Selectivity and escapement behaviour of five commercial fishery species in standard square- and diamond-mesh codends

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The Danish fishery for *Nephrops* (*Nephrops norvegicus*) is often conducted in a mixed-species setting, characterized by high rates of discards of several target species, including *Nephrops* and cod (*Gadus morhua*). Experiments were conducted to investigate and compare the selective properties of a standard 70 mm square-mesh codend (standard SMC) and a standard 90 mm diamond-mesh codend (standard DMC). Selectivity estimates for five commercial species are provided for both codends. The standard SMC yielded higher estimates of length at 50% retention/mesh size (hereafter SF) for *Nephrops* and roundfish than did the standard DMC, but no effect of codend type on SF was found for plaice (*Pleuronectes platessa*). Moreover, a novel codend cover design allowed assessment of the preferred direction of escapement in the codend. Whiting (*Merlangius merlangus*) and *Nephrops* showed pronounced, but opposite, vertical preference in the direction of escapement, with whiting escaping upwards and *Nephrops* downwards. A significant ($p < 0.05$) difference in the direction of escapement between the two codends was found for haddock (*Melanogrammus aeglefinus*) and whiting. Owing to the relatively small catches, the outcome is probably most applicable to *Nephrops*-directed fisheries under similar conditions, and caution should be taken not to extrapolate the results to other fisheries.

Keywords: cover, escapement behaviour, *Gadus morhua*, Kattegat, mixed-species fishery, *Nephrops norvegicus*, *Pleuronectes platessa*, selectivity, Skagerrak, square-mesh codend, trawl.

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Introduction

Discarding of commercial species takes place at high rates in Danish mixed-species fisheries in the Kattegat and Skagerrak (Krag *et al.*, 2008). Among other species, *Nephrops* (*Nephrops norvegicus*), cod (*Gadus morhua*), and plaice (*Pleuronectes platessa*) are targeted. Discarding of cod gives cause for particular concern, because the International Council for the Exploration of the Seas (ICES) states that the stock is at a historically low level in the Kattegat and overfished in the Skagerrak (ICES, 2009). In recent experiments with commercial trawls, >50% by number of *Nephrops* caught were below the minimum landing size (MLS; 40 mm carapace length, CL; Krag *et al.*, 2008; Frandsen *et al.*, 2009). Investigations have shown that survival of discarded *Nephrops* ranges from 12 to 85% (Evans *et al.*, 1994; Castro *et al.*, 2003; Harris and Ulmestrand, 2004), while survival of the *Nephrops* that escape from the trawl during the fishing process is ~82% (Wileman *et al.*, 1999). Hence, the overall survival of undersized *Nephrops* could be improved significantly by making the fishing gear more size-selective.

Theoretically and experimentally, both mesh size and mesh shape affects the L_{50} (L_x is the length at which x% is retained) and the SR (selection range = $L_{75} - L_{25}$) of *Nephrops* significantly (ICES, 2007; Frandsen *et al.*, 2010). Compared with diamond-mesh codends, square-mesh codends with the same nominal mesh size are more size-selective, i.e. have a higher L_{50} and a lower SR (ICES, 2007; Frandsen *et al.*, 2010). Square-mesh codends also have good selective properties for roundfish such as cod (Halliday *et al.*, 1999), haddock (Robertson and Stewart, 1988; Halliday *et al.*, 1999), and whiting (Robertson and Stewart, 1988). For some species of flatfish, however, square-mesh codends yield lower values of L_{50} than the equivalent diamond-mesh codends (Walsh *et al.*, 1992; He, 2007). Therefore, the selective properties of square- and diamond-mesh codends differ for different morphological groups, such as for flatfish, roundfish, and *Nephrops*. The optimum mesh shape is theoretically related to the cross-sectional shape of the species (Herrmann *et al.*, 2009).

With knowledge of species-specific behaviour and the different selective properties, selectivity can be optimized by combining different netting materials in the same codend. Many earlier studies on species-specific behaviour focused on species separation at the mouth of the trawl (Main and Sangster, 1982). Once the fish have entered a trawl, they usually stay clear of the netting panels unless the straight path is blocked (Glass *et al.*, 1993; Glass and Wardle, 1995), so they travel towards the codend, where most escape attempts are made just in front of the catch build-up (O'Neill *et al.*, 2003; Jones *et al.*, 2008). Previous investigations of species-specific behaviour in the aft end of a trawl and in the codend have shown that *Nephrops* tend to remain low in the net (Briggs, 1992; Krag *et al.*, 2009a). Plaice also seem to stay low in the aft end of the trawl, but cod have a more uniform vertical distribution (Krag *et al.*, 2009a), and haddock and whiting stay high (Krag *et al.*, 2009a). Cod, haddock, and whiting have been reported to escape through square-mesh windows in the extension and upper panel of the codend (cod:

Madsen *et al.*, 2010; haddock: Frandsen *et al.*, 2009; whiting: Briggs, 1992). We here document the vertical direction of escapement through the codend for five different species, so providing additional information on the selection process.

A 90 mm diamond-mesh codend with a 120 mm square-mesh window is included in the legislation for the Kattegat and the Skagerrak, and is commonly used. For most commercial species, however, the SR of this codend is high (e.g. cod 10.93 cm, haddock 18.56 cm; Frandsen *et al.*, 2009), so the risk of discarding and the loss of legal-sized fish is high. In addition, a 70 mm square-mesh codend is allowed, but only in combination with a rigid sorting grid (35 mm bar spacing). Selectivity experiments with square-mesh codends have been conducted in other *Nephrops* fisheries, using relatively small meshes (40–55 mm; Stergiou *et al.*, 1997; Bahamon *et al.*, 2006; Sala and Lucchetti, 2010), but only one experiment testing a square-mesh codend (60 mm) in the Skagerrak and Kattegat has been reported (Larsvik and Ulmestrand, 1992). The existing selectivity estimates for *Nephrops* in a 70 mm square-mesh codend are therefore based on extrapolations and assumptions.

To assess the selective properties of each type of netting, the codends we tested had no additional selective devices. Two codends, a commercial 70 mm (3 mm single twine) square-mesh codend (standard SMC) and a commercially used 90 mm (5 mm double twine) diamond-mesh codend (standard DMC), were investigated in terms of their selectivity for *Nephrops*, cod, haddock, plaice, and whiting. Also, the species-specific differences in the direction of escapement through the codend meshes were investigated with the aim of obtaining knowledge of the potential for species separation in the codend. Further, our experimental setup allowed between-trial variations in the estimated selection parameters to be assessed, because two trials using different vessels, trawls, and towing time were conducted.

Experimental methods

The selectivity of the codends was estimated using the covered codend method (Wileman *et al.*, 1996). Two codends were tested: a standard DMC with a nominal mesh size of 90 mm and a standard SMC with a nominal mesh size of 70 mm. Further information on the netting material is given in Figure 1. The standard DMC had 92 meshes around and the standard SMC had 90 bars around. On the basis of estimates of mesh openings in the standard DMC ranging from 0° to 35° and lengths of the tensionless bars in the standard SMC ranging from 47 to 94% of the stretched bar length (Frandsen *et al.*, 2010), the circumference of the two codends is estimated to be about the same. The netting material of both was the same as the netting used in commercial fisheries in the area.

Nephrops fishing is generally conducted on soft sediments, where the action of the trawl gear tends to cause resuspension of sediment. Hence, visibility is poor and divergence between visual observations and actual catch may arise under these conditions (Krag *et al.*, 2009b). Alternatives to visual observations for quantifying the reaction of fish to different netting panels are therefore needed. For this purpose, we developed a codend cover that was divided horizontally, providing an upper and a lower compartment (Figure 2). The horizontal partitioning panel in the cover constrained escapees to either the upper or the lower compartment, depending on the panel of the codend through which they escaped. The design, therefore, allowed estimation of the fractions of each species that escaped upwards or downwards through the codend. This novel cover design was developed and tested in full scale in the Hirtshals flume tank before the sea trials. Covers were made of polyethylene netting with a measured mesh size of 36.4 mm. A combination of kites, weights, and floats, as prescribed by Madsen *et al.* (2001), was used to maintain the geometry of the covers during fishing (Figure 2). The drag of this type of cover is expected to be relatively low (Madsen *et al.*, 2001). In both codends, the horizontal partitioning panel in the cover was attached to the seam of the codend, and the netting of the panel was orientated to form diamond-meshes. This design should minimize the influence of the cover on the mesh openings of the codend and leave the partitioning panel slack enough to allow movements of the codend. Inspection of the standard DMC with cover in the flume tank demonstrated that these requirements were met. Furthermore, the codend was clearly capable of assuming the bulbous shape characteristic for a diamond-mesh codend at catches as small as 150 kg. The bulbous shape causes the rows of meshes just in front of the catch build-up to be more open. To be able to conclude that fish and *Nephrops* that ended up in either the upper or the lower cover compartment had escaped through the corresponding panel of the codend, it is essential that no exchange between the two compartments is possible. The horizontal partitioning panel was made of the same small-mesh netting as the covers, and from the codline, the cover was divided into two separate compartments (upper and lower; Figure 2). As fish escape mainly through the open meshes just in front of the catch build-up, the distance they travel before they end up in the separate compartments is short. A potential exchange between the covers of the smallest fish is therefore restricted almost totally.

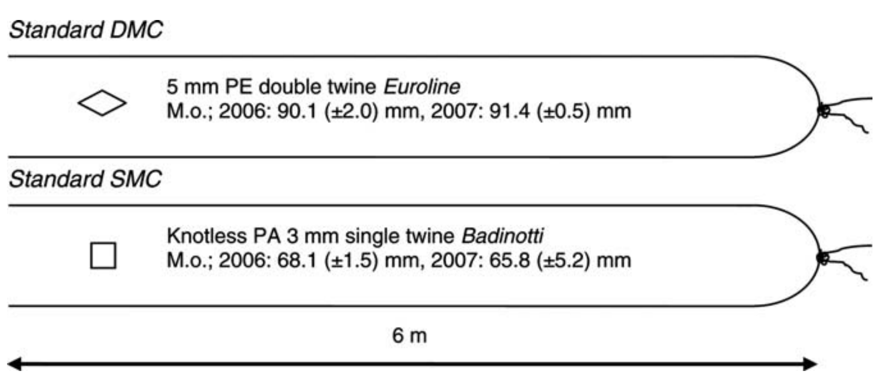

Figure 1. Experimental codends. M.o., mean mesh sizes measured by the ICES 4 kg wedge (95% confidence limits are in parenthesis); PE, polyethylene; PA, polyamide. Before and after the trials, 50 codend meshes were measured in a dry and a wet condition, respectively.

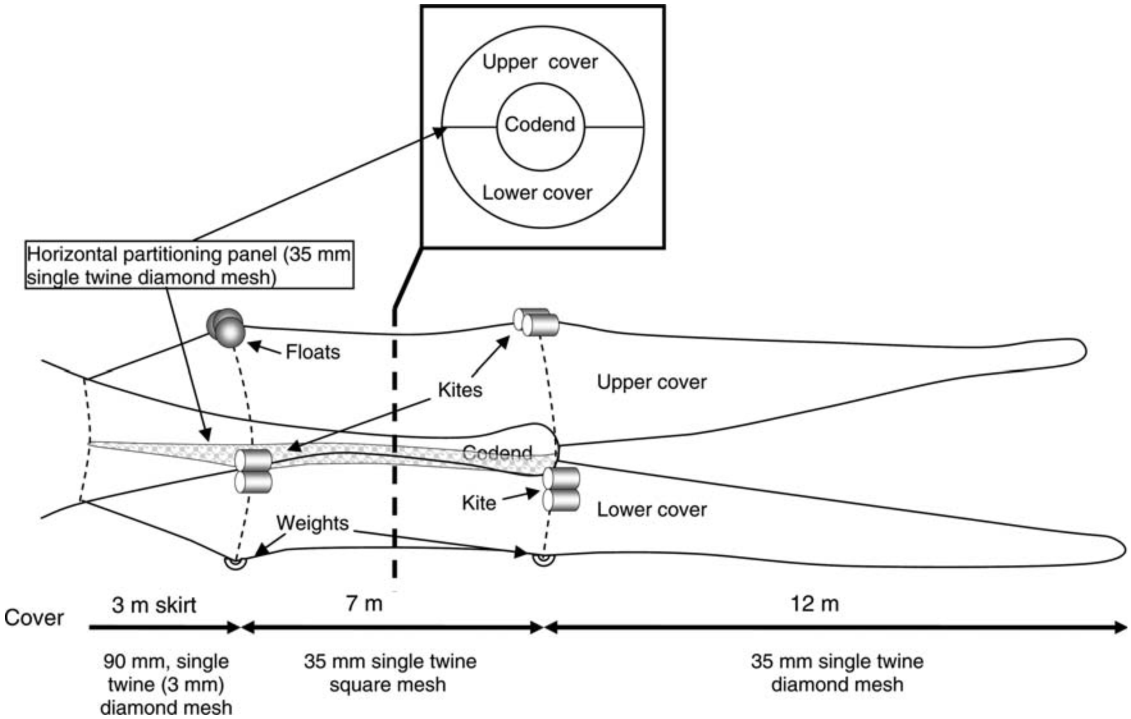

Figure 2. Cover design in cross section (upper drawing), and as seen from the side (lower drawing). The point at which the cross section is taken is indicated on the side view by a broken line.

Sea trials

Two cruises were conducted on-board commercial vessels in the Kattegat and the Skagerrak in 2006 and 2007 (Figure 3). In September 2006, the 294 kW stern trawler FN234 "Canopus" was used. It was rigged for twin-trawling with two identical trawls, which were combined fish and *Nephrops* trawls with a nominal mesh size of 80 mm and a circumference of 480 meshes. Design of the vessel limited the size of the cover catch that could be processed, so in 2007 a new vessel that allowed larger catches to be processed, and hence longer hauls, was chartered. In August 2007, the 386 kW stern trawler RS30 "Mette Amalie" was used. Like the "Canopus", it was rigged for twin-trawling with combined fish and *Nephrops* trawls with a nominal mesh size of 100 mm and circumference of 460 meshes. Choice of fishing ground was based on skipper knowledge of catch distribution of the primary target species of the study; *Nephrops*, cod, and plaice. The two cruises therefore differed in vessel, trawl, and catch size, so the results can indicate the sensitivity of the selectivity of the codends to such differences. In both years, the two test codends with covers fished simultaneously in the twin-trawl rig, and to avoid bias attributable to differences in performance between starboard and port trawls, the codends were interchanged throughout the cruises. In all, 24 daylight hauls with each codend design were made (Table 1).

Measuring the catch

To minimize selection at the surface, the covers and codends of both trawls were hauled onto the deck before processing the catch. In 2006, cod, plaice, haddock, and whiting were measured to the centimetre below, and the CL of *Nephrops* to the millimetre below with electronic calipers. We used the midpoints of the length classes in the analyses. In 2007, the number of days at sea was limited, so to optimize the number of hauls, only cod, plaice, and *Nephrops* were measured individually because these three species are the most important in this fishery. *Nephrops* and whiting catches were subsampled when large. Weight of the measured fish and *Nephrops* was estimated using month-specific length–weight conversion factors for fish (Coull *et al*., 1989) and gender-specific conversion factors for *Nephrops* (ICES, 1995). Total catch weight was taken as the sum of the weight of the measured fish and the weight of the rest of the catch, including debris.

Data analysis

Data from the two cruises were analysed separately. For estimating the selection parameters, data from the upper and the lower covers were summed for each haul of each codend. Estimates were based on unraised data, i.e. including both the raw data and the subsampling ratio. In cases of subsampling of the cover catch, a joint subsampling ratio was estimated for each length group according to the following equation: joint subsampling ratio = *count*/*raised*, where *count* is the total number of sampled animals in the upper and lower cover and the term *raised* refers to the estimated number of animals in the two cover compartments obtained by dividing the *count* in each compartment by the corresponding subsampling ratio, then adding the two estimates.

Initially, CC2000 software (www.constat.dk) was used to analyse the data on haul level. A goodness-of-fit test, referring the deviance to a χ^2 distribution (Wileman *et al*., 1996), showed that a logistic curve described the data well and that a lack of fit was indicated for one haul only (Table 2). Reasonable numbers

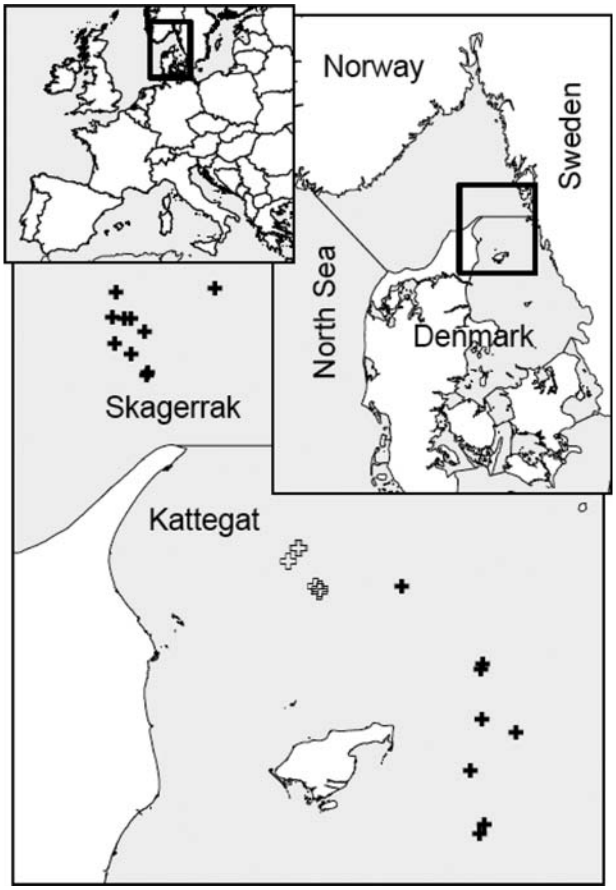

Figure 3. Distribution of hauls in 2006 (black crosses) and 2007 (white crosses). The overview map shows the location of the Danish fishing area.

of all species were caught in most hauls, with plaice in 10 hauls of the 2006 sea trials as the only exception (Table 2). The size distributions of haddock and whiting fitted their selective range in the standard DMC, but not in the standard SMC, and vice versa for *Nephrops*. The few individuals in the selective range resulted in a lack of convergence when analysing data on a haul level (Table 2). Subsequent combination of selection curves using Fryer's model (Fryer, 1991) would therefore not include all available data, so to optimize the use of our data, we used a generalized non-linear mixed model (GNLMM). The method is described by Millar *et al*. (2004), and the complete model includes the between-haul variations of both L_{50} and SR as random variables, and gear type as the dependent variable. In cases where the complete model did not converge, parameters on haul level were inspected to evaluate whether the smallest between-haul variation was on L_{50} or SR. Excluding the between-haul variation on this parameter would always make the model converge. Non-significant effects of gear type on either L_{50} or SR were excluded from the model, and the analysis was run again. The model was fitted with the NLMIXED procedure available in the statistical software package SAS, as prescribed by Millar *et al*. (2004). When comparing L_{50} or SR between the two codends, we used the significance estimates provided by the model. Overlap of the 95% confidence limits of the parameters was used to compare the selectivity of the codends between the two years.

The data were first raised by use of the subsampling ratio, then the direction of escapement was estimated for each haul as the number of escapees retained in the upper compartment divided by the total number of escapees. In cases in which the directions of escapement were normally distributed, the significance of the differences between the two gears was tested with a paired *t*-test. When the test for normality failed, data were instead tested using a Wilcoxon signed rank test. The correlation between direction of escapement and fish length was also tested; data for single length groups were treated as above, but length groups that contained fewer than five animals within a haul were excluded from that haul. Linear regressions based on the least-squares method were used to determine whether the slopes of the regression lines deviated significantly from zero.

Results

In 2006, 18 hauls were conducted, and in 2007 there were 6 hauls (Table 1). In 2006, the duration of haul was limited to about 1.5 h to preclude large catches in the covers. The design of the vessel used in 2007 allowed larger catches to be handled, and the duration of haul was extended to ~3.5 h, which increased the mean catches in the test codends from 184 to 284 kg and from 126 to 309 kg for the standard DMC and the standard SMC, respectively (Table 1). The composition of the catch differed between years (Table 2). By weight, the mean catches of *Nephrops* ranged from 18.5 to 21.5 kg per haul, with no difference between years, whereas catches of cod were ~85% lower in 2007 than in 2006 and catches of plaice were three times higher in 2007. Subsampling ratios of *Nephrops* and whiting ranged from 0.11 to 0.75.

Selection parameters

For the roundfish cod, haddock, and whiting, the NLMIXED model yielded significantly ($p < 0.001$) higher estimates of L_{50} for the standard SMC than for the standard DMC, differences ranging from 9 to 15 cm (Table 3). In 2006, the modelled SR estimates were significantly ($p < 0.05$) higher in the standard SMC for cod and haddock. For whiting in 2006 and cod in 2007, no significant ($p > 0.05$) difference between the estimated SR values for the two gear types was found, so the gear effect on SR was excluded from the NLMIXED model in these cases.

The NLMIXED model yielded significantly ($p < 0.001$) lower estimates of L_{50} for plaice for the standard SMC than for the standard DMC, differences ranging from 4 to 6 cm (Table 3). The reduction in L_{50} corresponds to the difference in mesh size between the codends, so the resulting selection factors (SF = L_{50}/mesh size) are similar (Table 3). A significant ($p < 0.05$) difference in SR estimates between codends was found only in 2007; the estimate of the standard DMC was 1.3 cm greater than that of the standard SMC.

Nephrops were collected both in 2006 and 2007, and estimates are given in Table 3. For both years, the NLMIXED model yielded significantly ($p < 0.0001$) higher estimates of L_{50} for the standard SMC than for the standard DMC. The SR estimates were significantly ($p < 0.01$) higher for the standard SMC in 2007, but there was no significant difference in 2006.

Cod, *Nephrops*, and plaice were measured in both years, and a small increase in the estimated L_{50} was detected for all three species in the standard DMC in 2007 compared with 2006. However, the increase in L_{50} was not significant ($p > 0.05$), nor were the differences in SR between years (Figure 4). For the standard SMC, the

Table 1. Operational conditions for all hauls in 2006 and 2007 together with mean and standard deviation.

Haul id	Vessel	Date	Latitude	Longitude	Duration (h)	Wave height (m)	Speed (knots)	Wire length (m)	Depth (m)	Door distance (m)	Total catch in test codend (kg)	
											Standard DMC	Standard SMC
1_2006	FN234	9/21/2006	57.5323	11.2361	1:00	0.75	2.6	125	43	85	110	121
2_2006	FN234	9/21/2006	57.4110	11.4523	1:00	0.75	2.6	150	60	85	101	94
3_2006	FN234	9/22/2006	57.4041	11.4464	1:30	0.5	2.5	150	62	85	174	159
4_2006	FN234	9/22/2006	57.3065	11.5369	1:30	0.75	2.6	150	63	86	85	57
5_2006	FN234	9/23/2006	57.3291	11.4442	1:30	1.25	2.6	150	66	85	151	120
6_2006	FN234	9/23/2006	57.2533	11.4085	1:30	1.25	2.6	150	67	85	233	124
7_2006	FN234	9/24/2006	57.1571	11.4269	1:30	0.5	2.6	150	64	85	298	313
8_2006	FN234	9/24/2006	57.1722	11.4413	1:00	0.5	2.6	150	73	86	541	315
9_2006	FN234	9/25/2006	57.9056	10.4538	1:00	0.5	2.6	200	106	86	122	62
10_2006	FN234	9/25/2006	57.8888	10.4997	1:30	0.5	2.6	200	110	86	152	59
11_2006	FN234	9/26/2006	57.9445	10.4492	1:30	0.5	2.6	200	103	85	198	70
12_2006	FN234	9/26/2006	57.9413	10.4999	3:00	0.5	2.6	200	114	85	216	137
13_2006	FN234	9/27/2006	57.9227	10.5380	1:30	0.5	2.6	200	120	86	102	59
14_2006	FN234	9/27/2006	57.9826	10.4606	1:30	0.7	2.6	200	109	86	166	100
15_2006	FN234	9/28/2006	57.9831	10.7382	1:30	0.7	2.6	300	184	86	120	160
16_2006	FN234	9/28/2006	57.9412	10.4822	1:30	0.6	2.6	200	110	87	176	84
17_2006	FN234	9/28/2006	57.8612	10.5442	1:30	0.5	2.6	200	106	87	190	124
18_2006	FN234	9/29/2006	57.8570	10.5409	1:30	0.5	2.6	200	109	87	167	106
				Mean	1:28	0.7	2.6	181.9	92.9	85.8	183.5	125.8
				s.d.	0:26	0.24	0.02	40.04	33.49	0.73	104.09	75.85
1_2007	RS30	8/22/2007	57.5360	10.9973	3:01	1.5	2.5	235	36	100	330	380
2_2007	RS30	8/22/2007	57.5738	10.9231	3:06	1.5	2.6	235	30	101	320	285
3_2007	RS30	8/23/2007	57.5299	11.0084	3:13	0.5	2.6	235	36	100	355	335
4_2007	RS30	8/23/2007	57.5923	10.9539	4:00	0.4	2.6	235	32	98	217	254
5_2007	RS30	8/24/2007	57.5269	11.0066	3:20	0.4	2.6	235	35	98	300	420
6_2007	RS30	8/24/2007	57.5935	10.9502	4:02	0.6	2.6	235	32	100	180	180
				Mean	3:27	0.8	2.6	235.4	33.5	99.5	283.7	309.0
				s.d.	0:27	0.55	0.04	0.00	2.43	1.22	69.30	87.50

only significant ($p < 0.05$) difference in selection parameter estimates between the two years was the L_{50} for *Nephrops*, which was higher in 2006 (Figure 4).

Vertical direction of escapement

Only *Nephrops* and whiting showed a pronounced preference in the direction of escapement in both gears and in all hauls based on all length groups combined (Figure 5). Therefore, depending on codend design, 85.0–93.7% of the *Nephrops* escaped downwards through the lower panel of the codend, whereas 66.8–90.9% of the whiting escaped upwards through the upper panel. For some species, the type of codend had a significant effect on escapement behaviour. Both haddock and whiting showed a significantly ($p < 0.05$) different preference in the direction of escapement in the two codend types. For both species, more fish escaped upwards in the standard SMC (Figure 5).

Plots of the direction of escapement vs. length revealed significant correlations for several species (Figure 6). Although significantly different from zero, the slope of the regression line was negligible (<0.01) usually. However, cod in both codends and haddock, plaice, and whiting in the standard DMC showed a pronounced negative relationship between the length and the direction of escapement. A pronounced positive relationship was found only for haddock and plaice in the standard SMC.

Discussion

Our novel cover design worked well and allowed estimation of both selection parameters and evaluation of the vertical direction of escapement. The relationship between length and preference of direction of escapement was consistent for the entire size range, demonstrating that any migration of small individuals between the two compartments of the cover was minimal. The results demonstrate that the selective properties of a standard SMC and a standard DMC differ significantly, and that the optimum mesh shape is species-specific. The selectivity of the two codends was consistent between trials, with *Nephrops* in the standard SMC being the only exception. Selectivity of *Nephrops* may be affected by the catch composition which, in 2006, was dominated by *Nephrops* and roundfish and, in 2007, by *Nephrops* and flatfish.

The relatively small vessel (characteristic for the fishery) and hence the difficulty in handling the covers restricted the catch weight that could be handled in the experiment. A rough estimate of commercial catch sizes, including discards, can be made from the Danish discard database by extracting data on standard 90 mm codends for the past 5 years. For vessels below medium size (<400 hp), catch weights ranged from 158 to 1400 kg for the Kattegat ($n = 27$, 24 of which were within the range of catches of the standard DMC, 85–541 kg), and from 92 to 1481 kg for the Skagerrak ($n = 50$, 20 of which were within the range of our experiments). The total catch rates obtained in the present study are therefore within the norm for the fishery, and also within the range of results previously reported as being similar to normal

Table 2. The number of each species caught in the codend/cover (upper+lower). Lack of convergence of the haul-based model is shown by an asterisk (*). A lack of fit ($p<0.05$) is shown by a double asterisk (**) if the goodness of fit, referring the deviance to a Chi-squared distribution, indicates it.

	Standard DMC					Standard SMC				
Haul	Cod	Haddock	*Nephrops*	Plaice	Whiting	Cod	Haddock	*Nephrops*	Plaice	Whiting
2006										
1	16/177	387/734	25/5	103/14	172/681	8/258	0/1246*	13/18	115/1	1/907*
2	43/159	143/243	244/10	130/47	187/433	14/391	0/399*	120/119	181/1	0/601*
3	73/289	80/393	1 477/98	151/74	225/394	38/268	3/631	758/927	195/13	0/635*
4	27/82	49/51	1 000/122	15/5	147/270	3/86*	2/112*	365/1 127	10/0*	0/443*
5	70/142	76/162	1 035/178	94/12	238/286	30/238	2/481	458/1 210	89/4	7/895
6	66/358	16/47	302/32	65/4	266/943	56/339	6/65	153/190	60/1	5/1 153
7	98/505	8/9	706/62	103/4	181/1 270	58/517	7/25	443/494	123/1	5/1 646
8	62/169	15/23	94/18	78/6	114/820	54/132	12/50	66/111	104/1	9/1 311
9	137/136	40/61	1 566/68	0/0*	153/14	23/201	4/99*	364/1 273	1/0*	2/150*
10	122/145	37/49	2 317/171	1/0*	108/24	25/172	2/76*	427/2 022	0/0*	2/129*
11	86/100	12/17	5 621/848	0/0*	60/11	29/226	1/36	897/5 075	0/0*	4/99
12	114/165	20/57	2 890/528	0/0*	131/22	45/217	5/53*	811/3 162	0/0*	6/111
13	87/74	23/32	615/80	1/0*	85/17	32/161	3/35	189/495**	0/0*	1/74
14	85/106	44/87	3 317/294	0/0*	104/29	33/186	0/87*	1 142/2 952	0/0*	4/121
15	34/0*	0/0*	28/0*	1/0*	6/1*	32/6	0/4*	14/32	0/0*	0/3*
16	91/95	15/27	4 504/420	1/0*	93/17	26/194	0/46*	1 353/4 004	0/0*	3/128
17	172/235	101/186	1 322/151	1/0*	213/28	47/380	29/283	302/1 012	0/0*	5/203
18	143/139	82/107	207/18	1/0*	349/39	63/210	14/214*	44/158	0/0*	8/515
Total	1 526/3 076	1 148/2 285	27 270/3 103	745/166	2 832/5 299	616/4 182	90/3 942	7 919/24 382	878/22	62/9 124
2007										
1	18/3	Na	2 158/106	90/104	Na	10/30	Na	1 673/1 164	170/9	Na
2	34/2	Na	42/3	147/172	Na	33/29	Na	13/38	268/58	Na
3	37/6	Na	2 519/30	208/107	Na	7/56	Na	1 651/642	181/17	Na
4	9/9	Na	148/4*	100/294	Na	11/62	Na	70/58	321/47	Na
5	18/13	Na	2 570/160	134/209	Na	4/28	Na	2 348/1 182	250/24	Na
6	17/17	Na	56/6	90/269	Na	3/17*	Na	56/42	209/19	Na
Total	133/50	Na	7 493/309	769/1 155	Na	68/222	Na	5 811/3 126	1 399/174	Na

Table 3. Parameter values estimated using the NLMIXED model.

		Standard DMC				Standard SMC			
Species	Year	L_{50} (cm)[a]	SR (cm)[a]	SF	L_{50}/SR	L_{50} (cm)[a]	SR (cm)[a]	SF	L_{50}/SR
Cod	2006[b]	15.03 (14.34 – 15.72)	3.28 (2.59 – 3.98)	1.60	4.58	26.92 (26.24 – 27.60)	4.40 (3.63 – 5.17)	3.80	6.12
	2007[c]	16.86 (14.03 – 19.68)	6.28 (3.63 – 8.93)	1.77	2.68	26.33 (23.77 – 28.90)	6.28 (3.63 – 8.93)	3.85	4.19
Haddock	2006[d]	15.17 (14.66 – 15.68)	3.25 (2.94 – 3.56)	1.62	4.67	26.30 (25.15 – 27.44)	4.07 (3.48 – 4.67)	3.72	6.46
Nephrops	2006[c]	16.71 (14.66 – 18.76)	14.71 (13.27 – 16.15)	0.18	1.14	41.18 (39.17 – 43.20)	14.71 (13.27 – 16.15)	0.58	2.80
	2007[d]	18.35 (12.44 – 24.25)	11.73 (9.21 – 14.23)	0.19	1.56	31.00 (26.31 – 35.69)	17.90 (14.89 – 20.91)	0.45	1.73
Plaice	2006[e]	19.07 (18.30 – 19.84)	3.45 (2.90 – 4.00)	2.03	5.53	14.61 (13.34 – 15.88)	3.45 (2.90 – 4.00)	2.06	4.23
	2007[b]	19.76 (18.93 – 20.59)	3.60 (2.85 – 4.35)	2.08	5.49	13.89 (12.98 – 14.79)	2.34 (1.58 – 3.11)	2.03	5.94
Whiting	2006[e]	18.10 (17.28 – 18.92)	3.61 (3.43 – 3.79)	1.93	5.01	33.47 (32.47 – 34.46)	3.61 (3.43 – 3.79)	4.73	9.27

SF = L_{50}/(measured mesh size × 1.04), where 1.04 is the approximated conversion factor between the ICES gauge and the EU wedge (Ferro and Xu, 1996). Data in parenthesis are the 95% confidence limits.
[a]Estimates for *Nephrops* are in mm.
[b]Complete model including gear effect and between-haul variation on both SR and L_{50}.
[c]Model including gear effect on L_{50}. and between-haul variation on both SR and L_{50}.
[d]Model including gear effect on SR and L_{50} but between-haul variation only on L_{50}.
[e]Model including gear effect and between-haul variation on L_{50} only.

practice in the Swedish *Nephrops* fishery (Valentinsson and Ulmestrand, 2008). Our results are therefore considered to be representative of smaller vessels in *Nephrops*-directed fisheries. However, this restriction in representativeness may change soon with the implementation of highly selective devices, such as grids (Catchpole *et al.*, 2006; Valentinsson and Ulmestrand, 2008; Frandsen *et al.*, 2009) and escape windows (Madsen *et al.*, 2010). These additional devices are expected to reduce the codend catch weight substantially, and they have already been enforced seasonally in part of the Kattegat, to protect the cod stock.

Selection parameters

Selection factors (SF = L_{50}/mesh size) can be used to compare our results with the results of previous experiments on *Nephrops*-directed fisheries. As twine thickness influences the selectivity of a codend (Lowry, 1995; Herrmann and O'Neill,

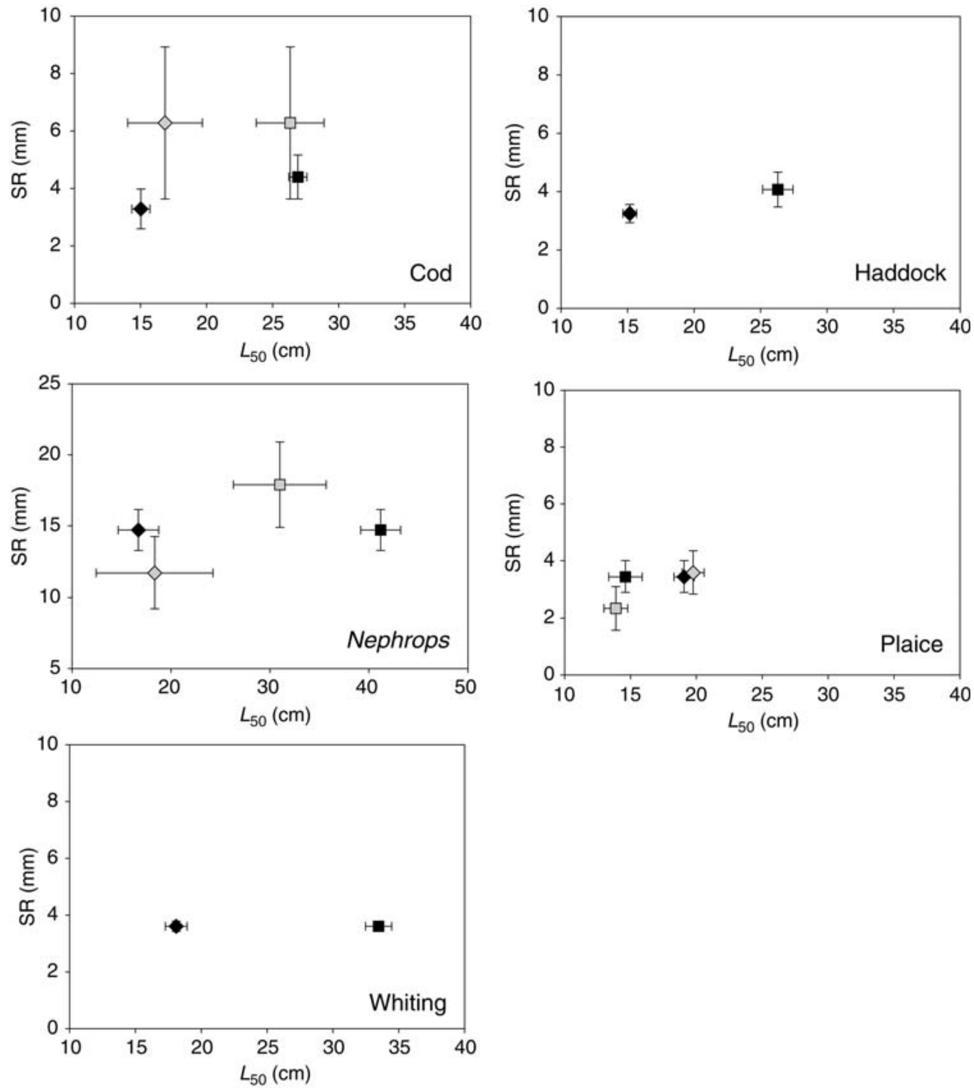

Figure 4. Parameter estimates for different species obtained using the NLMIXED model. Black symbol, 2006 data; grey symbol, 2007 data; squares, standard SMC; diamonds, standard DMC. Error bars indicate the 95% confidence limits around the mean.

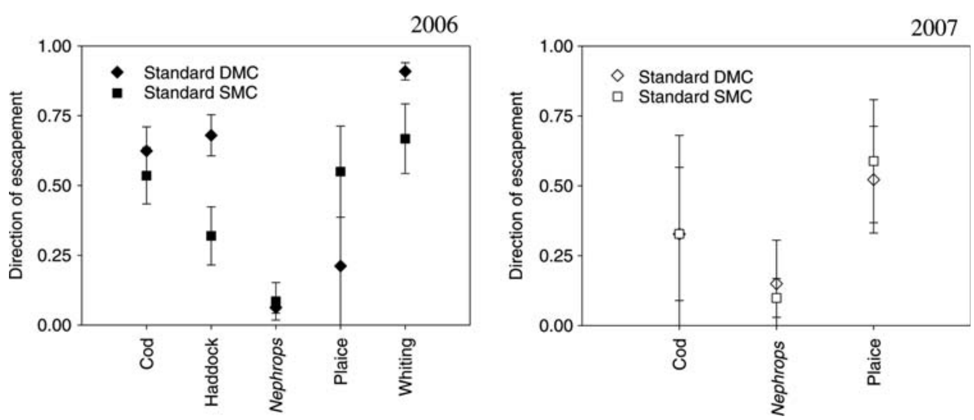

Figure 5. Vertical direction of escapement in 2006 and 2007. Estimates are based on raised data summed over all length groups. For each haul, the direction of escapement was estimated as the fraction of escapees retained in the upper cover. The symbols illustrate the means of all hauls, and the error bars show the 95% confidence limits.

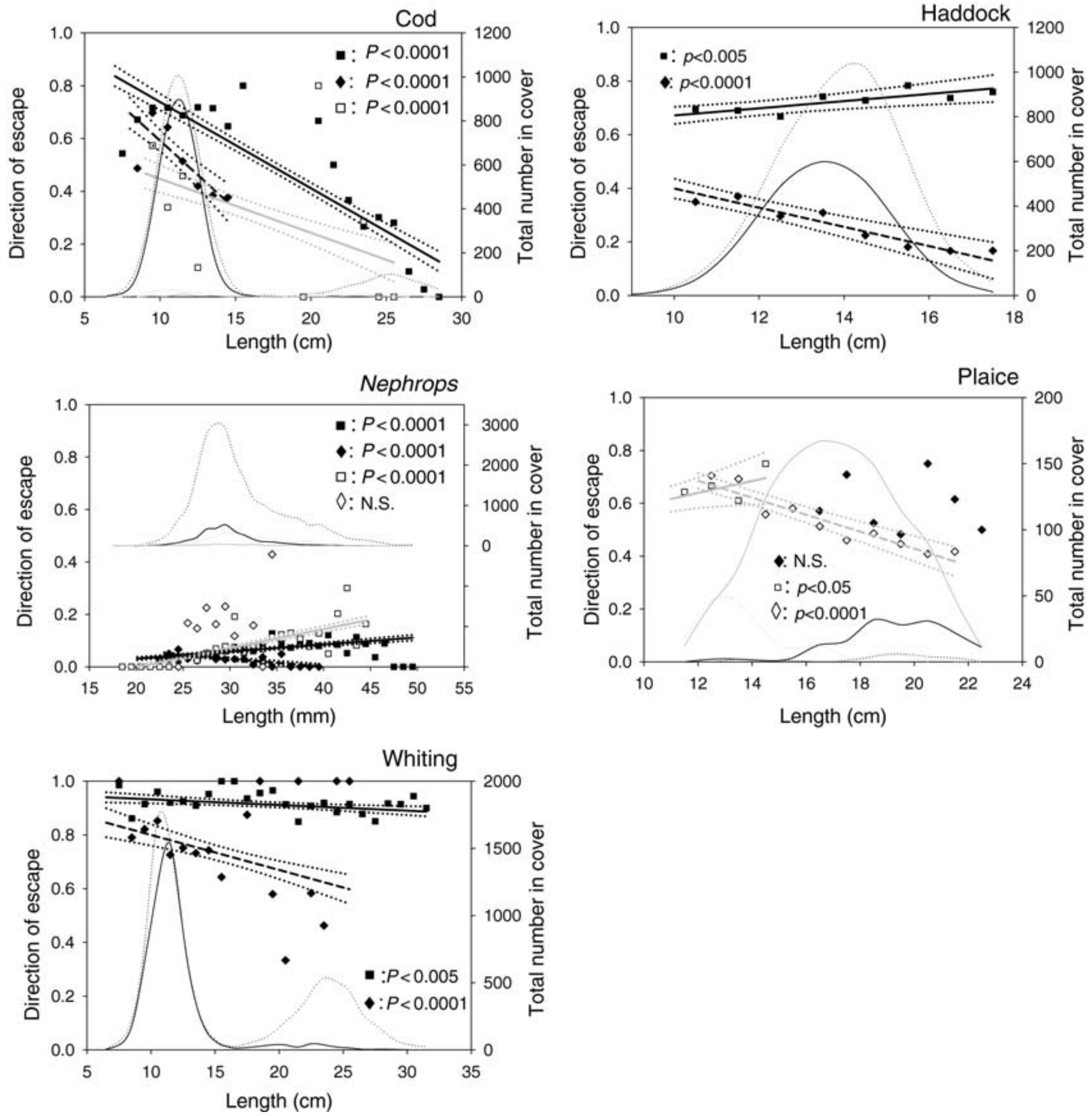

Figure 6. Relationship between the vertical direction of escapement and length (left *y*-axis) and length distribution of fish retained in the cover (right *y*-axis). For each length group, the direction of escapement was estimated as the fraction of escapees retained in the upper cover (squares and diamonds), and the regression lines based on the data at a haul level were estimated (bold lines), with standard SMC, squares and solid lines; standard DMC, diamonds and broken lines; dotted lines, the 95% confidence band of the regression; 2006, black symbols and black lines; 2007, white symbols and grey lines. Statistics on the slope of the regression are given. N.S., no significant deviation from zero. Numbers retained in the cover are shown as thin lines, with standard SMC, dotted lines; standard DMC, solid lines; 2006, black lines; 2007, grey lines.

2006), only experiments testing codends made of netting reasonably similar to that tested here were used when evaluating the estimated selection parameters.

The SF values for cod, haddock, *Nephrops*, plaice, and whiting in the standard DMC were all low compared with the SF estimates reported previously (cod, 2.4; haddock, 2.4–2.6; *Nephrops*, 0.28–0.38; plaice, 2.3; whiting, 2.7; Madsen *et al*., 2008; Frandsen *et al*., 2009). Small catches limit the opening of diamond-meshes and result in lower estimates of L_{50} (O'Neill and Kynoch, 1996; Herrmann, 2005), and this effect may be increased by the thick double twine used in this experiment. Although catches increased by >50% in 2007, they were still at the lower end of catches evaluated by the studies referred to above. The mean catch weights of those studies ranged from 300 to 393 kg. Based on simulations, it is predicted that an increase in catch weight from ~170 to ~290 kg in a diamond-mesh codend (100 mm, 100 meshes around) will lead to an increase in the L_{50} of haddock by 4–5 cm, whereas a catch increase from 170 to ~500 kg may increase the L_{50} of haddock by as much as 10 cm (Herrmann, 2005). The increase in catches in the standard DMC from 2006 to 2007 did not result, however, in a significant ($p > 0.05$) increase in the L_{50} of any of the three species that we measured in both years.

For the standard SMC, comparable selection estimates are available for *Nephrops* only. The SF estimate for *Nephrops* in the standard SMC was within the range of the earlier studies (*Nephrops*, 0.40–0.63; Larsvik and Ulmestrand, 1992; Stergiou *et al*., 1997; Campos *et al*., 2002; Bahamon *et al*., 2006; Sala *et al*., 2008; Sala and Lucchetti, 2010).

In general, the standard SMC yielded higher estimates of L_{50}/SR for all roundfish species and *Nephrops* than did the standard

DMC. For these species, therefore, an increase in L_{50} is not associated with a proportional increase in SR, and the standard SMC hence has better selective properties for roundfish and *Nephrops*. In contrast, plaice gave the highest estimates of L_{50} in the standard DMC; SF values of the two codends were, however, comparable. The standard DMC was expected to have better selective properties for plaice, but the relatively soft and thin netting (3 mm polyamide vs. 2 × 5 mm polyethylene) of the standard SMC, in combination with the relatively small catches, may explain why the difference between the two codends was not pronounced in the present experiment.

Vertical direction of escapement

In line with the results of previous investigations (Hillis and Earley, 1982), *Nephrops* escaped almost exclusively through the lower panel of the codend. Interestingly, the only fish species that exhibited a distinct preference in the direction of escapement was whiting, which primarily escaped upwards. Haddock, which has previously been shown to stay high in the extension piece (Krag *et al*., 2009a), and escape through square-mesh windows in the top panel of the codend (Madsen *et al*., 1999; Graham *et al*., 2003, Frandsen *et al*., 2009), only showed this preference in direction of escapement in the standard SMC; haddock caught in the standard DMC tended to escape downwards.

The swimming speed of fish is size-dependent (Breen *et al*., 2004), so because the fish escaping from the codend are small, their ability to navigate within the trawl cavity could be expected to be limited. However, the maximum sustainable swimming speed of a haddock 16 cm long is 0.8 knots (Breen *et al*., 2004), and at a towing speed of 2.9 knots, water flow in a partially fish-filled codend has been found to range from 0 to 0.6 knots (Main and Sangster, 1981). On the basis of this knowledge, we assume that a pronounced direction of escapement, at least for the larger escapees, reflects a species-specific preference.

The differences between the observed preferences in terms of direction of escape in this and in previous work are not necessarily contradictory, because the present setup did not include an alternative escape route, as do experiments with square-mesh panels. It is likely that introducing such a selective device in the standard DMC would alter the preferred direction of escape of species such as haddock, for which behaviour has previously been shown to be influenced by visual cues (Glass and Wardle, 1989).

The natural behaviour of most fish is to stay clear of netting, and this natural avoidance response can be modified by manipulating the visual stimulus presented by the netting panel (Glass *et al*., 1993). The contrast of the netting used for the two codends is expected to be different, because the standard DMC is constructed of dark (green) heavy (2 × 5 mm) twine, whereas the standard SMC is made of white thinner (1 × 3 mm) twine. All fishing was conducted during daylight, so we assume that the standard SMC presented a lower contrast in the light from the surface and may therefore appear a more attractive escape route. Rather than the difference in mesh shape, these factors may explain the different behaviour of some of the species in the standard SMC and the standard DMC.

Length-dependent differences in vertical preference of fish in trawls have been observed for several species, including haddock, cod, whiting, and plaice (Holst and Revill, 2009; Holst *et al*., 2009). In our study, cod in particular exhibited a pronounced length-dependence, with small fish escaping upwards and larger fish escaping downwards. This is in contrast to the behavioural pattern found farther forward in the trawl (Holst and Revill, 2009; Holst *et al*., 2009). However, those studies investigated larger fish, so the slope of the regression lines is not comparable with those found here.

Conclusions

The results of our study have confirmed the belief that the selectivity of the conventionally used standard DMC is poor, and they further suggest that this is particularly so in the cases of small catches and relatively thick double twine. Owing to the relatively small catches, the outcome of this study is most applicable to *Nephrops*-directed fisheries under similar conditions. In future, such conditions are probably to result from implementation of highly selective devices that are expected to reduce the codend catch weight substantially.

The selective properties of the 70 mm standard SMC are significantly better for *Nephrops* and roundfish than those of the 90 mm standard DMC. The use of a standard SMC is therefore expected to reduce discards of these species significantly. However, the estimated selection parameters for *Nephrops* in the standard SMC demonstrate that using a mesh size of 70 mm would result in loss of legal-sized (>40 mm CL) catch. In terms of plaice, the selectivity of the 70 mm standard SMC is more in conflict with the regulations on MLS (27 cm) than the selectivity of the 90 mm standard DMC. The use of a standard SMC would therefore be expected to increase the discarding of that species.

The positive effect of combining mesh shapes has previously been attained by inserting square-mesh windows in diamond-mesh codends, but the aim of those gears was primarily to reduce the discarding of roundfish. The results of the present study demonstrate the potential benefits of combining different nettings in the codend to improve the selectivity of a wider range of species in mixed-species fisheries.

Our study has shown that only whiting and *Nephrops* have a strong preference to escape either from the upper or the lower panel. For those species, an additional escape panel with an optimized netting configuration would theoretically influence the selectivity only if it is placed in their preferred direction of escapement. For all other species, we would expect such a panel potentially to improve the selectivity of the codend, irrespective of its vertical position. However, the behavioural patterns in the codend may be altered by the visual cues introduced when different nettings are combined. Further studies of such composite codends, designed to optimize multispecies selectivity by exploiting differences in behaviour and morphology, are therefore needed. Such studies should also take the length-dependent differences in behaviour into account.

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