} (cm)	14.00	15.00
L _{lim} (cm)	26.31	25.61
L50 _{haul-back} (cm)	22.55 (21.34 – 23.35)	22.42 (21.24 - 23.29)
SR _{haul-back} (cm)	2.8 (2.03 – 3.71)	2.69 (1.67 – 3.54)
<i>p-</i> value	0.9972	0.9999
deviance	34.82	28.48
DOF	61	61

calculated c_{tow} values were 0.72 (BACOMA) and 0.73 (T90), and they were not significantly different. Both values are significantly <1.0, meaning that not all plaice contacted the codend meshes during the towing phase and attempted to escape. Between the codends and between the phases of the fishing process, no significant differences were detected in the L50 or the SR values. As for cod, the limited escape probability during the towing phase at fishing depth was related to limited contact with the codend meshes during towing and not to changes in the selective potential of the codends between different phases of the fishing process.

Flounder

The escape patterns for flounder during the fishing process were very similar to those for plaice (Figure 6, Table 6). Due to the much smaller number of flounder in the experimental data (Table 2), the confidence limits (Figure 6, right column) were much wider compared to those for plaice. No significant differences in the escape patterns between the two codend types were found, and the estimated c_{tow} was < 1.0, meaning that not all flounder attempted to escape through the codend meshes during towing. Due to the limited number of flounder, especially those <25 cm in length, the confidence limits for the experimental data were very wide, resulting in the value for c_{tow} for the T90 codend not being significantly <1.0. No significant difference in the selective properties between the two codends, or between the two phases of the fishing process, was found. However, the data for flounder were weaker and therefore less conclusive compared to the data for the other two species investigated.

Discussion

In this study we developed and applied a model to investigate the escape pattern of cod, plaice, and flounder through codend meshes during the fishing process (inclusive of towing at fishing depth and haul-back of the fishing gear to the surface). In contrast to models that have traditionally been applied to study these processes, the model presented herein accounts explicitly for the fact that not all fish necessarily contact the codend meshes while the trawl is towed at fishing depth. Applying this new model to experimental data collected for the trawl fishery targeting Baltic Sea cod revealed that it is necessary to account for this phenomenon in order to describe the escape patterns observed for cod, plaice, and flounder. Using our modelling approach, it was possible to assess whether limited escape during the towing phase was related to behavioral aspects of the fish (i.e. potentially not attempting to escape through the codend meshes during towing) or if it was related to a lack of opportunities to escape through the codend meshes during the towing phase. The application of the model to the data collected demonstrated that a significant proportion of the cod and flatfish entering the codend during the fishing process do not attempt to escape through the codend meshes during the towing phase. This could explain the observed large fraction of escaping fish that do so during the haul-back phase of the fishing process.

That a large fraction of escape occurs late in the fishing process has been reported in other studies of other fisheries (Madsen et al., 2008; Grimaldo et al., 2009), and we speculate that the cause of this late escape may be related to fish behavior, with not all fish attempting to escape through the codend meshes while the gear is towed at fishing depth. This possibility was not assessed in those studies due to the methods used to analyse the data.

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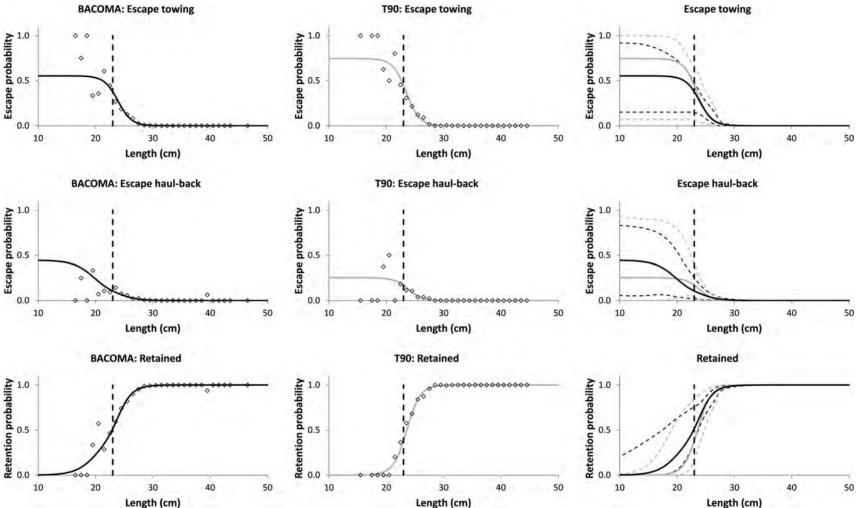


Figure 6. Escape likelihood for flounder (*Platichthys flesus*) during towing (top) and during haul-back (middle), and retention likelihood (bottom) for the BACOMA codend (left column) and the T90 codend (middle column). The diamonds represent the experimental datapoints. The right column compares the model curves for the BACOMA codend (black line) and the T90 codend (grey line) with the 95% confidence intervals for the models indicated by the stippled broken curves. The minimum landing size of 23 cm in the western Baltic Sea is indicated by the vertical broken line.

Table 6. Estimated model parameter and fit statistics for the temporal pattern of size selectivity of flounder in the BACOMA and T90 codends.

	BACOMA	T90
L50 _{total} (cm)	22.87 (17.42 – 23.71)	23.57 (19.01 – 24.70)
SR_{total} (cm)	4.39 (2.66 – 12.48)	2.58 (1.71 – 6.16)
c_{tow}	0.55 (0.15 – 0.92)	0.75 (0.07 – 1.00)
L50 _{tow} (cm)	23.9 (21.64 – -26.89)	23.47 (19.33 - 26.98)
SR_{tow} (cm)	2.64 (0.10 – 4.05)	2.56 (0.10 - 4.56)
L_{cut} (cm)	16.00	15.00
L _{lim} (cm)	27.44	26.90
L50 _{haul-back} (cm)	20.1 (11.83 – 22.29)	22.00 (17.68 - 23.43)
SR _{haul-back} (cm)	4.05 (2.68 – 8.32)	2.74 (1.48 – 4.70)
<i>p-</i> value	0.3633	0.9979
deviance	55.99	28.24
DOF	53	53

However, those data could be re-analysed by applying the method described in this paper. Relatively similar escape patterns were observed in our study, by Madsen *et al.* (2008), and by Grimaldo *et al.* (2009), even though the three studies were conducted in very different fisheries, at different depths, and with different relative duration of the towing and haul-back phases.

For the data collected in this study, the escape processes were sufficiently well described assuming a length-independent c_{tow} Data for cod <33 cm in length were excluded because the mesh size used in the covers resulted in potential overlap of selectivity between the cover and the test codend. One could question whether we could use data for cod <33 cm in the analysis because from model predictions in Madsen et al. (2002) it would seem very unlikely that a cod with length above 25 cm would be able to escape through a diamond codend with meshsize 80 mm (the cover mesh size we applied in our experiment). However the cover applied is made of thin single twine netting (Table 1), whereas the codends that the results in Madsen et al. (2002) are based on were made of thick double-twine netting. Based on Herrmann and O'Neill (2006) we therefore would expect that the results by Madsen et al. (2002) could potentially considerably underestimate the selective properties of the cover applied in our experiment. Given this, and the fact that Wienbeck et al. (2011) demonstrated the smallest cod, based on its morphology, that would not be able to pass through the meshes in cover under any circumstances had a length of 33 cm, we believe it is best not to use cod < 33 cm in the analysis. Due to limited swimming abilities, it might be expected that c_{tow} for smaller individuals would increase; this possibility should be investigated in a future experiment. Such an assessment would require changes in the cover construction to enable using cod <33 cm in the analysis.

Factors such as towing speed, water temperature, and fish condition could potentially also affect $c_{tow}(l)$ (Wardle, 1993; Winger et al., 1999; He, 2010). Additionally, it is unclear whether the value for c_{tow} is linked to the average ratio between towing time and the duration of the haul-back operation. It is also unclear if factors such as the amount of fish in the catch or the rate of fish entering the codend could affect c_{tow} . One could also speculate whether flatfish species like plaice and flounder may have low contact probability with the square mesh window installed in the top of the BACOMA codend during towing. Knowledge about reduced percentage of attempts to escape during the

towing phase in standard codends should foster the development of new gears that can address this issue. Such gears could include escape stimulation devices that would increase the contact probability between fish and codend mesh (Kim and Whang, 2010).

The precision in the assessments made in this study is affected by the relative small number of hauls carried out with each of the two codend types tested (six hauls for each). In particular for plaice and flounder, the relatively low numbers of individuals caught may have contributed to rather large confidence intervals for the escape and retention probabilities. This reduced our chance of detecting significant differences in performance of the two codend types for these species.

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