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Published in:
Canadian Journal of Fisheries and Aquatic Sciences

Link to article, DOI:
10.1139/cjfas-2016-0391

Publication date:
2017

Document Version
Peer reviewed version

A meta-analysis of vertical stratification in demersal trawl gears

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Abstract

A meta-analysis is presented of fishing trials that use trawl gear with horizontal separator panels to direct fish into an upper or lower codend. The analysis is applied to eight North Atlantic species: the gadoids cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), saithe (*Pollachius virens*) and whiting (*Merlangius merlangus*), the flatfish lemon sole (*Microstomus kitt*) and plaice (*Pleuronectes platessa*), and monkfish (*Lophius piscatorius*) and Nephrops (*Nephops norvegicus*).

The proportion of fish that rise above the separator panel decreases as the height of the leading edge of the panel increases, for six of the eight species. Only monkfish and Nephrops have no significant dependency on panel height. Cod is the only species for which separation depends on the horizontal distance of the leading edge of the panel from the ground gear, with the proportion of cod going above the panel increasing the further the panel is from the ground gear. The time of day only affects the separation of plaice, with a greater proportion going above the panel at night than during the day.

keywords: horizontal separator panels; vertical stratification; demersal trawls; species selectivity; fish behaviour

Introduction

Differences in the behavioural reaction of fish to trawl fishing gears, from when they first become aware of its approach and their interaction with the doors, sweeps and trawl mouth, to their possible entry into the net and passage to the codend, plays a key role in the selective performance of many trawl designs (Wardle 1993; Ryer 2008; Winger et al. 2010). Trawls have been developed with raised doors and sweeps to reduce the herding of some species into the path of the trawl mouth (Rose et al. 2010; He et al. 2015), and with raised fishing lines and low or cut-back headlines to exploit differences in how fish behave as they enter the gear (Chosid et al. 2011; Krag et al. 2015; Bayse et al. 2016). Fishing gears have been fitted with large mesh panels in the forward or centre sections of the trawl (Thomsen 1993; Madsen et al. 2006; Beutel et al. 2008; Holst and Revill 2009; Campbell et al. 2010; Kynoch et al. 2011) and with selective devices such as square mesh panels and rigid, flexible and netting grids (Isaksen et al. 1992; Catchpole and Revill 2008; Valentinsson and Ulmestrand 2008; Drewery et al. 2010) in the extension and/or the codend to encourage escape as fish pass through a gear. There has also been research into how mesh penetration and selectivity are influenced by netting material properties, such as twine colour and contrast, twine thickness and mesh size and mesh shape and by codend attachments and lifting bags (Glass et al. 1993; Tokaç et al. 2004; Kynoch et al. 2004; Sala et al. 2007; Herrmann et al. 2013; O'Neill et al. 2016).

Many of the insights into how fish behave during the capture process, and which have been used to develop these types of selective gears, have come from visual observations by divers (Main and Sangster 1981), underwater cameras footage (Reid at al. 2007; Jones et al. 2008; Bryan et al. 2014), laboratory experiments (Glass et al. 1995; Winger et al. 2004; Breen et al; 2004) and from experimental fishing trials at sea (Main and Sangster 1985; Engås et al. 1998; Ingolfsson and Jørgensen 2006; Ryer et al. 2010).

Here, we consider experimental fishing trials that have used trawl gears with horizontal separator panels to assess and quantify the behavioural reaction of fish as they pass through a gear. Horizontal separator panels are fitted across the width of a trawl and direct fish that go above the panel to an upper codend and those that go below to a lower one (Figure 1). The first report of this type of trial was by Dickson (1960), who fished two trawls, one above the other, to investigate the influence of increasing headline height. To our knowledge, the first trials using a horizontal panel are those of Symonds and Simpson (1971), who examined whiting (*Merlangius merlangus*) and Nephrops (*Nephops norvegicus*) behaviour with a horizontal panel in the codend of a Nephrops trawl. This was followed by Strzysewski (1972), who fitted a horizontal separator panel 1.5 m above the footrope of a demersal herring trawl (Figure 1). Subsequently there have been many attempts to develop species selective trawls using horizontal separator panels (e.g. Main and Sangster 1985; Stone and Bublitz 1995; Hickey and Brothers 1998; Engås et al. 1998). Trials have investigated gears where the panel has been fitted at different heights and positioned as far forward as the fishing line or as far back as the codend. Other trials have explicitly investigated the influence of panel position and the time at which trawling took place on separation (Main and Sangster 1982a; Main and Sangster 1982b; Valdemarsen et al. 1985; Ferro et al. 2007) or examined ways of modifying separation by using inclined netting sheets and rising ropes ahead of the separator panel (Graham 2010).

This paper presents a meta-analysis of catch data from 20 of these trials that were conducted in the North Sea, the Grand Banks, the Barents Sea, the Baltic Sea and the Skagerrak between 1970 and 2015. The trials included in the analysis are those which detail the number of fish entering the upper and lower codends and supply sufficient separator panel and gear design information. Results are presented for eight species: the gadoids cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), saithe (*Pollachius virens*) and whiting (*Merlangius merlangus*), the flatfish lemon sole (*Microstomus kitt*) and plaice (*Pleuronectes platessa*), and monkfish (*Lophius piscatorius*) and Nephrops (*Nephops norvegicus*).

Literature search

A meta-analysis is the process of synthesising the results from a series of studies, here fishing trials. See Borenstein et al. (2009) for a thorough description of meta-analysis principles and techniques. A key component of any meta-analysis is an exhaustive literature search (e.g. Normand 1999) and here we searched the following databases: ProQuest's Earth, Atmospheric and Aquatic Science Database (www.proquest.com); Google Scholar (http://scholar.google.co.uk); ICES historical CM documents (www.ices.dk); and Marine Scotland Science Library Catalogue (www.gov.scot). This yielded 57 articles with details of fishing trials that investigated species separation in trawl gears. However, some of these were automatically excluded as they were reviews, reproduced data presented in other articles or were not horizontal separator panel trials (e.g. they reported on escapement under the groundgear).

Of the remaining articles, those used in the analysis (Table 1) were chosen to provide as large a data set as possible, with a core set of common explanatory variables, and with data in a form that could be combined across trials. This resulted in 20 trials (testing 38 different panel configurations) where a) catch data (by number and species) in the upper and lower codends are available, b) the upper and lower codends have the same nominal mesh size and c) there is sufficient information on explanatory variables such as panel height, distance of panel from the ground gear, and the time of day at which trawling took place. Some of the trials involved multiple fishing trips on the same vessel but at different times of year and over different years (Table 1); these trips might normally have been considered as separate trials, but as the data were not available at the trip level, we had to regard them as a single trial for modelling purposes.

Publication bias, where studies are only reported if they generate significant results, is a common problem in meta-analyses (Easterbrook 1991). We followed no established protocol for checking for this, or other biases. However, trials investigating separator panels are relatively rare, and typically aim to quantify the proportions of fish retained in the upper codend across a range of species (rather than relying on the significance of effects for their relevance), so we feel that publication bias is unlikely to be a major issue here.

Data processing

The level of data aggregation varied widely across trials. Fish counts and sampling fractions were sometimes available by length class and haul. More often, however, fish numbers had been raised and aggregated and, to ensure comparability across trials, we therefore had to use raised data, aggregated across lengths and hauls. Since one of our objectives was to consider the effect of time of day (day / night) on separation, we summarised the separation of each panel configuration by the total number of fish (of each species) retained in the upper and lower codends by time of day. For those panel configurations where the data were not available by time of day we used the total number of fish in the upper and lower codends in all hauls and defined a third ‘mixed’ category. The availability of data by species is given in Table 2 and the proportions of fish retained in the upper codend are plotted in Figure 2.

The explanatory variables are described in Table 3 and plotted in Figure 2. Separator height and distance from ground gear both determine the position of the panel when the fish first encounter it. Headline height is also considered because it affects the geometry of the trawl at the start of the panel and, if it is low, may result in fish swimming over it. Time of day and trawl depth will both affect visibility within the trawl and panel mesh size will influence the ability of fish to pass through the panel. Finally, codend mesh size is included to accommodate any effects of codend selection on the estimates of panel separation: for example, if panel separation depends on length, then the proportion of fish that are retained in the upper codend will change depending on the codend mesh size. The headline height was not given for two studies (with six panel configurations); for analysis, the missing values were taken to be 3.5 m, the median headline height across the other trials.

Analysis

For haddock, cod, whiting, plaice and lemon sole (those species recorded in at least 9 trials), we modelled the proportion of fish retained in the upper codend by panel configuration and time of day. Thus, for each panel, we had two observations if trawling took place during both the day and night and the data were available as such, and a single observation otherwise (day hauls only, night hauls only, or an aggregated mixed category). The relationship between the proportions retained in the upper codend and the explanatory variables was investigated using generalised linear mixed models assuming binomial errors and a logistic link. We first fitted a ‘starting’ model:

proportion in upper codend ~ intercept + separator height

with binomial errors weighted by the total number of fish retained and random effects for trial, panel configuration (within trial) and time of day (within panel configuration). With only one observation for each combination of panel and time of day, the time of day random effect also incorporated any overdispersion in the data. Separator height was included in the starting model because it is the explanatory variable that we considered should have the most direct effect on separation. We then refined the starting model in a backwards and forwards stepwise procedure in which, at each stage, we considered dropping each of the explanatory variables in the current model or adding each of the explanatory variables not in the current model, and then selecting the model with the minimum AIC. This was repeated until there was no improvement in AIC. When time of day was in the current model, we also considered adding interactions between time of day and the other variables in the current model. All models were fitted by maximum likelihood. To avoid over-fitting, the model with the minimum AIC was then refined further by dropping any terms that were not significant at the 5% level. In generalised linear mixed models with small sample sizes, such as here, inferences made by comparing the likelihood ratio statistic to the standard reference chi-squared distribution can be unreliable so, instead, the likelihood ratio statistic was compared to a reference distribution obtained by simulating from the model fitted under the null hypothesis (see e.g. Bolker 2015).

The weighting of the binomial proportions by the total number of fish retained was a pragmatic decision, but one that appears acceptable based on residual plots (not shown). The proportions will be more precisely estimated if they are based on more fish, but the number of hauls will also be important. However, given the aggregation of the source data, it is not possible to model the between-haul and within-haul variation correctly. Fortunately, one of the effects of the overdispersion (time of day) variance component is to moderate the influence of observations based on very large numbers of fish, but possibly few hauls, on both the likelihood and the model estimates.

Simpler models were considered for monkfish, nephrops and saithe, as there were fewer data (Table 2) and little contrast in the explanatory variables apart from separator height. First, the data were aggregated over time of day (so there was only one observation for each panel configuration). We then fitted the model:

proportion in upper codend ~ intercept + separator height

with just two random effects, for trial and panel configuration (within trial), with the latter term now also including any overdispersion. Finally, we considered whether separator height should be retained in the model by a likelihood ratio test with a simulated reference distribution.

Results

The final models were:

haddock: ~ intercept + separator height

cod: ~ intercept + separator height + distance from ground gear

whiting: ~ intercept + separator height

plaice: ~ intercept + separator height + time of day

lemon sole: ~ intercept + separator height monkfish: ~ intercept

saithe: ~ intercept + separator height

Nephrops: ~ intercept

The fits are illustrated in Figure 3 and parameter estimates are given in Table 4.

For six of the eight species, the proportion of fish that rise above the separator panel decreases as the height of the leading edge of the panel increases (as would be expected). The species can be broadly characterised into three categories. Haddock, whiting and saithe behave in a similar way and almost all go above panels that are less than 1 m high. Cod, lemon sole and plaice can also be grouped, with about half swimming above panels that are 0.2 m high, but very few swimming over panels more than 1.5 m high. Only monkfish and Nephrops have no significant dependency on panel height; whilst, in some trials, individuals enter the upper codend when the separator height is low, in general most do not go above panels more than 0.2 m high.

Cod is the only species for which separation depends on the horizontal distance of the leading edge of the panel from the ground gear, with the proportion of cod going above the panel increasing the further the panel is from the ground gear. There is a suggestion that plaice behave similarly, but the relationship is not significant ($p = 0.063$). The time of day at which the trials were carried out only affected the separation of plaice ($p = 0.006$), with a greater proportion of plaice going above the panel at night than during the day ($p = 0.003$). (There was no significant difference between the mixed category and either day or night.) Again, there is a suggestion that time of day had a similar effect on lemon sole, but the relationship is non-significant ($p = 0.069$).

The estimates of the variance components are given in Table 5. The between-trial variance is the largest component for six species, and is similar to the other components for the remaining species. The between-trial variance will incorporate unexplained variability due to e.g. difference in vessels, area and time of year. Overdispersion in the data would be expected because of the aggregation over lengths and hauls, and this is reflected in the size of the between-time of day variance (when estimated) and the between-panel configuration variance (otherwise). The variances for monkfish and Nephrops should be treated with some scepticism as they are based on few trials, some of which had no fish retained in the upper codend; with estimation on the logistic scale, the zero proportions can lead to unrealistically large estimates.

Discussion

For six of the eight species, the height of the separator panel plays an important role in determining the proportion of fish which go above the panel. Only monkfish and Nephrops have no significant dependence on the height of the panel. These results are consistent with the observations and results of many related studies. For example, Main and Sangster (1981) describe differences in how fish react to and enter a demersal trawl. They report that haddock rise up, ahead of the fishing line, to a height of as much as 5 m; that whiting, who initially swim slightly higher off the seabed than haddock at about 1 to 2 m, do not tend to rise, but turn in the horizontal plane as they drop back; that cod swim close to the sea bed and into the net close to the belly panel; and that saithe swim between 1 and 2 m and are slowly overtaken by the gear. Newland et al. (1988) show that, following stimulation, the average swimming height of Nephrops is between 0.2 and 0.5 m from the seabed. In studies using collection bags behind the ground gear, 33% of cod, 23% of haddock and 7% of saithe escaped under the fishing line of a demersal trawl rigged with a 60 cm diameter rockhopper gear (Ingólfsson and Jørgensen 2006); 66% of cod and 21% of haddock swam under the fishing line of a survey gear that was 35 – 40 cm above the seabed (Engås and Godø 1989); 70% of cod escaped under the fishing line of a survey trawl whose bosom was 53 cm above the seabed (Walsh 1992); and 85% of monkfish went below the fishing line of a commercial gear with 40 cm diameter rockhoppers (Kynoch et al. 2015). The proportion of haddock which go under the ground gear in these studies is higher than would be expected from the results of our meta-analysis and may indicate that haddock were also escaping under the ground gear during the individual separator panel trials and hence not accounted for in the subsequent analysis.

For cod, there is a dependence on the horizontal distance of the panel from the ground gear. More cod go above the panel the further its leading edge is from the ground gear. This is consistent with Thomsen's (1993) observations of cod entering low and then gradually rising as they move through a trawl, a behaviour which he harnesses to obtain a 38% reduction of their capture by fitting large mesh netting panels in the upper sheets ahead of the straight section. Similarly, Holst et al. (2009) conclude that cod are close to the belly sheet when they first enter the gear but have redistributed upwards by the time they arrive at the extension.

We also found a dependency on time of day for plaice (and possibly lemon sole) with more plaice entering the lower compartment during the day than at night. This is consistent with the results of a number of authors who have shown that ambient light levels can influence avoidance and/or escape behaviour of fish (Glass and Wardle 1989). Poos and Rijnsdorp (2007) found that catch rates of Dover sole (*Solea solea*) were greater at night but did not find an effect for plaice and Ryer and Barnett (2006) found that in dark conditions flatfish were more likely to rise off the bottom in response to an oncoming footrope, whereas in the light they tended to swim away from the footrope and remain close to the seabed. Analysis of survey data has also found diel variation in trawl catch rates for many species which may be attributable to the reaction behaviour of fish under different light conditions (Walsh and Hickey 1993; Casey and Myers 1998; Petrakis et al. 2001). Furthermore, Hannah et al. (2015) and Weinberg and Munro (1999) found that with artificial light there was increased escape of eulachon (*Thaleichthys pacificus*) and flat head sole (*Hippoglossoides elassodon*) under the footrope.

The main limitations of our analysis arise from the need to work with raised data, aggregated across lengths and hauls. In particular, we could not investigate the influence of fish size. Each of the ground gear collection bags studies mentioned above (Walsh 1992; Engås and Godø 1989; Ingólfsson and Jørgensen, 2006; Kynoch et al. 2015) found that the proportion of fish which go above the fishing line depended on fish length, with smaller fish more likely to go under the fishing line than larger ones. Some of the separator panel studies used in our meta-analysis (e.g. Ferro et al. 2007; Holst et al. 2009) also reported length effects, but the direction of the effect was inconsistent, varying between species and with the height of the panel. From a pragmatic perspective, the estimates in Table 4 and the fitted proportions in Figure 3 must be interpreted as the values averaged across lengths, or at a ‘typical’ length.

Of course, the meta-analysis also averages across other variables that could affect the response of fish to a trawl and that cannot be modelled with the available data. Trials were conducted on different vessels, and in different areas and times of year, with consequent variation in water temperature and ambient light levels. This is reflected in the between-trial variance (Table 5), which was the largest variance component for six of the eight species and similar to the other variance components for the other two. However, a big advantage of a meta-analysis is that relationships are only significant if the effect can be demonstrated over and above any random trial effects and are thus far more likely to be generalizable that results from a single trial.

From a statistical perspective, raising and aggregating data within trials will lead to numbers retained in the upper-codend that are overdispersed relative to a standard binomial distribution, violating the assumptions of the mixed model. However, the time of day random effect acts as a ‘catch-all’ for overdispersion, so inference should still be reasonably robust. To investigate this, we simulated 1000 sets of haddock data using the same total numbers of fish as in the original trials and with the parameter estimates in Tables 4 and 5, but with the between-time of day variance set to zero and replaced by between-haul variation. We then compared the fits of the ‘correct’ mixed model (i.e. fitted to individual haul data with a haul random effect) and the ‘aggregated’ mixed model (i.e. the one used in this study, fitted to aggregated data and with a time of day random effect). The between-haul standard deviation was set to 1.00, which produced a between-time of day standard deviation similar to that in Table 5 when estimated using the aggregated model. The aggregated model estimated the mean proportion retained in the upper codend with negligible bias, but decreased the estimate of the separator height effect by about 10%. This suggests that the proportions in the upper codend shown in Figure 3 are underestimated when the separator panel is low (< 0.5 m) and overestimated when it is high (> 1.0 m). The standard error on the separator height effect decreased in line with the point estimate (i.e. by about 10%), suggesting the tests of significance in Table 4 are reasonable.

Our results will be useful in designing species selective fishing gears, which are becoming increasingly important as more jurisdictions prohibit discarding. In European Union fisheries, for example, there are concerns that, as the land-all obligation is applied to more species, fishermen are more likely to catch fish which they are not allowed to discard and for which they have no quota. In such circumstances, if species selective gears are not available, the only options may be to change fishing ground or to stop fishing altogether. Our meta-analysis quantifies the vertical distribution of a range of commercially important North Atlantic species as they enter and pass through a demersal trawl gear. Hence our results can be used to develop and adapt gears such as low headline and coverless trawls (Krag et al. 2015) and trawls with raised footropes (Chosid et al. 2011; Bayse et al. 2016) which have already been shown to be effective in a number of fisheries. Our analysis suggests that, in the first instance, it should be possible to separate the three categories of (i) haddock, whiting and saithe, (ii) cod, plaice and lemon sole and (iii) monkfish and nephrops. If these species can be directed to different parts of the gear it may then be possible to further select on a size or species basis. Furthermore, if such selection can take place during the early stages of the capture process, the fish will be less likely to be exhausted or to suffer physical damage while passing through the netting meshes and be more likely to survive (Breen et al. 2004; Suuronen and Erickson, 2010).

Acknowledgements

We thank the reviewers for their helpful comments, which have greatly improved this paper. This study was carried out under the Horizon 2020 project DISCARDLESS (633680). It does not necessarily reflect the views of the European Commission and does not anticipate the Commission’s future policy in this area.

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Table 1 A summary of the trials used in the meta-analysis, giving the number of panel configurations, the year, time of year and number of hauls available, and the range of each explanatory variable (with a single value denoting that the variable was fixed during the trial). The range across all trials is given at the bottom of the table. Further details of each explanatory variable are in Table 3. Blanks indicate missing data.

Trial	Year	No. panel config.	Time of year	Hauls	Separator height (cm)	Dist. from ground gear (m)	Headline height (m)	Separator mesh size (mm)	Codend mesh size (mm)	Time of day	Depth (m)	Reference
1	1970	1	Apr, Sept-Oct	42	150	0	3.1	40	40		85	Strzysewski (1972)
2	1981	2	Spring, Autumn	13	45	0	5	140	76	day, night	71 - 90	Main & Sangster (1982a)
3	1981	5		24	45 - 106	0	3.3	50 - 85	70	day	99 - 113	Main & Sangster (1982b)
4	1981-1982	1	Spring, Summer	16	75	0	3.1	50	70	day	108	Main & Sangster (1985a)
5	1982	2	Dec	8	200	0	5 - 7	20 - 140	20	day, night	113 - 120	Bailey et al. (1983)
6	1982	1		4	90	0.3	4.9	140	75	day	65	Galbraith (1983)
7	1983	1	Jun-Jul	4	100	0	3.3	50	70	day, night	59	Ashcroft (1983)
8	1983	1		8	75	0	3.4	70	70	day	108	Main & Sangster (1985b)
9	1984	4	Oct	16	50 - 150	0	6.5	144	135	mixed	235	Valdmarsen et al. (1985)
10	1989, 1990	2	May, Jan-Feb	29	75 - 120	0		140	140		80	Main & Sangster (1990)
11	1992	4	Oct	26	41 - 107	0.2		75	40	mixed	155	Hickey & Brothers (1998)
12	1994	2	Mar	30	100	0	3.3	115	60 - 100	mixed	51 - 53	Arkley et al. (1994)

13	1994	2	Nov	42	100	0	3.5	115	40 - 100	mixed	64	Swarbrick et al. (1995)
14	2004	3	Apr	14	80 - 135	0, 19.5	3.6	80	40	day, night	72 - 110	Ferro et al. (2007)
15	2004	1	Jun	11	25	28	2.4	42	42	day	60	Krag et al. (2009a)
16	2004	1	Nov	10	25	28	2.4	42	42	mixed	122	Krag et al. (2009b)
17	2005	1	Sept	11	135	10	3.5	120	50	day, night	108 - 121	Holst et al. (2009)
18	2006	1	Oct	28	60	0	8	40	40	day, night	95	Krag et al. (2010)
19	2014	2	Sept	17	20 - 80	1.6	2.2	60	40	day	81	Summerbell (unpub.)
20	2015	1	Mar	6	40	1.1	2.1	60	80	night	83	Summerbell (unpub.)
Overall range					**20 - 200**	**0 - 28**	**2.1 - 8**	**20 - 144**	**20 - 140**		**51 - 235**	

Table 2 Data availability by species: the number of trials, panel configurations, and observations (proportion retained in the upper codend aggregated over lengths and hauls) by time of day.

	trials	panel configurations	observations		
			day	night	mixed
haddock	18	33	21	10	11
cod	17	33	18	8	14
whiting	17	29	21	10	7
plaice	10	15	9	7	5
lemon sole	9	13	8	7	3
monkfish	6	7	5	2	1
Nephrops	5	9	8	1	1
saithe	5	8	3	2	5

Table 3 Explanatory variables used in the meta analysis and other supporting information

variable	unit	comments
hauls	#	The number of hauls across all panel configurations tested during the trial
separator height	m	The vertical distance from the leading edge of the separator panel to the netting sheet, fishing line or ground gear that is directly below it.
distance from ground gear	m	The horizontal distance from the leading edge of the separator panel to the ground gear. Very skewed (zero for 25 of the 38 panel configurations), so was 4^{th} root transformed for modelling purposes. When not specified, this variable was estimated from net drawings.
headline height	m	The vertical distance from the headline to the seabed, fishing line or ground gear that is directly below it.
time of day		Three categories: day, night and mixed. Mixed corresponds to panel configurations for which the data could not be disaggregated by day and night, or for which the time of day was not given.
trawl depth	m	The midpoint between the minimum and maximum trawl depth for each panel configuration (disaggregated by time of day where possible). This is a pragmatic choice based on the depth information that was typically available. Skewed, so was log transformed for modelling purposes.
panel mesh size	mm	The nominal mesh size. In general mesh shape was not specified.
codend mesh size	mm	The nominal mesh size. In general mesh shape was not specified.

Table 4 Parameter estimates, with standard errors (obtained from the inverse of the Hessian matrix) and p-values (based on likelihood ratio tests with a simulated reference distribution). The species are ordered by decreasing median proportion retained. For all but plaice, the proportions retained are related to the parameter estimates through logit (proportion retained) = α + β × separator height + γ × distance from ground gear, where α is the intercept parameter, β is the separator height parameter (saithe, haddock, whiting, cod and lemon sole) and γ is the distance from ground gear parameter (cod only). For plaice, the intercept and time of day effects are combined so that logit (proportion retained) = $\alpha_{time\ of\ day}$ + β × separator height, where $\alpha_{time\ of\ day}$ is the appropriate intercept parameter for day, night and mixed hauls respectively.

species	parameter	estimate	standard error	p-value
saithe	intercept	3.31	0.40	< 0.001
	separator height	-1.22	0.48	0.015
haddock	intercept	3.36	0.41	< 0.001
	separator height	-1.89	0.42	< 0.001
whiting	intercept	2.87	0.44	< 0.001
	separator height	-1.73	0.47	0.006
cod	intercept	-0.49	0.49	0.391
	separator height	-1.38	0.47	0.018
	distance from ground gear	1.00	0.26	0.002
lemon sole	intercept	0.89	0.68	0.265
	separator height	-2.58	0.72	0.003
plaice	intercept (day)	-0.30	0.78	0.754
	intercept (mixed)	-0.88	1.08	0.428
	intercept (night)	1.03	0.78	0.200
	separator height	-2.11	0.77	0.042
Nephrops	intercept	-7.2	3.1	0.125
monkfish	intercept	-10.5	4.2	0.108

Table 5 Estimates of the variance components, expressed as standard deviations. For haddock, whiting, cod, plaice and lemon sole, the between-time of day variance also incorporates any overdispersion. For saithe, monkfish and Nephrops, the data were aggregated over time of day and the between-panel configuration variance incorporates any overdispersion. The species are ordered by decreasing median proportion retained.

species	variance component		
	trial	panel configuration	time of day
saithe	0.57	0.14	
haddock	0.55	0.67	0.59
whiting	0.54	0.67	0.46
cod	0.74	0.34	0.57
lemon sole	1.22	0.00	0.52
plaice	1.30	0.46	0.11
Nephrops	5.28	1.54	
monkfish	11.08	0.00	

Figure 1 Demersal trawl fitted with horizontal separator panel which directs fish that goes above the panel to the upper codend and fish that go below the panel to the lower codend.

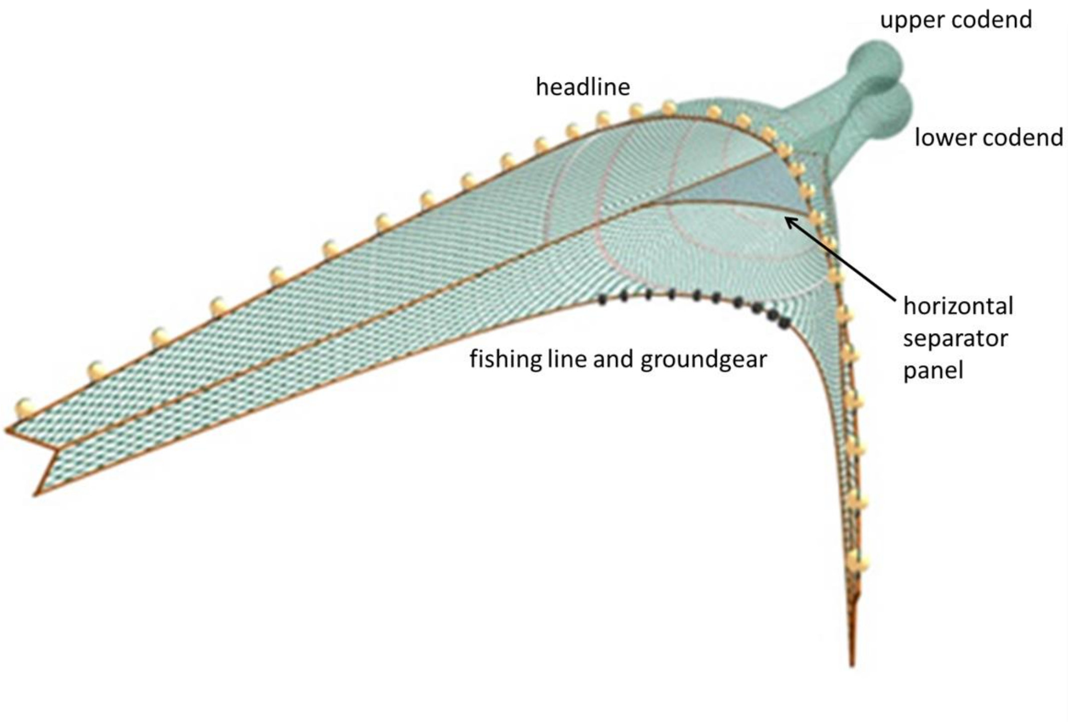

Figure 2 Scatter-plot matrix of the explanatory variables (upper triangle) and the proportions of each species retained in the upper codend (lower triangle). The species are ordered by increasing median proportion retained. The plotting symbol indicates the time of day: day (open circle), night (filled circle), mixed (+). Mesh sizes are measured in millimetres and depths, heights and distances in metres. Depth is plotted on the log scale and distance from ground gear on the fourth root scale.

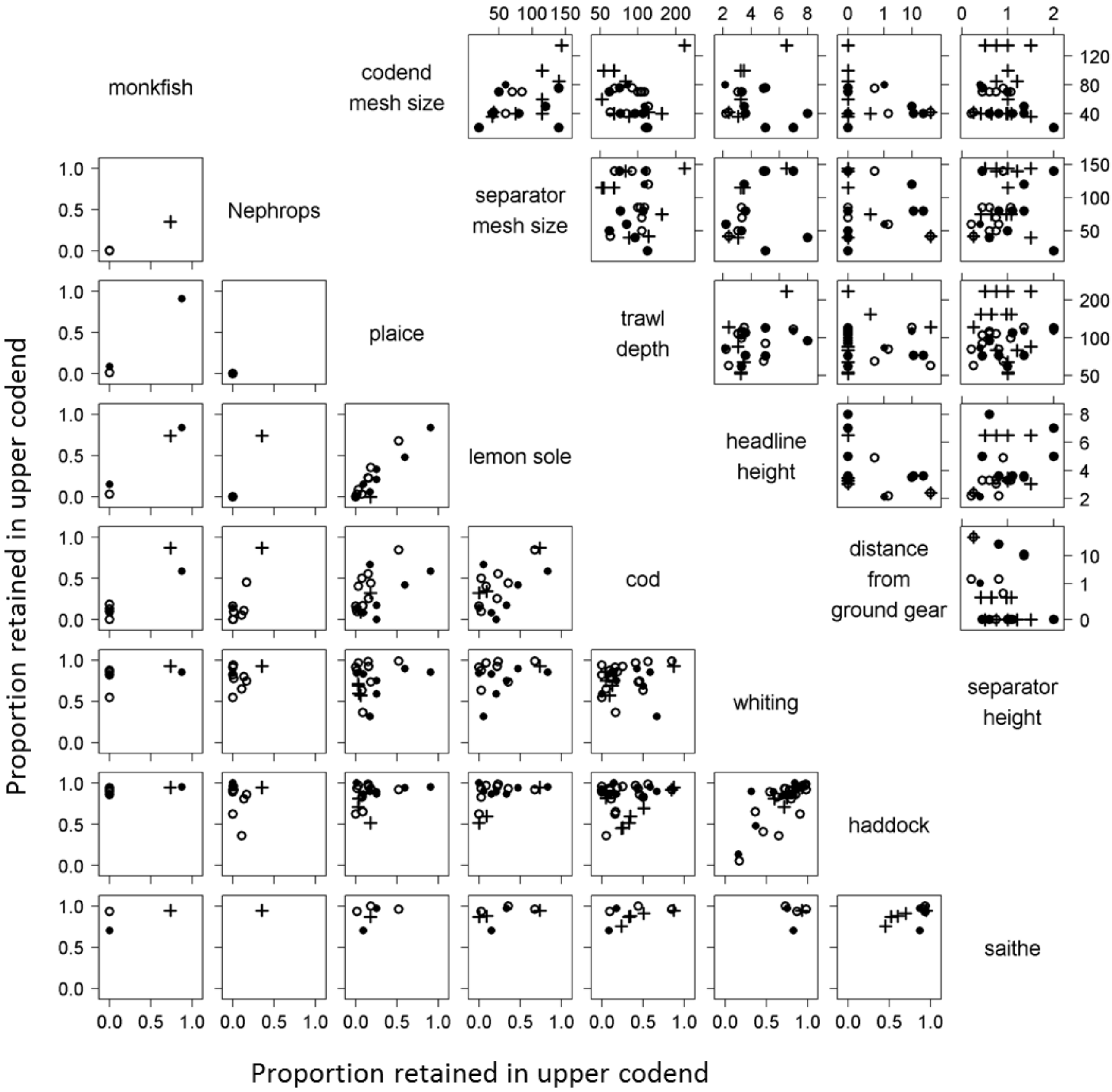

Figure 3 The proportion of fish retained in the upper codend plotted against separator height with the fitted relationship (solid line) and pointwise 95% confidence bands (grey shaded areas). The species have been ordered from bottom left to top right by decreasing median proportion retained. The plotting symbol indicates the time of day: day (open circle), night (filled circle), mixed (+). The proportions are those used for modelling so, for saithe, monkfish and Nephrops, the data have been aggregated across time of day with a + symbol indicating that day and night hauls were combined. For cod, the fitted values are standardised to a distance from ground gear of 1.6 m, the median of the non-zero values in the data set. For plaice, the three lines correspond to the three time of day categories: night (upper line), day (middle line), mixed (lower line). For monkfish and Nephrops, there was no significant relationship with separator height and the (back-transformed) intercept is shown: the very low values arise because the estimation is on the logistic scale and there are some trials with no fish retained in the upper codend.