

Original research article

# Understanding size selectivity of trawls using structural models: Methodology and a case study on fish sorting grids

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## ABSTRACT

Fish behaviour affects the performance of selection devices in fishing gears. Traditionally, fish behaviour in relation to selection devices is assessed by direct observation. However, this approach has limitations, and the observations are not explicitly incorporated in the selectivity models. Further, underwater observations and quantification of fish behaviour can be challenging. In this study we outline and use an indirect method to explicitly incorporate and quantify fish behaviour in trawl selectivity analysis. We use a set of structural models, which are based on modelling the actual processes believed to determine the size selection of the device, to discern which behaviours are most likely to explain the selectivity process. By bootstrapping we assess how confident we can be in the choice of a specific structural model and on discerning the associated behavioural aspects. We collected size selectivity data in the Barents Sea demersal trawl fishery targeting gadoids, where the use of a sorting grid is compulsory. Using our modelling approach, we obtained deeper understanding of which behavioural processes most likely affect size selectivity in the sorting grids tested. Our approach can be applied to other fishing gears to understand and quantify fish behaviour in relation to size selectivity.

## 1. Introduction

Selection devices in trawls are used to optimise the exploitation patterns for different species. For example, sorting grids are used in several trawl fisheries around the world to reduce the catch of unwanted species and sizes (Kennelly & Broadhurst, 2021; Larsen & Isaksen, 1993; Richards & Hendrickson, 2006; Sistiaga et al., 2018). The intended working principle of the grid is such that undersized individuals should be released through the grid bar spacings, and target-sized individuals should be guided towards the codend and retained there (Fig. 1).

In fisheries where sorting grids are used, problems are often still reported in terms of their sorting efficiency (Brinkhof et al., 2020; Kennelly & Broadhurst, 2021; Zeller et al., 2018). In the Barents Sea, large quantities of undersized fish can be retained during the capture process while many fish of targeted size are simultaneously released (Brinkhof et al., 2020; Sistiaga et al., 2016). This leads to fishing inefficiencies whereby fishermen must increase their effort to sort the catch or to catch their quota. Previous investigations have indicated that fish behaviour could significantly affect the size selectivity of sorting

grids (Herrmann et al., 2019; Sistiaga et al., 2011). For this reason, it is of relevance to understand the role that fish behaviour plays during capture for different species and to what extent this impacts the size selectivity.

To optimise grid size sorting efficiency, it is important that the sorting grid operates in such a way that it enables as large fraction as possible of the fish entering the grid section to interact with the grid. The most important commercial species caught in the Barents Sea demersal trawl fishery are cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*), while redfish (*Sebastes* spp.) is one of several important bycatch species (Grimaldo et al., 2016). There are several behavioural differences between cod, haddock and redfish, therefore this could lead to differences in the way that each species interacts with the sorting grid and the subsequent efficiency of the device (Herrmann, Sistiaga, Larsen, & Nielsen, 2013; Herrmann et al., 2009; Jacques et al., 2019; Larsen et al., 2016). Cod, for example, have been observed with a low activity level in the trawl compared to other species like haddock or redfish, which can impact the probability that cod seek out escape outlets and therefore interact with the grid section (Grimaldo et al., 2007, 2018;

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Melli et al., 2018; Sistiaga et al., 2018). As cod move aft towards the grid, they tend to follow the path of the lower netting panel, while haddock tend to orient themselves more upwards (Engås et al., 1998; Grimaldo et al., 2018; Krag et al., 2009; Larsen et al., 2021; Wardle, 1993). Redfish behaviour in the trawl has been less documented, but according to Larsen et al. (2016, 2021) and Sistiaga et al. (2018), the vertical distribution of redfish is understood to be relatively even in the grid section. Therefore, if fish are entering the sorting grid section in different ways, it could be expected that they would consequently need to orientate themselves in different ways to interact, and potentially escape, through the grid.

The ability of fish to orientate themselves optimally to be able to escape the trawl through the grid can be length-dependent (Hannah et al., 2003; He, 2010; Herrmann et al., 2019). This is explained by the stronger swimming capabilities of larger fish. However, smaller cod and haddock have been found to have a higher probability of escaping compared to larger cod and haddock, both for a square mesh panel and a rigid sorting grid in demersal trawls (Herrmann et al., 2019; Krag et al., 2014). This can be a result of the larger individuals displaying avoidance behaviour of the grid as they have a higher swimming capability compared to smaller fish at this point in the catch process.

A better understanding of fish behaviour is important to further improve size selectivity in trawls (Herrmann et al., 2019; Wardle, 1993). Therefore, the focus of the present study is to gain a deeper understanding of the mechanisms determining size selectivity of sorting grids.

In general, two different types of models may be applied to describe the size selectivity of a selection device (Fryer & Shepherd, 1996). The first are empirical models. These models simply fit a curve to the trend in the experimental data without the model parameters providing any explicit information about the processes involved in the size selection of the device. The second are structural models. These are based on explicitly attempting to model the individual processes believed to determine the size selection of the device. In this case the value of the parameters in the model will contain information about the processes involved in the size selection including fish behaviour (O'Neill & Herrmann, 2007; Zuur et al., 2001). Since we aim to obtain a deeper understanding of the size selection by grids including the fish behaviour involved, we base the study on a set of structural models.

However, when the parameter values in the structural models are to be applied to gain information on the internal processes involved, it raises the question on how confident one can be on selecting one specific model over another for the description of selectivity. It needs to be considered that there is a stochastic element in the specific experimental data obtained. To address this challenge, the present study outlines how a bootstrap model selection technique can be applied to selectivity data from sorting grids. This approach accounts for the uncertainty associated with selecting a particular structural model (Lubke et al., 2017). By using fish sorting grids employed in the Barents Sea as a case study, we demonstrate our approach and apply it to obtain a deeper understanding on sorting grid performance in this demersal trawl fishery.

## 2. Materials and methods

### 2.1. Modelling the size selection in a grid section

The internal processes governing the performance of the sorting grid were evaluated indirectly using experimental data from sea trials. This approach is indirect as it compares the inputs with the outputs of the grid selection process, rather than analysing the process directly by means of, for example, video observation. In this way, the sizes of the fish which either escaped through the grid (output) or passed towards the codend (output) were compared to the sizes of fish which entered the grid section (input). This procedure was carried out using five different structural models to describe the size selection  $r(l, \nu)$  of the tested grids. The value of the model expresses the retention probability as a function of fish length  $l$ .  $\nu$  is a vector for the parameters of the model.

Each of the models made unique assumptions regarding the underlying behavioural and morphological processes occurring during grid size selection. The first structural model we considered was a logistic model that assumed that all fish interact with the grid in the same way and independent of their size to be size sorted by it (Grimaldo et al., 2007; Sistiaga et al., 2018). Due to that only fish below a certain size would be able to physically pass through the grid bar spacings, the size selection of the grid can be modelled by using a traditional s-shaped selection curve (Wileman et al., 1996):

$$r(l, \nu) = \text{Logistic}(l, L50, SR) = \frac{\exp((l - L50) \times \ln(9)/SR)}{1 + \exp((l - L50) \times \ln(9)/SR)} \quad (1)$$

Where  $L50$  represents the length  $l$  of the fish that has a 50% probability of being retained by the grid. Thus, the  $L50$  value is linked to the sizes of fish that morphologically would be able to pass through a grid with a specific bar spacing.  $SR$  is the selection range defined as the difference between  $L75$  and  $L25$  which quantifies how precisely the process discriminates between the retained and released fish based on their size. A small  $SR$  value would describe a precise discrimination and a large  $SR$  value would describe an imprecise discrimination (Bak-Jensen et al., 2022).

The *Logistic* model does not account for situations where only a fraction of the fish interacts with the grid. Therefore, a more complex model based on the *Logistic* model was applied; the *Contact Logistic* model (*CLogistic*). This model accounts for that not necessarily all fish entering the gear interact with (contact) the selection device (Herrmann, Sistiaga, Larsen, & Nielsen, 2013; Sistiaga et al., 2010; Zuur et al., 2001). For sorting grids, the *CLogistic* model is described by the selection parameters  $C_1$  (grid contact probability),  $L50_1$  (length at which a fish has a 50% probability of passing through the grid conditioned that it contacts the grid) and  $SR_1 (=L75_1 - L25_1$  conditioned that the fish contacts the grid). In this model,  $C_1$  values range from  $0.0 \leq C_1 \leq 1.0$ , with a  $C_1$  value of 1.0 meaning that all fish contact the grid and are size sorted by it. The equation for the *CLogistic* model is:

$$r(l, \nu) = \text{CLogistic}(l, C_1, L50_1, SR_1) = 1.0 - C_1 \times (1.0 - \text{Logistic}(l, L50_1, SR_1)) \quad (2)$$

In the *CLogistic* model it is assumed that all fish contacting the grid do so in the same way and independent of their size. It is reasonable to

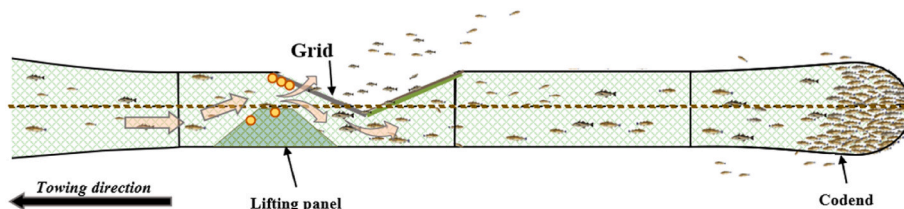


Fig. 1. The intended working principle of the grid section and the codend configuration used in the Barents Sea bottom trawl fishery.

consider that not necessarily all fish entering a sorting grid section contact the grid in the same way. Therefore, a model describing size selectivity in cases where more than one size-selection process contributes to the overall size-selection of the sorting device was tested. This model is the *Dual Logistic* model (*DLogistic*) (Herrmann et al., 2016; Jacques et al., 2019), and assumes that a fraction ( $C_1$ ) of the fish entering the grid section will be exposed to one logistic size-selection process described by the parameters  $L50_1$  and  $SR_1$ , while the remaining fraction ( $1.0 - C_1$ ) will be exposed to another also logistic size-selection process with the parameters  $L50_2$  and  $SR_2$ . In each of the selectivity processes only fish up to a certain size would be able to pass through the grid bar spacing while undergoing each of the specific processes. The equation for the *DLogistic* model is:

$$r(l, v) = DLogistic(l, C_1, L50_1, SR_1, L50_2, SR_2) = C_1 \times Logistic(l, L50_1, SR_1) + (1.0 - C_1) \times Logistic(l, L50_2, SR_2) \quad (3)$$

The *DLogistic* model can be used to account for that not all fish contact the grid with the same orientation so that their length-dependent chance of being able to pass through the grid is different. The chance that the fish contacts the grid in one specific way,  $C_1$  or  $1.0 - C_1$ , is assumed to be length-independent in the *DLogistic* model. These different orientations by which the fish can meet the grid are named contact modes (Jacques et al., 2019).

If two contact modes are not sufficient to describe the size selection process, the *Triple Logistic* model (*TLogistic*) (Jacques et al., 2019), which includes a third contact mode, can be used:

$$r(l, v) = TLogistic(l, C_1, C_2, L50_1, SR_1, L50_2, SR_2, L50_3, SR_3) = C_1 \times Logistic(l, L50_1, SR_1) + C_2 \times Logistic(l, L50_2, SR_2) + (1.0 - C_1 - C_2) \times Logistic(l, L50_3, SR_3) \quad (4)$$

If  $L50_3$  is assigned to a very small value, then the *TLogistic* model can account for a situation where a fraction of the fish is not subjected to a length-dependent chance of escape. The *CLogistic*, *DLogistic* and *TLogistic* do not account for potential length-dependency in the way fish contact the grid. Therefore, an additional model termed the *Length Contact Logistic* model (*LCLogistic*) was considered. This model considers scenarios where fish of the same species, but with different sizes, have different probabilities of contacting the grid to be size sorted by it (Herrmann et al., 2019). This model can be interpreted as a generalization of the *CLogistic* model but where the contact is length-dependent:

$$r(l, v) = LCLogistic(l, C_a, C_b, L50_c, SR_c, L50_1, SR_1) = 1.0 - C(l, C_a, C_b, L50_c, SR_c) \times (1.0 - Logistic(l, L50_1, SR_1)) \quad (5)$$

where

$$C(l, C_a, C_b, L50_c, SR_c) = C_a + (C_b - C_a) \times Logistic(l, L50_c, SR_c)$$

Where  $C(l, C_a, C_b, L50_c, SR_c)$  represents the length-dependent contact probability curve. Equation (5) is a flexible model that enables increasing, decreasing and constant values for fish contact with the grid to be modelled for different lengths of fish (see Herrmann et al. (2019) for further details).

## 2.2. Experimental design and model estimation

To collect data for assessing the size selection of a grid section, a configuration with a cover over the grid and a codend 'blinded' with a small mesh liner was used (Fig. 2). In such a configuration, the fish escaping through the grid are collected in the grid cover (*GC*) placed over the grid outlet, whereas fish that do not pass through the grid are collected in the codend (*BC*).

The expected number of fish retained in the blinded codend ( $n\widehat{BC}_l$ ) and the expected number of escapees collected in the grid cover ( $n\widehat{GC}_l$ ) can be directly related to the total number of fish entering the section of the grid  $n_l$  and the size selection curve  $r(l, v)$  modelled by either of equations (1)–(5):

$$\begin{aligned} n\widehat{BC}_l &= n_l \times r(l, v) \\ n\widehat{GC}_l &= n_l \times (1.0 - r(l, v)) \end{aligned} \quad (6)$$

Under the assumption that the retained ( $nBC_l$ ) and escaped ( $nGC_l$ ) fractions of the catch are determined by the size selection of the sorting grid, the size selection curves (1) to (5) and associated selectivity parameters can be estimated by maximum likelihood estimation. This is done by minimizing the negative of the binominal log-likelihood function:

$$- \sum_{i=1}^m \sum_t \{nBC_{it} \times \ln(r(l, v)) + nGC_{it} \times \ln(1.0 - r(l, v))\} \quad (7)$$

Expression (7) includes summation over hauls  $m$ , with  $nBC_{it}$  and  $nGC_{it}$  being the number of individuals captured in haul  $i$  belonging to length class  $l$  for the specific species being analysed. Expression (7) provides an estimate of the average selectivity properties for the sample of fish for each specific grid section tested.

Model selection in size selectivity research is often carried out using the Akaike Information Criterion (*AIC*) (Akaike, 1974) whereby the model resulting in the lowest value is picked. With this approach, this best model is selected one time based on the specific experimental data

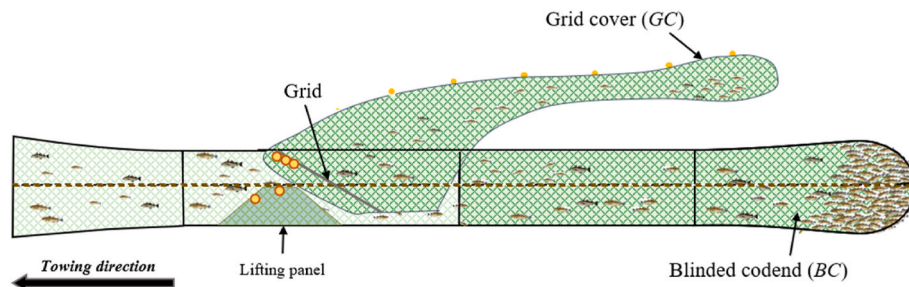


Fig. 2. The experimental design applied during the trials, displaying the sorting grid, grid cover (*GC*) and blinded codend (*BC*).

observed, hereafter referred to as One-time Model Selection (OMS). Selecting the best model based on *AIC* provides a trade-off between how well it describes the main trend in the experimental data and the complexity of it in terms of the number of parameters.

The five structural models (equations 1-5) were applied and ranked using the OMS approach. The best model was then applied to describe the size selection in the grid section. Further, to determine the weight of evidence in favour of one model compared to another, the relative likelihood ( $L_i$ ) between models was calculated. The relative likelihood can be used to describe how likely one model is relative to the model with the lowest *AIC* ( $AIC_{min}$ ) for providing the best representation of the data. We calculate  $L_i$  based on the approach from Wagenmakers and Farrell (2004):

$$L_i = \exp\left(-\frac{AIC_i - AIC_{min}}{2.0}\right) \quad (8)$$

Using equation (8), the difference in *AIC* corresponding to 95% confidence in model selection can be calculated by setting  $L_i = 1.0 - 0.95 = 0.05$  and rearranging, which leads to:

$$\Delta AIC = AIC_i - AIC_{min} = -2.0 \times \ln(0.05) = 5.99 \approx 6 \quad (9)$$

Therefore, models that had an *AIC* value within 6 of the model with the lowest *AIC* were considered as potential candidates to describe the data (Melli et al., 2023). The ability for the chosen model to describe the experimental data was determined based on calculating the corresponding *p*-value. In the case of poor fit statistics (*p*-value < 0.05), the residuals of the data were inspected to confirm whether the problems could be attributed to structural problems in the data or overdispersion (Wileman et al., 1996).

To account for within- and between-haul variation (Fryer, 1991) in the size selectivity when estimating the uncertainty for the selection curve and associated parameters, we applied a double bootstrapping technique (Efron, 1982; Herrmann et al., 2012; Millar, 1993). Specifically, Efron percentile (95%) confidence intervals (CIs) were estimated using 1000 double bootstrap iterations (Chernick, 2007; Efron, 1982; Herrmann et al., 2012; Millar, 1993).

### 2.3. Accounting for uncertainty in the model-selection process

The OMS model selection process (section 2.2) has been criticised as it does not consider the uncertainty in the experimental data (Burnham & Anderson, 2002; Efron, 2014; Preacher & Merkle, 2012). When fitting a set of models to a set of finite samples taken from the population, the chance that the same model would be selected in all samples could be affected because of sampling fluctuation (Lubke & Campbell, 2016). It is important to account for that a different sample taken from the same population could lead to a different model being selected (Burnham & Anderson, 2002; Efron, 2014; Preacher & Merkle, 2012).

Multi-model inference is an approach earlier used to address uncertainty due to uncertainty in model selection (Burnham & Anderson, 2002; Herrmann et al., 2015, 2017). This includes weighting the different model contributions relative to each other by using the *AIC* weights. However, this approach does not account for the challenges in model selection under circumstances of sample size fluctuations. Lubke and Campbell (2016) outline the advantages of using a bootstrap model selection (BMS) approach to quantify model selection uncertainty. This is done by drawing multiple bootstrap samples from the original sample and conducting model selection in each iteration (Lubke & Campbell, 2016). In the present study we adapted the BMS approach inspired by Lubke and Campbell (2016) to investigate sorting grid size selectivity specifically. Size selectivity data obtained from sea trials was analysed using the five structural models described earlier: *Logistic*, *CLogistic*, *DLogistic*, *TLogistic*, *LLogistic*. This was executed using the software tool SELNET (Herrmann et al., 2012). The BMS approach was applied by conducting 1000 bootstrap iterations and selecting the model which

resulted in the lowest *AIC* in each iteration. The counts for the number of times each model was selected were aggregated. A model which attained a high selection count could be interpreted as having a high probability of representing the process in a different sample of data (Lubke & Campbell, 2016). Models which were selected in less than 5% of the bootstrap iterations were rejected as potential candidate models as they were deemed unlikely to be chosen to model the selection process given a different dataset. We then used the double bootstrap method outlined in Millar (1993) and in Sistiaga et al. (2010) to account for the uncertainty related to selecting a structural model and the corresponding uncertainty on the selection curve.

### 2.4. Data collected during sea trials

Experimental data were collected during sea trials in the Barents Sea demersal trawl fishery on board the research vessel Helmer Hanssen (LOA 63.8 m, 4080 HP), from the 14th to the December 18, 2020. The trawl used for the data collection was a commercial Alfredo No. 3 design (for further details regarding this, see Brinkhof et al. (2020)). Two sorting grid designs which were tested had different bar spacings measured to be  $54.78 \pm 1.12$  mm (mean  $\pm$  SD) (55 mm nominal bar spacing) and  $44.70 \pm 1.30$  mm (45 mm nominal bar spacing), respectively. The specific bar spacing was measured using callipers following the protocol described by Wileman et al. (1996). The sorting grids were 1650 mm long and 1234 mm wide and were each mounted following the guidelines of the Directorate of Fisheries at an inclination angle of 25–26°, which is considered optimal for its selectivity (Norwegian Directorate of Fisheries, 2022; Sistiaga et al., 2010).

The grids were each mounted in standard 2-panel Sort-V sections (Sistiaga, Herrmann, Brinkhof, & Larsen, 2023). These grid sections were both 59 ½ meshes long and constructed in a two-panel configuration of 135 mm mesh size. The grid section was attached after the trawl belly, and in front of an extension piece (58 meshes long), which was followed by the codend (Fig. 2). The codend was approximately 11 m long in stretched length. The performance of the sorting grids was evaluated by comparing the sizes of the fish retained in the *GC* and *BC* (output) in respect to fish entering the grid section (input) (Fig. 2). The *GC* was constructed following the design by Larsen and Isaksen (1993) and had a mesh size of  $45.23 \pm 0.89$  mm which was measured using an OMEGA gauge (Fonteyne et al., 2007). To avoid blockage of the grid outlet by the *GC*, seven floats were mounted to it (Fig. 2). Fish which did not pass through the grid were collected in the *BC* ( $52.38 \pm 1.21$  mm mesh size) (Fig. 2). When the catch was brought onboard, fish from the *GC* and *BC* (Fig. 2) were kept separate by emptying each compartment into separate holding bins. The total length of all cod, haddock and redfish above 20 cm were measured to the nearest centimetre below.

### 2.5. 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 commercial fishing practice in accordance with the local legislation and institutional requirements. 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 were 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.



**Table 1**

Haul details showing the haul number, grid bar spacing tested, date, fishing time, depth and number (*n*) of cod, haddock and redfish length measured from the BC and GC.

Haul	Grid	Date (dd.mm.yyyy)	Fishing time (hh:mm)	Depth (m)	Cod ( <i>n</i> )		Haddock ( <i>n</i> )		Redfish ( <i>n</i> )	
					BC	GC	BC	GC	BC	GC
1	45 mm	December 14, 2020	01:30	299	442	11	261	124	5	20
2	45 mm	December 14, 2020	01:00	300	260	7	186	84	9	12
3	45 mm	December 14, 2020	01:02	300	340	15	341	110	20	20
4	45 mm	December 14, 2020	01:00	295	529	8	320	147	9	13
5	45 mm	December 15, 2020	01:00	256	522	11	329	63	29	17
6	45 mm	December 15, 2020	01:01	310	71	8	88	98	6	27
7	45 mm	December 15, 2020	01:13	334	62	11	81	120	2	15
8	45 mm	December 15, 2020	01:30	323	80	11	147	147	5	14
9	45 mm	December 15, 2020	02:00	321	136	19	176	277	9	34
10	45 mm	December 15, 2020	02:00	324	128	23	182	246	7	29
11	45 mm	December 15, 2020	02:00	318	111	9	151	245	8	37
12	45 mm	December 16, 2020	02:00	320	129	8	126	203	4	30
13	45 mm	December 16, 2020	02:00	312	153	14	235	217	11	12
14	45 mm	December 16, 2020	02:00	308	180	23	179	245	9	23
15	55 mm	December 16, 2020	02:00	318	204	44	96	347	13	33
16	55 mm	December 16, 2020	02:00	322	312	45	292	422	5	17
17	55 mm	December 16, 2020	02:00	314	315	39	329	353	7	22
18	55 mm	December 16, 2020	02:02	321	226	65	164	596	10	80
19	55 mm	December 16, 2020	02:00	319	164	39	115	448	6	38
20	55 mm	December 17, 2020	02:00	318	228	47	149	571	13	56
21	55 mm	December 17, 2020	02:03	321	223	53	192	504	11	37
22	55 mm	December 17, 2020	02:02	319	105	40	67	312	3	54
23	55 mm	December 17, 2020	02:00	322	161	50	86	356	12	58
24	55 mm	December 17, 2020	02:00	331	183	55	142	348	10	30
25	55 mm	December 17, 2020	02:00	323	281	52	175	368	8	30
26	55 mm	December 17, 2020	02:01	323	405	55	251	401	12	40
27	55 mm	December 18, 2020	02:00	321	280	40	197	454	15	31
28	55 mm	December 18, 2020	02:00	332	257	72	223	621	–	–
Total					6487	874	5280	8427	258	829

### 3. Results

#### 3.1. Overview of sea trials

During the data collection period, a total of 28 hauls were conducted. Of these, 14 hauls used the 45 mm grid, and 14 hauls used the 55 mm grid (Table 1). In total 7361 cod, 13,707 haddock and 1087 redfish were captured and length-measured (Table 1). Cod were within the length range of 20–139 cm, haddock were within 20–85 cm and redfish were within 20–63 cm. All hauls were conducted in the Barents Sea within 72°01'–72°19' N and 30°46'–31°56' E.

#### 3.2. Analysis based on the OMS approach

The mean selection curves obtained for each of the structural models were plotted together to compare how well each of them described the main trend in the experimental data (Fig. 3). Plotting these curves together also provided insight into how much deviation there was between them. The curves followed a similar tendency for cod and haddock (Fig. 3-a:d), however they deviated more from each other in the lower tails. This was expected due to the dispersion in the experimental data for smaller length classes as they were captured at lower frequencies compared to central length classes. The deviation between model curves was greatest for redfish, also likely as a result of the experimental data dispersion for redfish (Fig. 3-e:f). Deviation among the mean selection curves was greater for the 55 mm grid compared to the 45 mm grid for all three species.

Model selection based on the OMS approach indicated that several models were competing for providing the 'best' explanation of the experimental data (Table 2, Supplementary material S1). Multiple candidate models were found due to that the difference in AIC between the best model and the remaining candidate models was not large enough under the relative likelihood ( $L_i$ ) estimation ( $\Delta AIC < 6$ ; Table 2). Therefore, a single explanation for the underlying behavioural processes

taking place could not be determined. To confirm that a model could be a potential candidate model, the fit statistics were checked to ensure that  $P > 0.05$ .

According to the OMS approach, cod and haddock passage through the 45 mm grid was best described by a model including three modes of contact (*TLogistic* model) (Table 2, Supplementary material S1). However, all remaining models were potential candidate models for cod while the *DLogistic* and *LCLogistic* models were considered in addition to the *TLogistic* model for haddock ( $\Delta AIC < 6$ ; Table 2). Redfish selection with the 45 mm grid was best described by the *CLogistic* model according to the OMS approach, suggesting therefore that all fish which contacted the grid did so in the same way (Table 2, Supplementary material S1). However, all remaining models were found to be potential candidate models for redfish with this grid design when using this model selection approach ( $\Delta AIC < 6$ ; Table 2). The same situation was true for redfish with the 55 mm grid as all remaining models scored significantly low under the relative likelihood estimation ( $\Delta AIC < 6$ ; Table 2). However, the *DLogistic* model provided the best explanation of selection with the wider bar spacing for redfish (Supplementary material S1). For cod, the 55 mm bar spacing led to a more simplistic modelled behaviour compared to the 45 mm design as the *DLogistic* model had the lowest AIC value, rather than the *TLogistic* model (Table 2). The number of potential alternative explanations was reduced compared to the 45 mm grid as the difference in AIC was too high for the *CLogistic* and the *Logistic* models to be considered (Table 2). For haddock, the model considering that three modes of contact occur during passage through the grid (*TLogistic* model) was picked for both grid designs (Table 2). Multiple potential explanations for behaviour still existed however, as the *DLogistic* and *LCLogistic* were still potential candidate models for haddock with the 55 mm grid (Table 2). Thus, only the two most simplistic models (*Logistic* and *CLogistic*) could be disqualified with certainty for haddock with both grid designs and for cod with the 55 mm grid ( $\Delta AIC > 6$ ,  $P < 0.05$ ; Table 2).

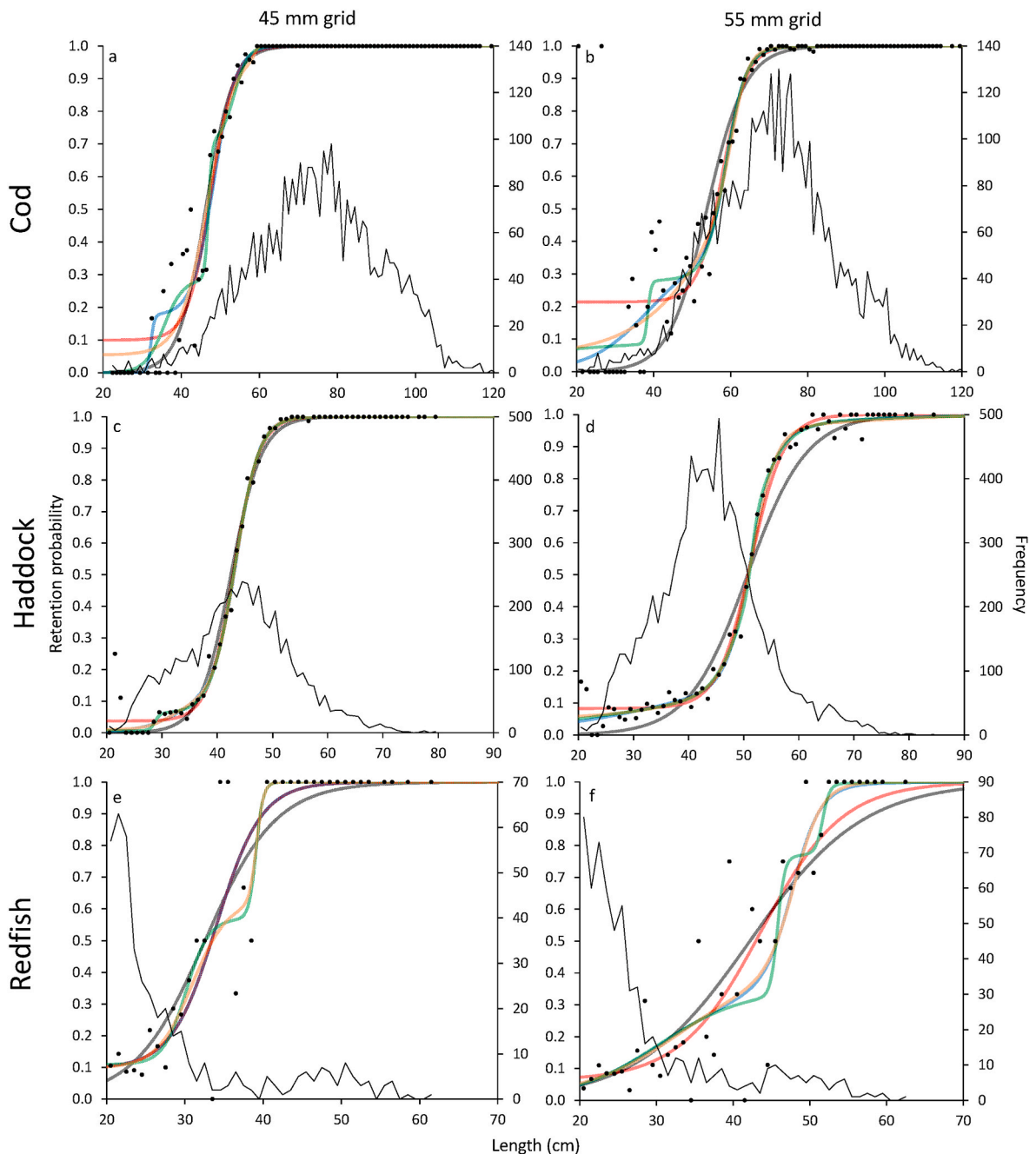


Fig. 3. Mean selection curves using the *Logistic* (grey), *CLogistic* (red), *DLogistic* (blue), *TLogistic* (green) and the *LCLogistic* (yellow) models. Solid black lines show length frequencies with the experimental rates (black dots).

### 3.3. Analysis using the BMS approach

The BMS approach quantified the frequency for how often each structural model was selected in the 1000 bootstrap repetitions (Fig. 4). By applying the BMS approach, both the *DLogistic* and *TLogistic* models were found to be potential candidate models among all cases, while the model assuming length-dependent contact was supported among all cases except for redfish with the 45 mm grid. In this case, the length-dependent contact model was not supported as it was selected in just 18 bootstrap iterations (i.e., selected in <5% of bootstrap iterations). The only instance where the more simplistic *Logistic* and *CLogistic* models were significant was also for redfish with the 45 mm grid (Fig. 4-e). As this case had the smallest dataset, this was likely to have led to greater power to discriminate against more complex models in each of the

bootstrap samples. When accounting for model selection uncertainty for redfish with the 45 mm grid, the number of potential candidate models was reduced from five with the OMS approach to four with the BMS approach (Table 2, Fig. 4-e). With the 55 mm design for redfish, the BMS approach identified that the *Logistic* and the *CLogistic* models could be rejected (Fig. 4-f). Rejecting these models was not possible under the relative likelihood estimate of the OMS approach (Table 2). For cod and haddock, the BMS approach aligned with the OMS approach regarding model selection except for cod with the 45 mm grid whereby the BMS approach enabled the two most simplistic models to be rejected. Therefore, for all three species the OMS approach led to the same models or more being considered as potential candidate models compared to the BMS approach.

The most favoured model resulting from the BMS approach was the

Table 2

Fit statistics for the five structural models for the two different grid bar spacings. The values in bold highlight the model chosen based on the OMS approach.

	Model	<i>Logistic</i>	<i>CLogistic</i>	<i>DLogistic</i>	<i>TLogistic</i>	<i>LLogistic</i>
	<b>Grid design</b>	<b>45 mm</b>				
<b>Cod</b>	$\Delta AIC$	5.27	2.33	1.27	<b>0.00</b>	0.67
	Li (%)	7.17	31.19	52.99	100.00	71.53
	<i>P</i>	>0.9999	>0.9999	>0.9999	>0.9999	>0.9999
<b>Haddock</b>	$\Delta AIC$	156.87	7.13	0.35	<b>0.00</b>	1.18
	Li (%)	<0.01	2.83	83.95	100.00	55.43
	<i>p</i> -value	<0.0001	0.2481	0.5546	0.6894	0.5619
<b>Redfish</b>	$\Delta AIC$	5.03	<b>0.00</b>	4.00	4.51	0.96
	Li (%)	8.09	100	13.53	10.49	61.88
	<i>P</i>	0.8035	0.9600	0.9378	0.9832	0.9899
	<b>Grid design</b>	<b>55 mm</b>				
<b>Cod</b>	$\Delta AIC$	91.24	9.78	<b>0.00</b>	1.73	0.07
	Li (%)	<0.01	0.75	100.00	42.11	96.56
	<i>P</i>	<0.0001	0.6071	0.8844	0.9077	0.9001
<b>Haddock</b>	$\Delta AIC$	308.90	20.51	0.15	<b>0.00</b>	2.21
	Li (%)	<0.01	<0.01	92.77	100.00	33.12
	<i>P</i>	<0.0001	0.0050	0.1903	0.2679	0.1650
<b>Redfish</b>	$\Delta AIC$	5.03	<b>0.00</b>	4.00	4.51	0.96
	Li (%)	8.09	100.00	13.53	10.49	61.88
	<i>P</i>	0.8035	0.9600	0.9378	0.9832	0.9899

model selected in most BMS iterations (Fig. 4). In our study, the outcome of this was consistently different compared to the particular model selected according to the OMS approach (Table 2, Fig. 4). Further, the selection curve estimated based on the BMS approach had comparable or wider estimated confidence limits compared to the selection curve from the model selected based on the OMS approach, which was to be expected. This was evident for both grid designs for cod (Fig. 5-a:b), particularly for length groups where data was weaker. The larger data set attained for haddock did not lead to additional uncertainty between the confidence limits calculated for the two model selection approaches (Fig. 5-c:d). For redfish, applying the BMS approach almost always led to wider confidence limits compared to the OMS approach (Fig. 5-e:f). This was shown for most length sizes for both grid designs except for some central length classes of redfish using the 45 mm design. For this, a small sample size resulted in the simplistic *CLogistic* model being applied with the OMS approach, resulting in wider CIs (Fig. 5-e).

### 3.4. Deconstructing the structural models

The underlying processes decisive for the size selection in the grid section were revealed by deconstructing the structural model picked into its individual components (Figs. 6 and 7). According to the BMS approach, the *Logistic* model was identified as a potential candidate model for describing selection only for redfish with the 45 mm grid (Fig. 4-e, 6-c). If this model reflects the nature of redfish selectivity, then we would assume that all individuals contacted the grid using the same mode and independent of their size. This assumption is illustrated by the horizontal line crossing the second axis at a value of 1.0 (Fig. 6-c).

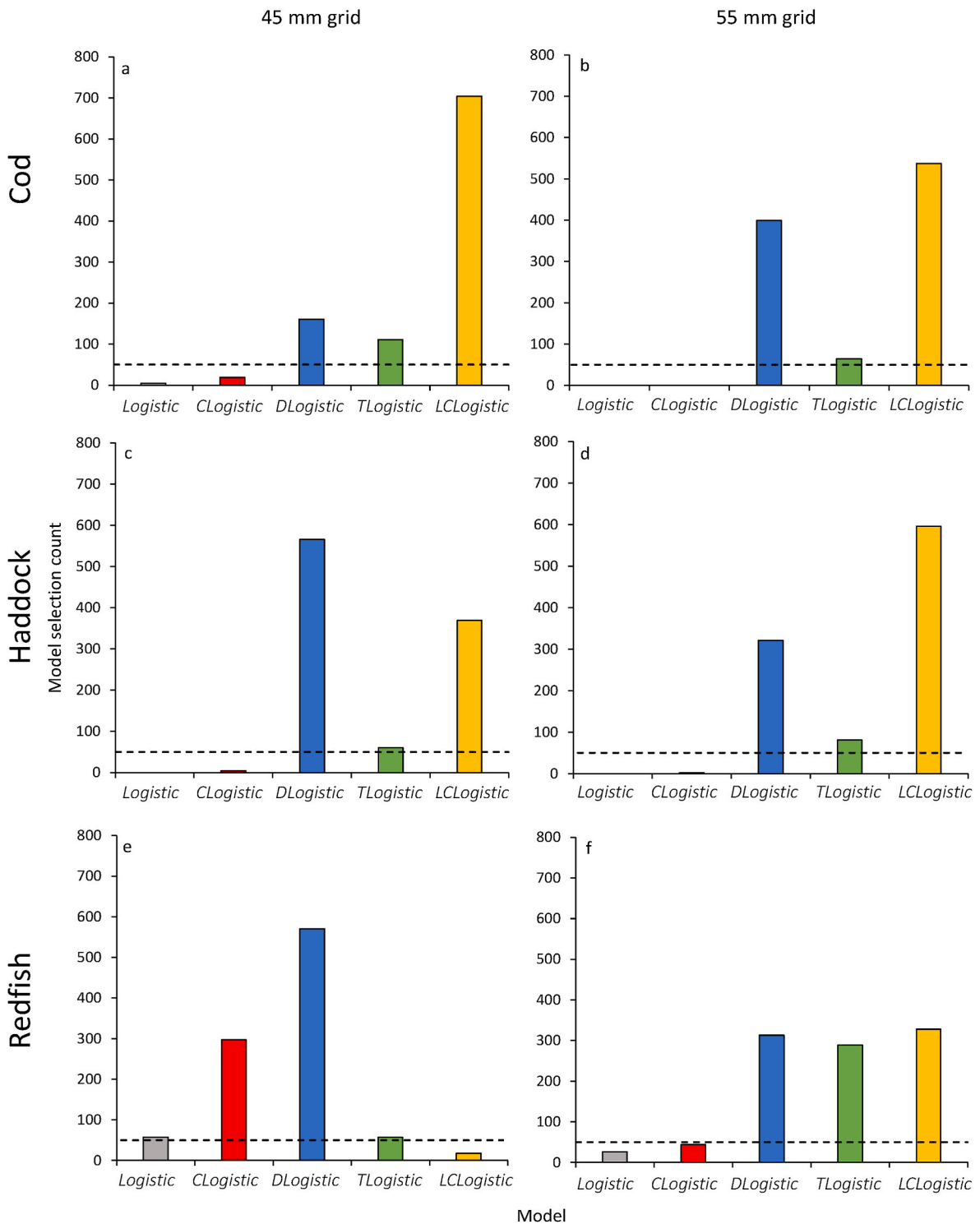
The *CLogistic* model assumed that only a fraction of the fish made contact with the grid and that this fraction is independent of the size of the fish. The probability that fish made contact was then illustrated by the horizontal line crossing the second axis at a value of  $C_1$ . This model was only a potential candidate model for redfish with the 45 mm grid (Fig. 6-f). The horizontal line in this case shows that approximately 90% of redfish contacted the grid. For the smallest individuals (<30 cm) which made contact, the corresponding selectivity curve showed that most (approximately 80%) of these individuals were able to escape. However, as the selectivity curve did not reach 0 for these sizes (100% escapement), we can assume that this was due to that some individuals did not make selectivity contact with the grid (Fig. 6-f).

For the *DLogistic* model, the most optimal contact mode was described by the  $C_1$  selectivity curve (Figs. 6 and 7). The *DLogistic* model predicted that fish using this mode consistently had a significantly lower

retention probability compared to the second mode for central length classes (Figs. 6 and 7). Thus, it is more likely that this mode would explain the loss of target sized fish compared to the mode represented by  $1.0-C_1$ . Conversely, the size selectivity curve associated with this less favourable mode of contact accounted for a higher retention probability for the smallest sizes compared to the selectivity curve of the most favourable mode. Therefore, individuals adopting the second mode of contact were less likely to be able to escape through the grid if they were small. For example, the *DLogistic* model predicted that almost all cod below 50 cm adopting the most optimal mode of contact with the 55 mm grid were predicted to escape (Fig. 7-g). However, individuals of this length which made contact using the second mode of contact had >70% probability of being retained. The horizontal lines crossing the second axis showed that individuals which contacted the grid had a 62% probability of adopting the most optimal contact mode and a 38% probability of adopting the second mode. However, this difference was not significant due to that the corresponding 95% CIs overlapped.

Across all species, the effect of bar spacing was apparent according to parameter predictions made with the *DLogistic* model (Figs. 6 and 7). Specifically, the selectivity curve of the second mode was consistently flatter for the 55 mm grid compared to the 45 mm grid (Figs. 6 and 7). Thus, smaller individuals which adopted the second mode had a greater probability of being able to pass through the 55 mm grid compared to the 45 mm grid. The size selectivity curve of the most favourable mode (mode with  $C_1$ ) was more similar between grid bar spacings compared to the less favourable mode. With the *DLogistic* model, the retention probability was most dependent on the mode adopted when it came to haddock compared to cod or redfish. For haddock the two *DLogistic* contact modes led to significantly different retention probabilities for fish of the Minimum Legal Size (40 cm in length; Norwegian Directorate of Fisheries, 2022) and the probability that individuals used the most optimal mode was significantly greater compared to the second mode (Fig. 6-h, 7-h). This trend was common among the two grid designs. For redfish the probability that either of the two contact modes were used was significantly different according to the *DLogistic* model with the 45 mm grid (Fig. 6-i). Redfish were likely to adopt the two modelled contact modes at more similar rates with the 55 mm grid (Fig. 7-i). However, the two modes resulted in significantly different probabilities of escape for redfish sizes up to 36 cm and 45 cm with the 45 mm and 55 mm grid, respectively.

The uncertainties estimated for each of the modelled parameters of the *TLogistic* model were greater with the 55 mm case compared to the 45 mm case (Figs. 6 and 7). With the *TLogistic* model the difference

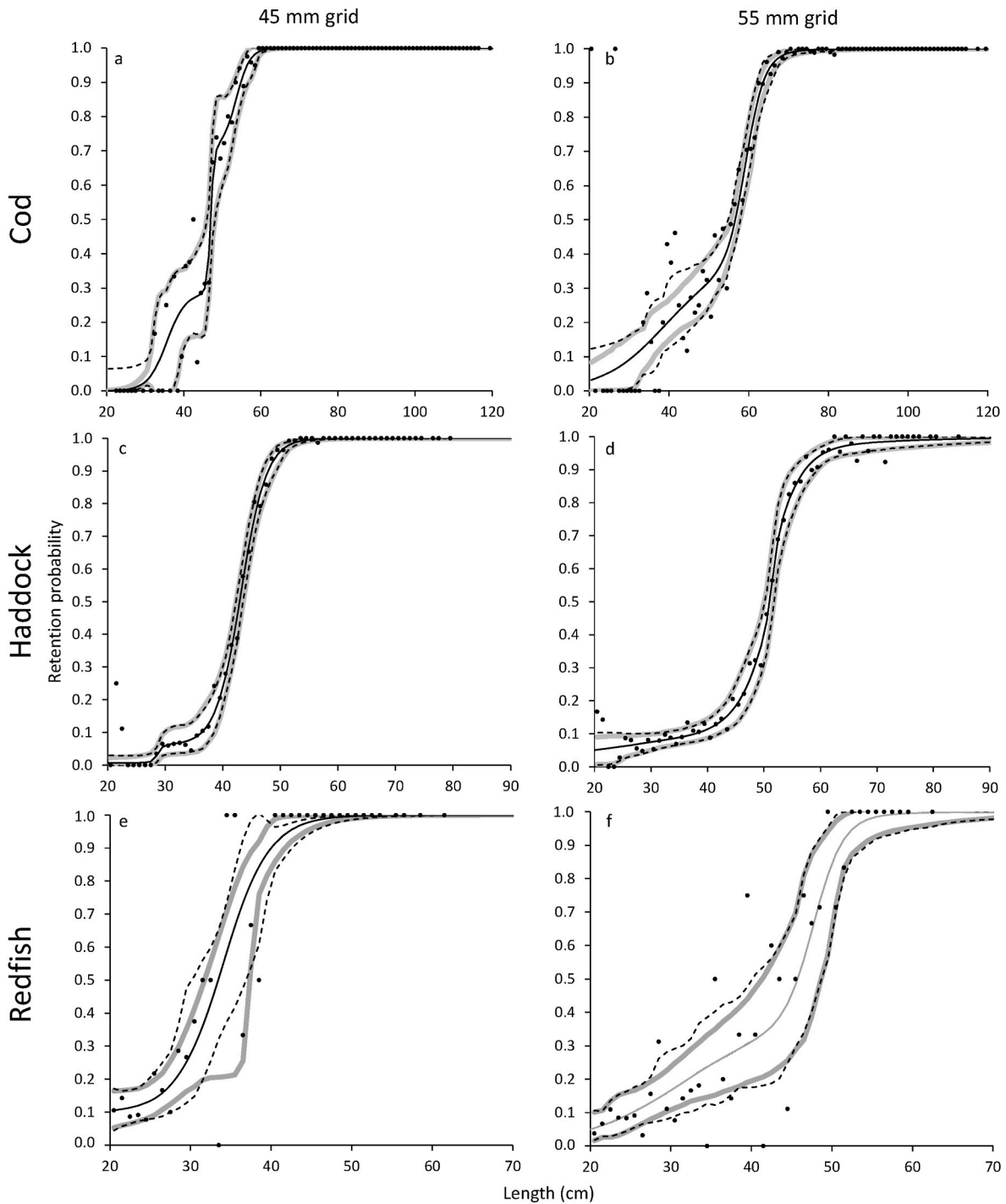


**Fig. 4.** BMS count bar plots for the *Logistic* (grey), *CLogistic* (red), *DLogistic* (blue), *TLogistic* (green) and the *LCLogistic* (yellow) models, with the horizontal dashed line corresponding to the point at which a model is selected 50 times out of the 1000 bootstrap resamples, i.e., at least 5%.

between the probability that fish adopted either of the three contact modes was lower compared to the *DLogistic* model for all species (Figs. 6 and 7). Thus, there were no cases where a particular mode was clearly preferred over another. This was shown as there was no significant difference detected between the horizontal lines for the *TLogistic* model (Figs. 6 and 7). Utilising either the first- or third-most optimal contact mode resulted in a significant difference in retention probability for central length classes for all species with this model (Figs. 6 and 7). However, the predicted retention resulting from using the second mode

was always similar to the first and/or the third most optimal modes according to the 95% CIs estimated. With the *DLogistic* model, the probability that individuals used the most optimal mode was always predicted to be larger compared to the probability for the second mode. However, this trend was not consistent among the three modes modelled by the *TLogistic* model. For example, the second mode was predicted to be used most frequently by cod which contacted the 45 mm grid (Fig. 6-j), for haddock contacting the 55 mm grid (Fig. 7-k) and for both instances of redfish selection (Fig. 6-l, 7-l). If the most optimal mode was



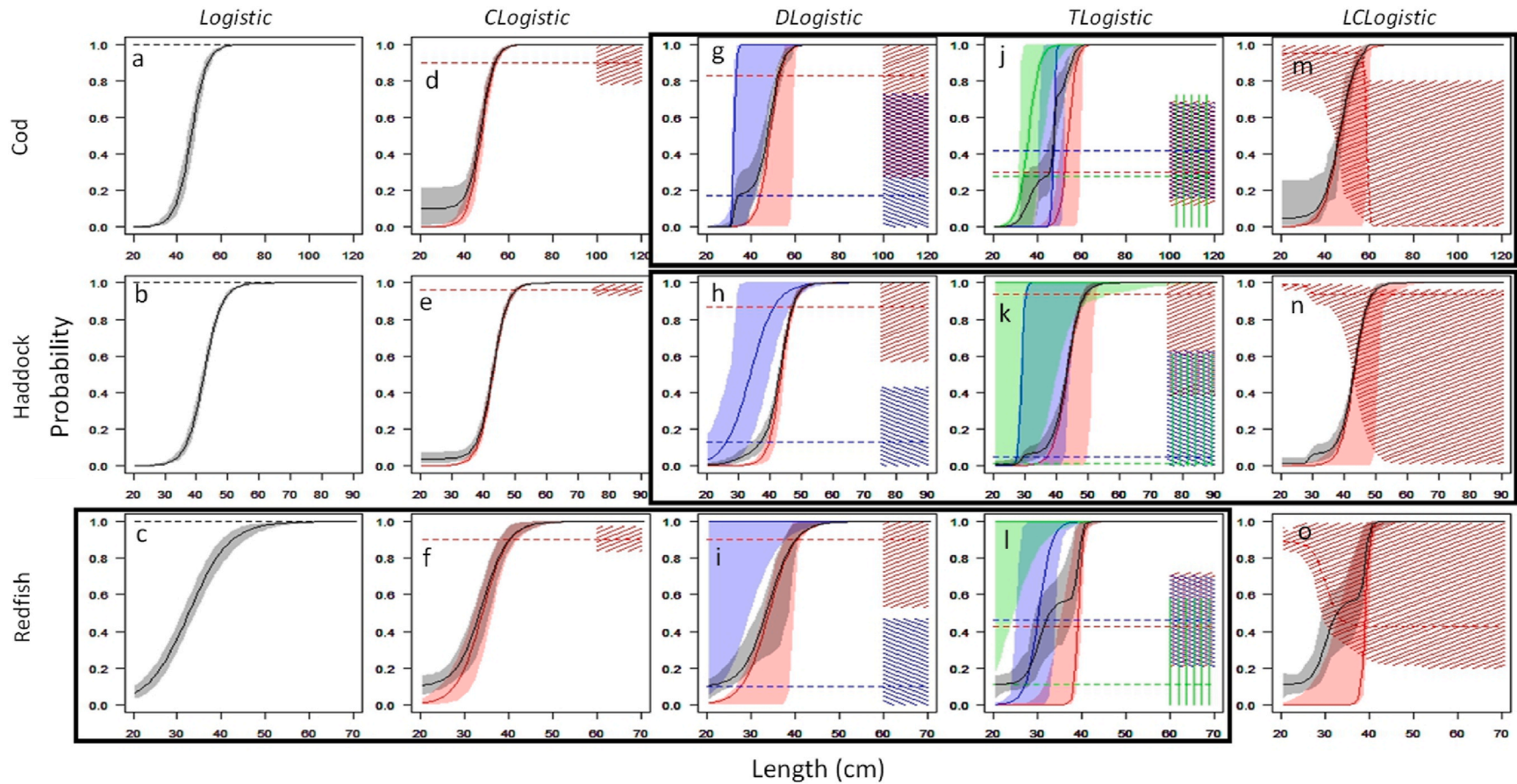


**Fig. 5.** The selection curves for the model selected based on the OMS approach (grey solid 95% CI curves) compared to the model selected using BMS (black dashed 95% CI curves) with the experimental rates (black dots).

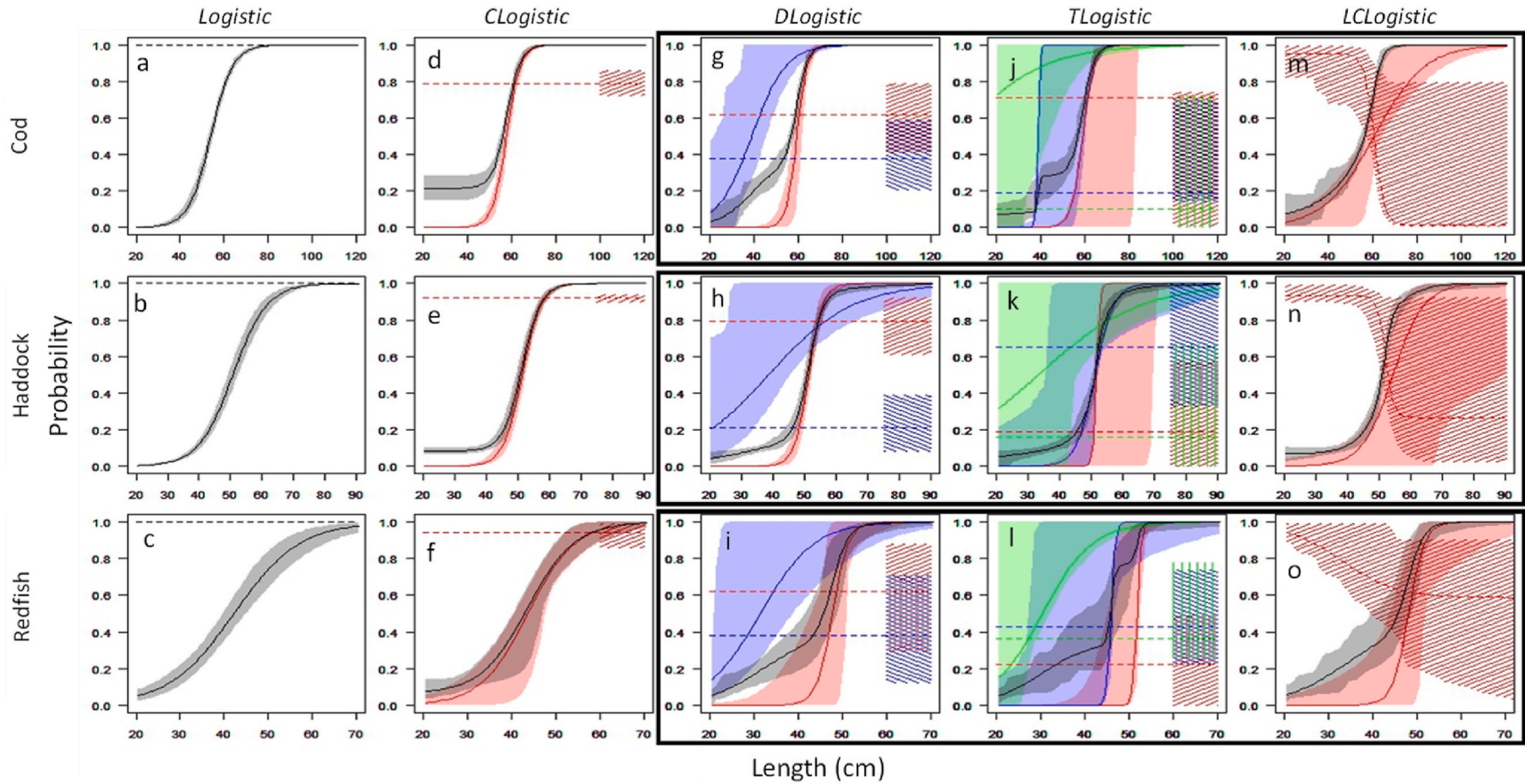
used most often for these cases, this may have led to a more favourable size selection.

By deconstructing the *LCLogistic* model, we could visualise the length-dependent contact probability ( $C(l)$ ) captured by the parameters of the model (Figs. 6 and 7). The selection curve for the *LCLogistic* model for cod showed that <10% of the smallest individuals (<30 cm) were retained by the 45 mm grid (Fig. 6-m). The size selectivity curve for those that made contact (equation (5)) showed that all individuals of this size that made contact escaped (Fig. 6-m). Thus, it could be concluded that the reason for that a small fraction of juveniles were retained was due to that they did not make contact. The contact

probability ( $C(l)$ ) in this case was predicted to remain constant for individuals up to almost 60 cm in length before it dropped abruptly. This trend was similar for the 55 mm grid for cod, however, the  $C(l)$  decreased for smaller individuals compared to the 45 mm grid (for individuals larger than ~55 cm) (Fig. 6-m, 7-m). Fish above 60 cm are too large to pass through the bar spacing used and therefore no size selection was possible. Thus, for these sizes contact was considered by the model to have no relevance. For haddock, the probability  $C(l)$  that the smallest individuals made contact with the 45 mm grid was slightly higher compared to the 55 mm grid (Fig. 6-n, 7-n). This decreased for individuals larger than approximately 27 cm with the 45 mm design



**Fig. 6.** Deconstructed selectivity plots for the 45 mm grid for the *Logistic* (a:c), *CLogistic* (d:f), *DLogistic* (g:i), *TLogistic* (j:l) and *LCLogistic* (m:o) model. The black solid curve is the selectivity curve showing the retention probability with corresponding 95% CIs. The solid red, blue and green curves are the  $C_1$ ,  $1.0-C_1$  and  $1.0-C_1-C_2$  selectivity curves, respectively, with 95% CIs. The horizontal lines with 95% CIs illustrate the length independent contact probabilities for the *Logistic*, *CLogistic*, *DLogistic* and *TLogistic* models. The *Logistic* line crosses the second axis at 1.0 (black dashed line), the *CLogistic* at  $C_1$  (red dashed line), the *DLogistic* at  $C_1$  and  $1.0-C_1$  (blue dashed line), the *TLogistic* at  $C_1$ ,  $C_2$ ,  $1.0-C_1-C_2$  (green dashed line). For the *LCLogistic* model, the red dashed curve with 95% CIs illustrates the length dependent contact probability curve ( $C(l)$ ). A black box surrounds the potential model candidates identified according to the BMS approach.



**Fig. 7.** Deconstructed selectivity plots for the 55 mm grid for the *Logistic* (a:c), *CLogistic* (d:f), *DLogistic* (g:i), *TLogistic* (j:l) and *LLogistic* (m:o) model. The black solid curve is the selectivity curve showing the retention probability with corresponding 95% CIs. The solid red, blue and green curves are the  $C_1$ ,  $1.0-C_1$  and  $1.0-C_1-C_2$  selectivity curves, respectively, with 95% CIs. The horizontal lines with 95% CIs illustrate the length independent contact probabilities for the *Logistic*, *CLogistic*, *DLogistic* and *TLogistic* models. The *Logistic* line crosses the second axis at 1.0 (black dashed line), the *CLogistic* at  $C_1$  (red dashed line), the *DLogistic* at  $C_1$  and  $1.0-C_1$  (blue dashed line), the *TLogistic* at  $C_1$ ,  $C_2$ ,  $1.0-C_1-C_2$  (green dashed line). For the *LLogistic* model, the red dashed curve with 95% CIs illustrates the length dependent contact probability curve ( $C(L)$ ). A black box surrounds the potential model candidates identified according to the BMS approach.



(Fig. 6-n). With the 55 mm grid,  $C(l)$  was constant (approximately 93%) until individuals reached approximately 45 cm in length (Fig. 7-n). For redfish, the  $L$ Logistic model was only a potential candidate model for the 55 mm grid under the BMS approach (Fig. 7-o). Here, the model predicted a decrease in  $C(l)$  for individuals which would have a lower chance for escape based on their morphology (approximately 45 cm in length).

#### 4. Discussion

This study outlined and demonstrated how structural models can be applied to gain deeper understanding of the behavioural processes of fish during grid size selection. Further, it demonstrated how a BMS approach can help quantify how confident one can be in selecting a specific structural model for describing the size selection process and the underlying behavioural processes. More specifically, by comparing the model selection counts, it showed that the inference made regarding fish behaviour during grid selection changed compared to inference based on the OMS approach (Table 2, Fig. 4). Finally, the model selection counts quantified the probability that underlying behaviours assumed in the structural models would describe the data (Fig. 4).

Inference based on indirect fish behaviour analysis with structural models has to varying extents previously been conducted within several size selectivity investigations (e.g. Brčić et al., 2015; Herrmann et al., 2013a,b, 2016, 2019; Jacques et al., 2019; Krag et al., 2017; O'Neill et al., 2006; Santos et al., 2016; Sistiaga et al., 2010; Zuur et al., 2001). During such indirect analysis, it is important to specify whether the analytical goal of fitting a model is to improve understanding of the underlying processes or to provide quantitative predictions regarding the effect of changing the gear design in some way. This is because either of these goals can lead to differences in the type of model picked. Empirical models can provide a quantified effect on selectivity resulting from a particular change in gear design. However, these models are limited by their ability to provide predictions on selectivity beyond the range of data available (Fryer & Shepherd, 1996). Empirical models are also limited to providing estimations of the contribution from individual components in a complex selectivity system (Lövgren et al., 2016). Conversely, structural models are defined by a set of assumptions regarding the physical and biological mechanisms underlying the gear selection process (O'Neill & Herrmann, 2007). Due to this, they are able to provide predictions regarding the impact on the overall selectivity when a particular component of the selection system is changed (Lövgren et al., 2016). These components, described by the model parameters in structural models, can be used to provide improved extrapolations, compared to empirical models (Fryer & Shepherd, 1996).

The study by Zuur et al. (2001) was one of the first to outline how some basic assumption-driven parametric models such as structural models, could improve the model fit of size selectivity data. However, the authors warned against making interpretations from the parameters too literally. Earlier studies have acknowledged the need for gaining deeper understanding of behaviour regarding size selectivity of sorting devices as it can support future gear developments to improve catch efficiency for the industry (Petetta et al., 2021; Sistiaga et al., 2010, 2023b). Fish behaviour can be particularly complex within the dynamic environment of a demersal trawl (He, 2010). As several competing models assuming different behaviours were able to reproduce the same size selectivity curve (Fig. 3), we were limited in being able to discern the underlying behaviour determining the size selection. In such situations we have a case of so-called 'model-dependent realism' (Hawking & Mlodinow, 2010). In the present study, we encourage consideration of the BMS approach, or similar, as part of the investigation in such cases, to protect against inference being made which could not be replicated in a different sample (Lubke & Campbell, 2016). Future analysis of the grid selection process could reduce the uncertainty in the fish behaviour interpretations by implementing direct analysis techniques (for example, using video observation). This would enable specific

probabilities to be assigned to certain behaviours observed by a subset of fish during grid selection. The probabilities attained could be related to the behavioural and morphological structures embedded in the model to make more accurate predictions.

There is diverse literature on behavioural responses to sorting grids (e.g. Grimaldo et al., 2008, 2018; Herrmann et al., 2019; Larsen et al., 2018). Typically, model selection in such studies is carried out by using criteria such as the  $AIC$  value to determine the best-fitting model. The OMS approach has limitations under conditions of low power in the data, or if different samples are taken from the same population, adding to ambiguity in the results (Burnham & Anderson, 2002; Preacher & Merkle, 2012). Further, as the OMS approach leads to a single 'best-fitting' model being selected, it can lead to oversimplification of the understanding of the underlying behaviours taking place (Symonds & Moussalli, 2011). These limitations are addressed in the present study by implementing the BMS approach (Lubke & Campbell, 2016; Lubke et al., 2017). The BMS approach has been well documented in the literature regarding other fields, such as social sciences (Cudeck & Henly, 1991; Linhart & Zucchini, 1986; Lubke & Campbell, 2016; Preacher et al., 2013). However, to our knowledge, this is the first time that this has been implemented in a size selectivity study in fisheries.

The BMS approach discourages choosing a single best-fitting model for making inference as the BMS counts provide a quantifiable way of assessing model selection uncertainty. As often acknowledged in statistical modelling, "all models are wrong, but some are useful" (Box, 1976). Model selection counts are attained by including each of the models within each of the bootstrap repetitions (Cudeck & Henly, 1991; Linhart & Zucchini, 1986; Lubke & Campbell, 2016). These enable the replicability of the chosen model to be quantified when fitted to a different sample taken from the same population (Lubke & Campbell, 2016). As a result, the BMS approach shifts the perspective of the analysis from focusing on a single model towards measuring the degree by which one model can compete with another. This aspect is important when it comes to making behavioural inference based on parameter estimates from structural models due to that another model may have been chosen under a different sample of data. Comparing the model selection counts using the BMS bar plots (Fig. 4) enabled easy inference on the probability that either of the models had to be chosen from another sample as well as the power to discriminate between competing models (Lubke et al., 2017). Therefore, we encourage future selectivity analyses to adopt this form of model selection procedure with the accompanying model selection counts. Accounting for model selection uncertainty was expected to create significantly wider CIs compared to the CIs from the OMS approach. However, this was not consistently found and could be associated to that several of the models included in this study produced a similar selection curve in many of the bootstrap iterations. Thereby we could speculate that it would not make any major effect on the CIs whether the bootstraps were based on fixed or varying models.

Multi-model inference as well as other methods considering applications of fit indices such as the  $AIC$  weights have been applied previously to find a 'best-fitting model and/or models' (Burnham & Anderson, 2002; Herrmann et al., 2016, 2017). While multi-model inference can account for uncertainty due to uncertainty in model selection, we cannot be sure that the same model(s) would be chosen if we were using a different sample taken from the same population (Lubke & Campbell, 2016; Lubke et al., 2017). This was highlighted in the present study as accounting for stochasticity in the sample data consistently led to a different model being selected compared to the OMS approach. Further, the BMS approach consistently identified several potential candidate models for describing grid selection, therefore there was never enough evidence to clearly discriminate for one behavioural explanator. Instead, multiple, equally valid candidate models were found.

Fish interactions with sorting grids may be length-dependent as larger fish have stronger swimming capabilities compared to smaller



fish. This was supported by the present study as length-dependent contact was an important determinant of passage through the grids for both haddock and cod according to the BMS approach (Fig. 4). Herrmann et al. (2019) found clear behavioural differences among different lengths of haddock interacting with square mesh panels and grids. Specifically, smaller haddock were more active and made contact with the grid more frequently compared to larger individuals. Larger fish have a better chance of being able to manoeuvre themselves to avoid the grid, while small fish are more subjected to water turbulence and may not be able to manoeuvre themselves effectively to escape (Jacques et al., 2019). The individual model parameters extracted from the *LCLogistic* model (Figs. 6 and 7) suggested that above the length classes with full retention, we cannot determine with high precision whether individuals were retained due that they did not contact the grid or that they contacted the grid but could not pass through (Figs. 6 and 7). This is a confounding factor as we are unable to say with certainty what causes the high retention probability for individuals that would not be physically able to pass through the grid bars. An explanation for this tendency could be that larger individuals had a degree of self-perception for their body shape and size, which could have influenced their willingness to attempt escape.

Without accounting for uncertainty due to model selection, the most favoured model to describe haddock and cod selectivity would have been the models assuming multiple modes of contact (*DLogistic*, *TLogistic*) (Table 2). When the BMS approach was applied, the model of length-dependent contact (*LCLogistic*) was selected most frequently for both species, except for haddock with the 45 mm grid. This highlights the problem of model selection when differences in model fit among different samples from the population are not accounted for, as in the OMS approach. To our knowledge, it has not been previously shown that cod selectivity could be best described by assuming length-dependent contact. When making inference based on this, it would be reasonable to consider that the sorting process for these species involved a combination of both length-dependent and contact orientation processes. This was supported by the results of this study (Table 2; Figs. 3, 4, 6 and 7). A wider length range measured for redfish may have helped to determine with more certainty whether length-dependent contact played a more determinant role in the probability that they are retained using this design (Fig. 4).

It should be noted that the uncertainty of model selection is expected to be higher when models are similar in structure (Preacher & Merkle, 2012). This can describe why two and three modes of contact were often significant descriptors simultaneously among the species studied here

(Fig. 4). Despite this, a single explanation could not be given due to that multiple potential explanations exist.

We included the simplistic *Logistic* and the *CLogistic* models which have been commonly used previously (Brinkhof et al., 2020; Grimaldo & Larsen, 2005; Kvamme & Isaksen, 2004; Larsen et al., 2016; O'Neill et al., 2006; Sistiaga et al., 2008; Wileman et al., 1996; Zuur et al., 2001). According to the BMS approach, these models were rejected as potential candidate models more often compared to when the OMS approach was used (Table 2, Fig. 4). From a perspective of making inference about behaviour, it is as our results have demonstrated, not realistic to expect that all fish interact with the grid during capture (*Logistic*) and that they all do so in the same way if they make contact (*CLogistic*). This conclusion can also find support by observations taken from video recordings of fish contacting sorting grids investigated in this study (Fig. 8). Fig. 8 provides examples of individuals following the lower netting without making contact or contacting the grid in a way that does not allow a length-dependent chance for escaping through. Further, these observations provide support for modelling the fish interaction with the grid as described by the models *DLogistic* and *TLogistic* as fish are seen contacting the grid with different orientations (contact modes) (Fig. 8).

The *CLogistic* model was a potential candidate model for describing selectivity only in the case of redfish with the 45 mm grid. However, this dataset was the weakest dataset in the study (Table 1). Thus, it is likely that *AIC* penalised the complex models more heavily and favoured one with significantly fewer parameters. With weak data there is a higher chance of oversimplifying a process due to the model selection approach not finding sufficient support in the data to attribute it to a more complex model. Herrmann et al. (2019) showed how conclusions of the true underlying process can depend on the quality of the data used. Specifically, when haddock <20 cm were included, contact likelihood was found to be length-dependent, which differed compared to results when individuals <20 cm were excluded (Herrmann et al., 2019). Including model selection uncertainties in the case of weak data can support researchers in handling such cases.

The grid selection process has been investigated many times in past years, however, targeted fish retention as well as bycatch reduction are not yet optimized (Brinkhof et al., 2020; Grimaldo et al., 2007; Herrmann, Sistiaga, Larsen, & Nielsen, 2013, 2019; Sistiaga et al., 2009, 2016, 2018). Why can we not achieve a sharp selection curve when we have a well-defined escape geometry for this device? The results from this study outline that this may be explained by the behavioural processes taking place during size selection and that they are more complex

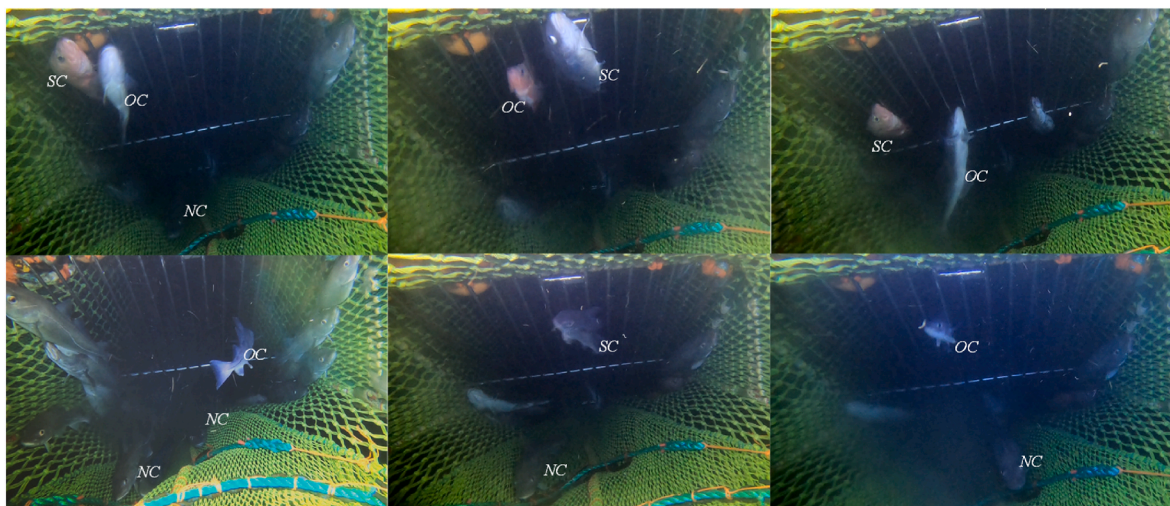


Fig. 8. Photos from video recordings of the sorting grid during trawling showing cod, haddock and redfish not contacting the grid (NC) as well as fish contacting the grid optimally (OC) and sub-optimally (SC).

than assumed in previous studies. The variation among the modelled mean curves captured the range of potential grid interactions that could occur during grid passage (Fig. 3). Ideally, the selectivity curve produced by a sorting grid should have a steep slope to reflect a smaller proportion of targeted catch loss with minimal juvenile fish retention. As expected, reducing the grid bar spacing in the current study led to a reduction in  $L50$  for all species. In particular, the narrower bar spacing could lead to a greater complexity of the behaviour needed to enable fish to escape (Table 2; Fig. 4). However, to achieve a smaller  $SR$ , more detailed examination of fish behaviour in relation to technical changes made to this device is needed. The deconstructed selectivity plots allowed us to deepen our understanding of how fish behaviour and morphology were depicted in the structural model parameters (Figs. 6 and 7). This provided a helpful visual representation for the model composition and how individual model elements accompanied by their uncertainty combine to provide more detail of the selectivity. More precise understanding also of how different species interact with the grid can explain the different patterns in the size selectivity curves obtained in this study.

This study has presented different models intended to capture the processes determining size selectivity of fish sorting grids. Even the most complex of our models (*DLogistic*, *TLogistic*, *LCLogistic*) are based on modelling a relatively low number of processes. These could be considered as idealizations which try to grasp the main processes involved in the more complex reality of grid selection (Stevens, 2013). Therefore, one could ask the question whether applying an even more complex model than equations (3)–(5) would be able to deepen our understanding on the processes determining size selection of fish sorting grids. This is supported by that both the OMS and BMS procedure tended to favour our more complex models compared to the simpler, except for the more data weak case of redfish. However, considering the success of our existing models in being able to accurately reproduce the output of the grid size selection in all cases we examined, we would conclude that our models are sufficiently complex and flexible enough to grasp the main processes involved. In addition, it should also be considered that we already face a situation where models based on assuming quite different internal processes, i.e., different modes of contact versus length-dependent contact, are able to reproduce a comparably accurate output. Therefore, instead of directing future research towards even more complex models, there seems to be a need to use external knowledge about some of the processes. In this way, we could potentially better discriminate between models and thereby solve the issue of model-dependent realism. This external knowledge could include details regarding the size limits of fish that in reality could morphologically pass through a certain grid bar spacing. Thereby the maximum values the parameters  $L50_1$ ,  $L50_2$  and  $L50_3$  could adopt in the *DLogistic* and *TLogistic* models could be constrained. For example, such information could be obtained by applying FISHSELECT methodology (Herrmann et al., 2009) or variants of it to fish sorting grids for the species investigated in this study. This could adapt the approach used by Frandsen et al. (2010) which studied different modes of contact with codend meshes to gain deeper understanding of size selectivity of *Nephrops* (*Nephrops norvegicus*) in trawls.

#### CRedit authorship contribution statement

**Nadine Jacques:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Bent Herrmann:** Writing – review & editing, Writing – original draft, Validation, Supervision, Software, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Jesse Brinkhof:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Investigation, Funding acquisition, Data curation, Conceptualization. **Manu Sistiaga:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Data

curation, Conceptualization.

#### 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.2024.03.003>.

#### References

- Akaike, H. (1974). A new look at the statistical model identification. *IEEE Transactions on Automatic Control*, 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.
- Box, G. E. P. (1976). Science and statistics. *Journal of the American Statistical Association*, 71(356), 791–799.
- Brčić, J., Herrmann, B., De Carlo, F., & Sala, A. (2015). Selective characteristics of a shark-excluding grid device in a Mediterranean trawl. *Fisheries Research*, 172, 352–360.
- Brinkhof, J., Larsen, R. B., Herrmann, B., & Sistiaga, M. (2020). Size selectivity and catch efficiency of bottom trawl with a double sorting grid and diamond mesh codend in the North-east Atlantic gadoid fishery. *Fisheries Research*, 231, Article 105647. Article.
- Burnham, K. P., & Anderson, D. R. (2002). *Model selection and Multimodel inference: A practical information-Theoretic approach* (2nd ed.). New York: Springer.
- Chernick, M. R. (2007). What is bootstrapping?. In *Bootstrap methods: A guide for practitioners and researchers* (2nd ed., pp. 1–25). New York: John Wiley & Sons, Inc.
- Cudeck, R., & Henly, S. J. (1991). Model selection in covariance structures analysis and the “problem” of sample size: A clarification. *Psychological Bulletin*, 109(3), 512–519.
- Efron, B. (1982). The Jackknife, the bootstrap and other resampling Plans. In *SIAM Monograph No. 38*. Philadelphia: Society for Industrial and Applied Mathematics.
- Efron, B. (2014). Estimation and accuracy after model selection. *Journal of the American Statistical Association*, 109(507), 991–1007.
- Engås, A., Jørgensen, T., & West, C. W. (1998). A species-selective trawl for demersal gadoid fisheries. *ICES Journal of Marine Science*, 55(5), 835–845.
- Fonteyne, R., Buglione, G., Leonori, I., & O’Neill, F. G. (2007). Review of mesh measurement methodologies. *Fisheries Research*, 85(3), 279–284.
- Frandsen, R. P., Herrmann, B., & Madsen, N. (2010). A simulation-based attempt to quantify the morphological component of size selection of *Nephrops norvegicus* in trawl codends. *Fisheries Research*, 101(3), 156–167.
- Fryer, R. J. (1991). A model of between-haul variation in selectivity. *ICES Journal of Marine Science*, 48(3), 281–290.
- Fryer, R. J., & Shepherd, J. G. (1996). Models of codend size selection. *Journal of Northwest Atlantic Fishery Science*, 19, 51–58.
- Grimaldo, E., & Larsen, R. B. (2005). The cosmos grid: A new design for reducing by-catch in the Nordic shrimp fishery. *Fisheries Research*, 76(2), 187–197.
- Grimaldo, E., Larsen, R. B., & Holst, R. (2007). Exit windows as an alternative selective system for the Barents Sea demersal fishery for cod and haddock. *Fisheries Research*, 85(3), 295–305.
- Grimaldo, E., Sistiaga, M., Herrmann, B., & Larsen, R. B. (2016). Trawl selectivity in the Barents Sea demersal fishery. In H. Mikkola (Ed.), *Fisheries and Aquaculture in the modern world* (pp. 69–94). London: IntechOpen.
- Grimaldo, E., Sistiaga, M., Herrmann, B., Larsen, R. B., Brinkhof, J., & Tatone, I. (2018). Improving release efficiency of cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) in the Barents Sea demersal trawl fishery by stimulating escape behaviour. *Canadian Journal of Fisheries and Aquatic Sciences*, 75(3), 402–416.
- Grimaldo, E., Sistiaga, M., & Larsen, R. B. (2008). Evaluation of codends with sorting grids, exit windows, and diamond meshes: Size selection and fish behaviour. *Fisheries Research*, 91(2), 271–280.

- Hannah, R. W., Jones, S. A., & Matteson, K. M. (2003). *Observations of fish and shrimp behavior in ocean shrimp (Pandalus jordani) trawls*. Oregon Department of Fish and Wildlife, Marine Resources Program.
- Hawking, S., & Mlodinow, L. (2010). *The grand design*. London: Bantam Press.
- He, P. (2010). *Behavior of marine fishes: Capture processes and conservation challenges* (1st ed.). Ames, USA: Wiley-Blackwell.
- Herrmann, B., Krag, L. A., Feekings, J., & Noack, T. (2016). Understanding and predicting size selection in diamond-mesh cod ends for Danish seining: A study based on sea trials and computer simulations. *Marine and Coastal Fisheries*, 8(1), 277–291.
- 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(1), 59–71.
- Herrmann, B., Sistiaga, M., Grimaldo, E., Larsen, R. B., Olsen, L., Brinkhof, J., & Tatone, I. (2019). Size selectivity and length-dependent escape behaviour of haddock in a sorting device combining a grid and a square mesh panel. *Canadian Journal of Fisheries and Aquatic Sciences*, 76(8), 1350–1361.
- Herrmann, B., Sistiaga, M., Larsen, R. B., & Nielsen, K. N. (2013a). Size selectivity of redfish (*Sebastes* spp.) in the Northeast Atlantic using grid-based selection systems for trawls. *Aquatic Living Resources*, 26(2), 109–120.
- Herrmann, B., Sistiaga, M., Larsen, R. B., Nielsen, K. N., & Grimaldo, E. (2013b). Understanding sorting grid and codend size selectivity of Greenland halibut (*Reinhardtius hippoglossoides*). *Fisheries Research*, 146, 59–73.
- Herrmann, B., Sistiaga, M., Nielsen, K. N., & Larsen, R. B. (2012). Understanding the size selectivity of redfish (*Sebastes* spp.) in North Atlantic trawl codends. *Journal of Northwest Atlantic Fishery Science*, 44, 1–13.
- Herrmann, B., Sistiaga, M., Rindahl, L., & Tatone, I. (2017). Estimation of the effect of gear design changes on catch efficiency: Methodology and a case study for a Spanish longline fishery targeting hake (*Merluccius merluccius*). *Fisheries Research*, 185, 153–160.
- Herrmann, B., Wienbeck, H., Karlsen, J. D., Stepputtis, D., Dahm, E., & Moderhak, W. (2015). Understanding the release efficiency of Atlantic cod (*Gadus morhua*) from trawls with a square mesh panel: Effects of panel area, panel position, and stimulation of escape response. *ICES Journal of Marine Science*, 72(2), 686–696.
- Jacques, N., Herrmann, B., Larsen, R. B., Sistiaga, M., Brčić, J., Gökçe, G., & Brinkhof, J. (2019). Can a large-mesh sieve panel replace or supplement the Nordmore grid for bycatch mitigation in the northeast Atlantic deep-water shrimp fishery? *Fisheries Research*, 219, Article 105324. Article.
- 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., Feekings, J., Lund, H. S., & Karlsen, J. D. (2017). Improving escape panel selectivity in *Nephrops*-directed fisheries by actively stimulating fish behavior. *Canadian Journal of Fisheries and Aquatic Sciences*, 74(4), 486–493.
- Krag, L. A., Herrmann, B., & Karlsen, J. D. (2014). Inferring fish escape behaviour in trawls based on catch comparison data: Model development and evaluation based on data from Skagerrak, Denmark. *PLoS One*, 9(2), Article e88819.
- Krag, L. A., Madsen, N., & Karlsen, J. D. (2009). A study of fish behaviour in the extension of a demersal trawl using a multi-compartment separator frame and SIT camera system. *Fisheries Research*, 98(1), 62–66.
- Kvamme, C., & Isaksen, B. (2004). Total selectivity of a commercial cod trawl with and without a grid mounted: Grid and codend selectivity of north-east Arctic cod. *Fisheries Research*, 68(1), 305–318.
- Larsen, R. B., Herrmann, B., Brčić, J., Sistiaga, M., Cerbule, K., Nielsen, K. N., & Jacques, N. (2021). Can vertical separation of species in trawls be utilized to reduce bycatch in shrimp fisheries? *PLoS One*, 16(3), Article e0249172.
- Larsen, R. B., Herrmann, B., Brinkhof, J., Grimaldo, E., Sistiaga, M., & Tatone, I. (2018). Catch efficiency of groundgears in a bottom trawl fishery: A case study of the Barents Sea haddock. *Marine and Coastal Fisheries*, 10(5), 493–507.
- Larsen, R. B., Herrmann, B., Sistiaga, M., Grimaldo, E., Tatone, I., & Onandia, I. (2016). Size selection of redfish (*Sebastes* spp.) in a double grid system: Estimating escapement through individual grids and comparison to former grid trials. *Fisheries Research*, 183, 385–395.
- Larsen, R. B., & Isaksen, B. (1993). Size selectivity of rigid sorting grids in bottom trawls for Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*). *ICES Marine Science Symposia*, 196, 178–182.
- Linhart, H., & Zucchini, W. (1986). *Model selection*. New York: John Wiley & Sons.
- Lövgren, J., Herrmann, B., & Feekings, J. (2016). Bell-shaped size selection in a bottom trawl: A case study for *Nephrops* directed fishery with reduced catches of cod. *Fisheries Research*, 184, 26–35.
- Lubke, G. H., & Campbell, I. (2016). Inference based on the best-fitting model can contribute to the replication crisis: Assessing model selection uncertainty using a bootstrap approach. *Structural Equation Modeling*, 23(4), 479–490.
- Lubke, G. H., Campbell, I., McArthur, D., Miller, P., Luningham, J., & van den Berg, S. M. (2017). Assessing model selection uncertainty using a bootstrap approach: An update. *Structural Equation Modeling*, 24(2), 230–245.
- Melli, V., Herrmann, B., Frandsen, R. P., Malta, T. V., & Feekings, J. P. (2023). Escape panels in trawls: Does placement matter when every individual contacting the panel can escape? *Canadian Journal of Fisheries and Aquatic Sciences*, 80(5), 866–891.
- Melli, V., Krag, L. A., Herrmann, B., & Karlsen, J. D. (2018). Investigating fish behavioural responses to LED lights in trawls and potential applications for bycatch reduction in the *Nephrops*-directed fishery. *ICES Journal of Marine Science*, 75(5), 1682–1692.
- Millar, R. (1993). Incorporation of between-haul variation using bootstrapping and nonparametric estimation of selection curves. *Fishery Bulletin*, 91(3), 564–572.
- Norwegian Directorate of Fisheries. (2022). *Forskrift om gjennomføring av fiske, fangst og høsting av viltlevende marine ressurser (Høstingsforskriften)* [In Norwegian]. Retrieved from <https://lovdata.no/dokument/LTI/forskrift/2021-12-23-3910>.
- O'Neill, F. G., & Herrmann, B. (2007). PREMEMO—a predictive model of codend selectivity—a tool for fishery managers. *ICES Journal of Marine Science*, 64(8), 1558–1568.
- O'Neill, F. G., Kynoch, R. J., & Fryer, R. J. (2006). Square mesh panels in North Sea demersal trawls: Separate estimates of panel and cod-end selectivity. *Fisheries Research*, 78(2), 333–341.
- Petetta, A., Herrmann, B., Virgil, M., Bargione, G., Vasapollo, C., & Lucchetti, A. (2021). Dredge selectivity in a Mediterranean striped venus clam (*Chamelea gallina*) fishery. *Fisheries Research*, 238, Article 105895. Article.
- Preacher, K., & Merkle, E. (2012). The problem of model selection uncertainty in structural equation modeling. *Psychological Methods*, 17(1), 1–14.
- Preacher, K. J., Zhang, G., Kim, C., & Mels, G. (2013). Choosing the optimal number of factors in exploratory factor analysis: A model selection perspective. *Multivariate Behavioural Research*, 48(1), 28–56.
- Richards, A., & Hendrickson, L. (2006). Effectiveness of the Nordmore grate in the Gulf of Maine Northern shrimp fishery. *Fisheries Research*, 81(1), 100–106.
- 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., Brinkhof, J., Herrmann, B., Grimaldo, E., Langård, L., & Lilleng, D. (2016). Size selective performance of two flexible sorting grid designs in the Northeast Arctic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) fishery. *Fisheries Research*, 183, 340–351.
- Sistiaga, M., Grimaldo, E., & Larsen, R. B. (2008). Size selectivity patterns in the Northeast Arctic cod and haddock fishery with sorting grids of 55, 60, 70 and 80 mm. *Fisheries Research*, 93(1), 195–203.
- Sistiaga, M., Herrmann, B., Brinkhof, J., & Larsen, R. B. (2023). Effect of grid section design on trawl size selectivity. *Regional Studies in Marine Science*, 63, Article 103023. Article.
- Sistiaga, M., Herrmann, B., Brinkhof, J., Larsen, R. B., Santos, J., Stepputtis, D., Brinkhof, I., Jacques, N., Cerbule, K., Petetta, A., Cuende, E., & Kvalvik, L. (2023b). Is there a limit to the potential effects of shortening lastridge ropes on the size selectivity of diamond mesh codends? *Fisheries Research*, 262, Article 106671. Article.
- Sistiaga, M., Herrmann, B., Grimaldo, E., & Larsen, R. B. (2010). Assessment of dual selection in grid based selectivity systems. *Fisheries Research*, 105(3), 187–199.
- Sistiaga, M., Herrmann, B., Grimaldo, E., Larsen, R. B., Olsen, L., Brinkhof, J., & Tatone, I. (2018). Combination of a sorting grid and a square mesh panel to optimize size selection in the North-East Arctic cod (*Gadus morhua*) and redfish (*Sebastes* spp.) trawl fisheries. *ICES Journal of Marine Science*, 75(3), 1105–1116.
- Sistiaga, M., Herrmann, B., & Larsen, R. B. (2009). Investigation of the paired-gear method in selectivity studies. *Fisheries Research*, 97(3), 196–205.
- Sistiaga, M., Herrmann, B., Nielsen, K., & Larsen, R. B. (2011). Understanding limits to cod and haddock separation using size selectivity in a multispecies trawl fishery: An application of FISHSELECT. *Canadian Journal of Fisheries and Aquatic Sciences*, 68(5), 927–940.
- Stevens, M. (2013). No understanding without explanation. *Studies In History and Philosophy of Science Part A*, 44(3), 510–515.
- Symonds, M. R. E., & Moussalli, A. (2011). A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behavioral Ecology and Sociobiology*, 65(1), 13–21.
- Wagenmakers, E. J., & Farrell, S. (2004). AIC model selection using Akaike weights. *Psychonomic bulletin & review*, 11(1), 192–196.
- Wardle, C. S. (1993). Fish behaviour and fishing gear. In *The behaviour of teleost fishes* (pp. 463–495). Boston, MA: Springer US.
- Wileman, D. A., Ferro, R. S. T., Fonteyne, R., & Millar, R. B. (1996). Manual of methods of measuring the selectivity of towed fishing gears. In *ICES Cooperative research Reports (CRR)*.
- Zeller, D., Cashion, T., Palomares, M., & Pauly, D. (2018). Global marine fisheries discards: A synthesis of reconstructed data. *Fish and Fisheries*, 19(1), 30–39.
- Zuur, G., Fryer, R. J., Ferro, R. S. T., & Tokai, T. (2001). Modelling the size selectivities of a trawl codend and an associated square mesh panel. *ICES Journal of Marine Science*, 58, 657–671.