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1 **Using vertical distribution to separate fish from crustaceans in a mixed species trawl fishery**

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14

15 **Abstract**

16 A major challenge in mixed fisheries is achieving acceptable size selectivity for morphologically different
17 species using the same fishing gear. Separator trawls can have different selective properties in the upper and
18 lower compartments provided successful separation of species. We used a horizontally divided codend with
19 small square meshes (40 mm) and a simple frame to stimulate fish to swim into the upper compartment. The
20 majority of the fish were separated successfully from *Nephrops* (*Nephrops norvegicus*), but their preference were
21 uniform. Less than 10% of the *Nephrops* entered the upper compartment. Length-based analysis revealed three
22 patterns of separation efficiency among nine commercial species: length-dependent separation, and preference
23 for the upper or lower compartments. The separation efficiency should be improved for small roundfish and
24 flatfish. There was little diel effect on the separation efficiency. The preference of fish for a compartment taking
25 the relative height of that compartment into account was established for this and similar previous studies to
26 enable comparison of results. We recommend length-based analysis to account for the fished population when
27 interpreting the results.

28

29 Key words: horizontally divided codend, mixed fish-crustacean fisheries, length-based separation efficiency,
30 vertical distribution, vertical preference

31

32 **Introduction**

33 The ability to catch different target species and sizes is crucial for the incomes of fishermen. The proportion of
34 the catch that comprises unwanted species and sizes has traditionally been discarded. This practice no longer
35 conforms with the increased societal demand for sustainable fisheries. The landing obligation under the EU
36 Common Fisheries Policy does not allow European fisheries to sell landings of regulated species under the
37 minimum conservation reference size (MCRS, previously called Minimum Landing Size, MLS) for human
38 consumption (EU 2013). If alternative sales channels offers lower prices per kg, landing fish below the MCRS
39 likely reduces the economic value of the quota. Horizontally divided codends may be used to reduce the large
40 proportion of unwanted catch in mixed trawl fisheries that target crustaceans. An upper compartment made of
41 large, open meshes would be ideal for fish escapes along the whole length of the compartment similar to the
42 BACOMA codend, which, in contrast to some square mesh panels, efficiently releases roundfish such as cod
43 (*Gadus morhua*) (Herrmann et al. 2015). A small-mesh lower compartment may reduce the loss of valuable
44 crustaceans that has been observed in standard gears targeting *Nephrops* (*Nephrops norvegicus*) (Krag et al.
45 2008; Frandsen et al. 2010). Apart from reducing unwanted catches, the separation of fish from species with hard
46 outer surfaces can significantly improve the catch quality and thus have prospects of increasing the catch value
47 (Karlsen et al. 2015). Furthermore, the sorting time may be reduced, especially in fisheries involving crustaceans
48 (Main and Sangster 1985a).

49
50 Separating species into different compartments is the first step when developing a horizontally divided codend
51 with different selective properties for fish and crustaceans. A separator panel can separate species that are closely
52 associated with the seabed from species that distribute themselves higher in the gear. The height of the separator
53 panel above the fishing line, ground gear, or bottom panel affects the proportion of individuals that enters the
54 different compartments for several species (Fryer et al. 2017). For example, if a species has a uniform vertical
55 distribution when encountering the leading edge of the separator panel, then lowering the separator panel will
56 increase the proportion of individuals entering the upper compartment. However, in mixed fisheries involving
57 many species and vertical distributions, changing the height of the separator panel may not be sufficient to give
58 the wanted species separation. Additional gear modifications may be required to alter the vertical distribution of
59 of some species while maintaining the vertical distribution of others.

60

61 Separator frames and grids at the entrance of the horizontal separation have been used to separate the majority of
62 roundfish and a large proportion of flatfish from *Nephrops* in the codend (Graham and Fryer 2006; Holst et al.
63 2009; Krag et al. 2009a, 2009b). Graham and Fryer (2006) used grids to guide fish into the upper compartment.
64 The grid had horizontal gaps in the bottom making the separation process a combination of mechanical selection
65 by the grid bars, and vertical behaviour where fish either could be guided by the grid, enter the upper
66 compartment directly, or contact the lower gap and enter the lower compartment. Krag et al. (2009b) used a rigid
67 separator frame with two horizontal bars to separate fish into three vertically stacked compartments, and
68 compared the results with those when using a similar frame, but with additional two vertical bars across the
69 lowest and middle compartments. They concluded that the vertical bars were able to increase the catches of
70 several commercial species into the upper compartment.

71
72 The development of optimal designs can be facilitated if vertical distribution patterns are identified and
73 understood. To interpret the vertical distribution inside the gear, the overall proportion of species entering the
74 different compartments is not an appropriate measure for two reasons. First, it depends on the height of the
75 compartments. For example, if the proportion of a species is distributed 50:50 in upper and lower compartment,
76 it can be interpreted as the vertical distribution of the species is uniform in the gear. This is also true if the height
77 of the compartments are apportioned 50:50 of the total height of the gear at the entrance of the compartments.
78 However, if they are not, e.g., the height of the upper compartment is 67% and the lower compartment is 33% of
79 the total height, and the proportion of the species entering each compartment still is 50%, the vertical distribution
80 of the species can be misinterpreted to be uniform in the gear. In fact, a larger proportion enters the lower
81 compartment relative to the size of this compartment, i.e. the species is overall distributed low in the gear.
82 Second, the proportions are affected by changes in the length distribution of the fished population when the catch
83 of a species in a given compartment depend on its body length. For example, Graham and Fryer (2006) used a
84 gear in which each of the two compartments constituted 50% of the total height of the gear. They found that
85 more than 50% of dab (*Limanda limanda*) larger than 15 cm were caught in the upper compartment, and thus
86 they preferred the upper compartment. The opposite was true for dab smaller than 15 cm, i.e. more than 50%
87 went into the lower compartment, and thus they preferred the lower compartment. If this study was repeated with
88 everything identical, except for an increased proportion of large fish in the fished population, an increased
89 proportion caught in the upper compartment due to the preference for this compartment by larger individuals
90 could be misinterpreted as an overall change in vertical distribution due to a change in fish behaviour. This

91 example demonstrates that the proportion of a species that enters the e.g. upper compartment cannot be
92 compared between studies when the fished population differs or is unknown.

93
94 The main aim of the present study was threefold. First, to use a separator frame with two vertical bars at the
95 entrance of the horizontally divided codend to stimulate fish to swim into the more open upper compartment
96 while maintaining *Nephrops* in the lower compartment in the economically important and discard-heavy
97 *Nephrops*-directed fishery. The design was inspired by the two guiding bars used in Krag et al. (2009b) and by
98 the observation made by Glass et al. (1995) that fish are reluctant to pass through large meshes when a clearer
99 passage is available. Second, to perform a length-based quantification of the species specific separation
100 efficiency. By giving the proportion of a species entering a compartment for each length class, comparisons of
101 the same length classes of the same species across studies is enabled. I.e. the approach is population independent
102 and can be used to identify size-specific separation patterns and separation limitations, as well as making our
103 results comparable with those of other studies. The latter also required presenting our results as overall and size-
104 specific preferences for specific compartments, which are independent of the height of the compartments. Third,
105 we investigated the length-based diel differences in species separation. Vision appear to be important for fish
106 when they orientate relative to the gear, and so the vertical distribution of fish may be influenced by the light
107 intensity (Glass and Wardle 1989; Wardle 1993). Further, Krag et al. (2009a) observed that gadoids responded to
108 a separator frame without vertical guiding bars by holding in front of it. If the gadoid response was due to the
109 visual stimuli caused by the frame, it may change if their visual perception of the frame changes with changes in
110 ambient light levels.

111 **Materials and methods**

112 **Gear design and sea trials**

113 The experiment used a codend made of four net panels. The diamond mesh netting (40 mm mesh made of 1.8
114 mm polyethylene twine) was turned 45 degrees and mounted as square meshes to the tapered section to obtain
115 more stable mesh geometry and to maximize the water flow through the small meshes. The codend was divided
116 into upper and lower compartments by a horizontal net panel. In the aft end, the codend was split to give separate
117 collecting bags for the two compartments that eased handling during hauling (Fig. 1, enlarged section). The
118 entrance of the upper compartment was about 60 cm high and comprised two-thirds of the total height of the
119 gear. The height of the lower compartment was fixed to 30 cm by a frame made from 20 mm stainless steel pipes

120 mounted at its entrance, and comprised the remaining one-third of the total height. The frame had two vertical
121 guide bars placed 30 cm apart to encourage fish to swim into the upper compartment. A similar frame without
122 the vertical bars was mounted 4 m aft of the compartment entrance to aid full opening in the lower compartment.
123 Five 1-L floats were attached across the top panel above both frames to ensure good opening in the upper
124 compartment and to compensate for the weight of the frames (Fig. 1). To further optimize the catch separation,
125 the foremost frame was placed in the transition between the tapered and non-tapered section of the gear, where
126 the inclination of the bottom netting of the trawl ended (Fig. 1). At this point, we expected *Nephrops* to be closer
127 to the bottom netting panel in the trawl than the untapered codend section. Measurements of the codend mesh
128 size were conducted using dry netting before sea trials with OMEGA mesh gauge (Fonteyne et al., 2005).

129
130 The experiment was conducted aboard the commercial trawler FN-136 Tove Kajgaard (162 BT, 22 m, 299 kW)
131 using a three-wire towing rig. The codend was attached to the vessel's commercial trawl used in the mixed
132 species *Nephrops*-directed fishery. The trawl had a 47.5 m floatline and the groundgear measured 54.5 m. The
133 circumference comprised 500 meshes (80 mm diamond) and the headline height was ca. 2 m. Fishing was
134 conducted during day and night hours from 23 September to 1 October, 2013, in commercial fishing grounds in
135 Skagerrak. To separate the day and night tows, the day tows were performed in the time interval between one
136 hour after sunrise to one hour before sunset, and night tows from one hour after sunset until one hour before
137 sunrise. The overall geometry of the towing rig was monitored continuously using double spread sensors
138 (Marport) and the values were recorded every 15 min. The geometry of the entrance of the upper compartment
139 was monitored by underwater video recordings. The camera (GoPro Hero 3+) was attached to the top panel
140 about 1.5 m in front of the entrance of the upper compartment facing towards the entrance of the divided codend.
141 The haul time was less than that normally used in the commercial fishery to avoid the risk of large catches
142 reaching the separation point of the small mesh non-selective codend, thereby mixing the catches in the two
143 compartments. The catches from the two compartments were kept separate during handling and measurements.
144 The total lengths of cod, whiting (*Merlangius merlangus*), haddock (*Melanogrammus aeglefinus*), saithe
145 (*Pollachius virens*), hake (*Merluccius merluccius*), plaice (*Pleuronectes platessa*), witch flounder
146 (*Glyptocephalus cynoglossus*), and lemon sole (*Microstomus kitt*) were measured to the nearest centimetre
147 below, and the carapace length of *Nephrops* was measured to the nearest millimetre below. In the subsequent
148 analysis, 0.5 cm was added for fish and 0.5 mm for *Nephrops* (Krag et al. 2014). All individuals from each

149 species were measured in each haul, except for saithe, which was subsampled in the upper compartment in one
150 haul due to a large catch size, where 25% of the saithe were measured in this haul.

151 **Data analysis**

152 The mean body length (\pm standard deviation, SD) and mean proportions of individuals (with confidence interval,
153 CI) caught in the upper compartment was calculated separately for all fish, roundfish, flatfish and each species,
154 and separately for those caught during the day and during the night, and for fish smaller than MCRS. To evaluate
155 the length-dependent vertical separation efficiency for each species separately, and separately for the day and
156 night hauls, we used the numbers of individuals nu_{li} and nd_{li} in each length class l caught in each of the two small
157 mesh compartments (u : upper, d : lower) in each haul i . We defined the experimental vertical separation
158 efficiency VS_{li} as the proportion of fish with length l caught in the upper compartment compared with the total in
159 a haul i , as follows.

160

$$161 \quad VS_{li} = \frac{nu_{li}}{nu_{li} + nd_{li}} \quad (1)$$

162

163 The averaged vertical separation curves, $VS(l)$, for the three cases of all, day, and night hauls were estimated by
164 pooling the data from the different hauls. A parametric model for $VS(l)$ was defined by $VS(l, \mathbf{v})$, where \mathbf{v} is a
165 vector comprising the parameters in the model. Therefore, the analysis was reduced to a maximization problem
166 to estimate the values of the parameters \mathbf{v} , which made the observed experimental data averaged over hauls most
167 likely, assuming that the model was able to describe the data sufficiently well. Thus, the negative logarithm of
168 likelihood function for binomial data (2) was minimized with respect to \mathbf{v} , which is equivalent to maximizing the
169 probability for the observed data:

170

$$171 \quad - \sum_l \sum_{i=1}^h \{ nu_{il} \times \ln(VS(l, \mathbf{v})) + nd_{il} \times \ln(1.0 - VS(l, \mathbf{v})) \}, \quad (2)$$

172

173 where the summations were over length classes l and over the h hauls belonging to the case analysed, i.e. all,
174 day, or night hauls, respectively. We needed to find a model for $VS(l, \mathbf{v})$ that was sufficiently flexible to account
175 for the trends in the experimental data for the different species. Eq. (1) is on a form which is often applied in
176 catch-comparison studies for the efficiency/selectivity of fishing gears (Krag et al. 2014, 2015). Therefore we
177 adapted a model often applied for such data also to model $VS(l, \mathbf{v})$:

$$178 \quad VS(l, \mathbf{v}) = \frac{\exp(f(l, \mathbf{v}))}{1.0 + \exp(f(l, \mathbf{v}))}, \quad (3)$$

179 where f is a polynomial of order k with coefficients v_0, \dots, v_k so $\mathbf{v} = (v_0, \dots, v_k)$. We considered f up to an order of 4
 180 with parameters v_0, v_1, v_2, v_3 , and v_4 . $VS(l, \mathbf{v})$ expresses the probability of finding a fish of length l in the upper
 181 compartment given that it was observed in the upper or lower compartment. We used $f(l, \mathbf{v})$ in the following
 182 formula.

$$183 \quad f(l, \mathbf{v}) = \sum_{i=0}^4 v_i \times \left(\frac{l}{100}\right)^i = v_0 + v_1 \times \frac{l}{100} + v_2 \times \frac{l^2}{100^2} + \dots + v_4 \times \frac{l^4}{100^4} \quad (4)$$

184 By omitting one or more of the parameters $v_0 \dots v_4$ in Eq. (4), we obtained 31 further potential models for
 185 describing $VS(l, \mathbf{v})$. Model averaging was applied to describe $VS(l, \mathbf{v})$ according to how likely the individual
 186 models were when compared with each other (Burnham and Anderson 2002). In the resulting combined model,
 187 the individual models were ranked and weighted according to their AIC values (Burnham and Anderson 2002).
 188 Models yielding AIC values within +10 of the value obtained by the model with the lowest AIC (Akaike 1974)
 189 were considered to contribute to $VS(l, \mathbf{v})$ based on the procedure described by Katsanevakis (2006) and Herrmann
 190 et al. (2017). The ability of the combined model to describe the experimental data was assessed based on the p -
 191 value, which expresses the likelihood of obtaining a discrepancy at least as large as that observed between the
 192 fitted model and the experimental data by chance. Therefore, when the p -value was >0.05 a combined model was
 193 accepted (Wileman et al. 1996). In the case of poor fit statistics (p -value < 0.05 ; deviance \gg DOF (Degree Of
 194 Freedom)), the deviations between the experimentally observed vertical separate data and the fitted curve were
 195 examined to determine whether the difference was due to structural problems when describing the experimental
 196 data with the combined model, or data over-dispersion.

197 Confidence intervals (CI) were estimated for the length-dependent vertical separation efficiency using a double
 198 bootstrap method with the software SELNET released by 08.03.2017 (Millar 1993; Herrmann et al. 2012). The
 199 procedure accounted for uncertainty due to between-haul variation in the vertical separation efficiency by
 200 selecting h hauls with replacement from the h hauls available from the pool of hauls in the three specific cases
 201 investigated (i.e., all, day, or night hauls) during each bootstrap repetition. The within-haul uncertainty in the
 202 size structure of the catch data for the upper and lower compartments was accounted for by randomly selecting
 203 fish with replacement from each of the selected hauls from the upper and lower compartments. The number of
 204 fish selected from each haul was the number of fish with length measurements in that haul in the upper and
 205 lower compartments. The data were then combined as described above and the vertical separation efficiency was

206 estimated. Only hauls containing at least 10 individuals in the summed upper and lower compartments were
207 investigated for a given species. In total, 1000 bootstrap replicates were performed and the Efron 95% CI (Efron
208 1982) was calculated for the vertical separation curve. Incorporating the combined model approach described
209 above in each of the bootstrap replicates allowed us to consider additional uncertainty regarding the vertical
210 separation efficiency due to uncertainty in model selection (Krag et al. 2015).

211 Our null hypothesis (H_0) was uniform vertical distribution in the gear, i.e. when the proportion of individuals
212 entering a compartment corresponds to the proportion of the compartment relative to the total height of the
213 fishing gear at the location of the separation (Krag et al. 2009b). As the upper compartment constituted 2/3 of the
214 total height of the gear, the vertical distribution was considered uniform when the separation efficiency $V_S(l, \nu)$
215 was 0.67 (67 % of the individuals of length l entered the upper compartment), and in cases when the confidence
216 interval contained 0.67 with respect to the upper compartment. On the other hand, when the proportion of a
217 species was larger than the proportion of the height of the compartment it entered, the species was considered to
218 have a preference for that compartment, i.e., at separation efficiencies > 0.67 individuals preferred the upper
219 compartment, whereas they preferred the lower compartment at efficiencies < 0.67 . We use the term ‘preference’
220 quantitatively (Melli et al. 2018). Our use is analogous to that used for habitat preference defined as ‘the ratio of
221 the use of habitat over its availability, conditional on the availability of all habitats to the individual’ (Aarts et al.
222 2008). Habitat preference is considered the consequence of habitat selection that is ‘the process by which an
223 animal chooses which habitat component to use’ (Johnson 1980), thus resulting in the disproportional use of
224 some resources over others (Hall et al. 1998). Similarly, the vertical preference for either compartment in our
225 experiment is not used to imply behavioural choices at the point of codend separation, but is considered the
226 outcome of the vertical distribution selected in the natural habitat and any changes individuals made when
227 encountering the trawl gear and along the gear. ‘Preference’ has previously been used in relation to spatial
228 distribution inside trawls (Krag et al. 2009a, 2009b; Graham 2010; Winger et al. 2010).

229 **Results**

230 **Fishing gear and fishing operation**

231 The average mesh size (\pm SD) was 44.03 mm (\pm 1.35 mm) for the upper codend compartment ($n = 30$) and 43.63
232 mm (\pm 1.27 mm) for the lower codend compartment ($n = 30$). Fourteen valid hauls were conducted during good
233 fishing conditions in commercial fishing grounds (Table 1). The duration of the hauls varied between 1.25 and
234 3.50 h (mean: 2.63 h). Underwater video recordings showed that the net was open and stable at the entrance of

235 the divided codend (Fig. 2). There were no problems handling the two frames in the lower compartment during
236 the fishing process and the two vertical bars in the foremost frame did not collect any objects.

237

238 **Ability of the model to describe the data**

239 The p -value was above 0.05 in most cases, thereby implying that the deviation between the experimental data
240 and the fitted model might well be a coincidence and did therefore not cause any concern using the model to
241 describe the data (Table 2). The deviance residuals were checked for the five cases where the p -value was below
242 0.05. We found no systematic patterns in the deviations and the fitted model in any of these cases, and thus the
243 low p -values were probably a consequence of over-dispersion in the data. Therefore, we were confident that the
244 model could also be used to describe the length-dependent separation efficiency in these cases.

245

246 **Vertical distribution**

247 In total, 20,205 individuals comprising cod, whiting, haddock, saithe, hake, plaice, witch flounder, lemon sole,
248 and *Nephrops* were included in the analysis (Table 3). Although most of the fish (65%, CI: 60.0–69.1) entered
249 the upper compartment, the overall vertical distribution of fish was close to uniform (Table 4). The level of
250 separation differed between species. In general, a larger proportion of the roundfish than flatfish entered the
251 upper compartment. The flatfish were caught in the lower compartment in a larger proportion (58%, CI: 50.8–
252 64.2) than expected if their vertical distribution was uniform, considering that the entrance of this compartment
253 only comprised one-third of the total height in this part of the gear. Of the *Nephrops*, 90.6% (CI: 87.9–92.1)
254 entered the lower compartment of the divided codend (Table 4). Three patterns of separation efficiencies were
255 identified among the nine study species: 1) a strong length dependency for cod and whiting; 2) preferences for
256 the upper compartment by haddock and saithe; and 3) preferences for the lower compartment by hake, plaice,
257 witch flounder, lemon sole, and *Nephrops*.

258 *Length-dependent vertical distribution*

259 Cod

260 The mean length of the cod ($n = 3688$) was 39 cm (range: 9–96 cm) (Table 3–4). Overall, the individuals entered
261 the upper compartment less than expected if their vertical distribution was uniform (Table 4). There was a strong
262 length dependency in terms of the vertical distribution by cod, with a mean vertical separation efficiency of 0.22
263 for individuals measuring less than the MCRS of 30 cm, and 0.68 for individuals measuring greater than or equal

264 to the MCRS (Fig. 3). Of the total cod analysed, 32% measured less than the MCRS and they had a mean size of
265 25 cm (SD: \pm 14.0). The preference for the lower compartment was significant for cod $<$ 45 cm. Cod \geq 45 cm
266 showed a uniform vertical distribution (Fig. 3).

267 Whiting

268 The mean length of the whiting (n = 793) was 24 cm (SD: \pm 4.8). The individuals entered the upper compartment
269 less than expected if their vertical distribution was uniform (Table 4). Like cod, the separation observed for
270 whiting was length-dependent (Fig. 3). The mean vertical separation efficiency was 0.30 for individuals
271 measuring less than the MCRS of 23 cm and 0.65 for individuals measuring greater than or equal to the MCRS.
272 Individuals with a total length $<$ 20 cm had a significant preference for the lower compartment. Whiting
273 measuring \geq 20 cm were uniformly distributed in the two compartments. The proportion of individuals
274 measuring less than the MCRS was 37% and their mean size was 20 cm (SD: \pm 5.3). The undersized whiting
275 were caught in the upper compartment less than expected if their vertical distribution was uniform (Table 4).

276 *Preference for the upper compartment*

277 Haddock

278 Haddock (n = 1317) entered the upper compartment more than expected if their vertical distribution was uniform
279 (Table 4). Haddock had a significant preference for the upper compartment in the size interval (22, 31) cm (Fig.
280 3). There was a non-significant length-dependent separation efficiency for individuals $<$ 20 cm. The MCRS for
281 haddock is 27 cm. The proportion of individuals measuring less than this size was 22% and their mean size was
282 22 cm (SD: \pm 10.5). Undersized haddock were caught in the upper compartment more than expected if their
283 vertical distribution was uniform (Table 4).

284 Saithe

285 Like haddock, saithe (n = 9112) entered the upper compartment more than expected if their vertical distribution
286 was uniform (Table 4). The preference for this compartment was significant for the size interval (29, 58) cm
287 (Fig. 3). Saithe \geq 58 cm had a uniform vertical distribution when taking the proportion of the compartment
288 heights into account. The separation of saithe was weakly dependent on length, i.e. 0,12 when comparing the
289 smallest and largest size classes with $>$ 20 individuals (21 cm vs 53 cm, Table A1 in Appendix). The proportion
290 of individuals measuring less than the MCRS of 30 cm was 36% (mean size \pm SD: 25 \pm 11.7 cm). The

291 undersized saithe entered the upper compartment more than expected if their vertical distribution was uniform
292 (Table 4).

293 *Preference for the lower compartment*

294 Hake

295 Hake was caught in lower numbers than most of the other species, thus the number in the analysis was also lower
296 (n = 288). In contrast to the gadoids, hake had a clear behavioural preference for the lower compartment, where
297 most of the individuals were caught (Table 2). This preference was observed in almost all the size classes present
298 in the catch and it was statistically significant for the sizes ≤ 58 cm (Fig. 3). Length-dependent separation was
299 observed for individuals < 35 cm. Of the total hake, 18% measured less than the MCRS of 27 cm, and their mean
300 size was 23 cm (SD: ± 13.3). Undersized hake was caught much less in the upper compartment than expected if
301 their vertical distribution was uniform (Table 4).

302 Plaice

303 Plaice (n = 1357) were caught in the upper compartment less than expected if their vertical distribution was
304 uniform (Table 4). The preference for the lower compartment was statistically significant for individuals < 41 cm
305 (Fig. 3). The difference in separation efficiency between lengths was small, only 0.04 when comparing the
306 smallest and largest size classes with > 20 individuals (20 cm vs 36 cm, Table A1 in Appendix). Beyond these
307 size classes the confidence intervals widen. Of the plaice, 35% was less than the MCRS. Their mean size was 24
308 cm (SD: ± 4.8) (Table 4). These undersized fish were caught in the upper compartment less than expected if their
309 vertical distribution was uniform.

310 Witch flounder

311 Like plaice, witch flounder (n = 984) had a statistically significant preference for the lower compartment for the
312 size interval (19, 42) cm, i.e., most of the size range caught (Fig. 3). The separation efficiency did not change
313 much with length, only 0.04 when comparing the smallest and largest size classes with > 20 individuals (24 cm
314 vs 37 cm, Table A1 in Appendix). The upper compartment caught less of the 984 witch flounders than expected
315 if their vertical distribution was uniform (Table 4). No official landing size is defined by ICES, but individuals
316 measuring less than 28 cm have no market. In total, 26% were under the marketable size, and less than expected
317 if their vertical distribution was uniform were caught in the upper compartment (Table 4).

318 Lemon sole

319 The number of lemon sole analysed (n=274) was lower than most other species because, like hake, they were
320 caught in lower numbers. Preference for the lower compartment was statistically significant for the size interval
321 (20, 33) cm (Fig. 3). Like the two other flatfish species, the separation efficiency changed little (0.06) when the
322 smallest and largest size classes with > 20 individuals were compared (24 cm vs 29 cm, Table A1 in Appendix).
323 As many as 46% of the analysed lemon sole measured less than the MCRS of 26 cm. The mean size of these
324 undersized individuals was 22 cm (± 4.1), and less than expected if their vertical distribution was uniform were
325 caught in the upper compartment (Table 4).

326 Nephrops

327 The *Nephrops* analysed (n=2392) had a statistically significant preference for the lower compartment for the size
328 interval (25, 70) mm, i.e., for most of the size range found in the catch (Fig. 3). The separation efficiency
329 changed by 0.08 when the smallest and largest size classes with > 20 individuals were compared (29 mm vs 62
330 mm, Table A1 in Appendix). I.e., there was weak length-dependent vertical separation for *Nephrops*, where
331 smaller individuals had a stronger preference for the lower compartment than larger ones. The MLS comprising
332 a carapace length of 40 mm was reduced to a MCRS of 32 mm due to the implementation of the EU landing
333 obligation. Thus, the proportion of undersized individuals was reduced from 44% to 6%. Among all the analysed
334 *Nephrops* with a size greater than or equal to MCRS, 10% (CI: 7.8–11.8) could potentially be lost through the
335 larger meshes in the upper compartment (Table 4).

337 **Day/night effects**

338 We compared the length-based vertical separation curves plotted pairwise with their 95% confidence limits, and
339 a significant difference between day and night was only observed for plaice in the size interval (25–31] cm (Fig.
340 5). No significant differences in the vertical separation efficiency were detected between day and night for any of
341 the other fish species or *Nephrops* based on the data collected (Figs 4–5).

342
343 During the day, cod in the size interval [9, 45) cm had a significant preference for the lower compartment. At
344 night this preference was significant for individuals ≤ 37 cm (Fig. 4). The significant preference for the upper
345 compartment in haddock during the day was limited to individuals ≥ 49 cm. This shifted to the size interval (12,
346 31) cm at night. For saithe, the preference for upper compartment during the day was significant for the size

347 interval (24, 56) cm. During the night, this significant preference was limited to the size interval (46, 56) cm.
348 Hake ≤ 57 cm had a significant preference for the lower compartment during the day while only those in the size
349 interval (28, 34) cm had the same preference during the night. Similarly, the preference of plaice for the lower
350 compartment that was significant for the size interval (19, 39) cm during the day, was reduced to the size interval
351 [33, 38] cm at night (Fig. 5). The size interval for which witch flounder had a significant preference for the lower
352 compartment was similar during the day and night ((21, 41) cm and (20, 39] cm, respectively). This was also the
353 case for lemon sole ((19, 32) cm during the day and [23, 34) cm during the night). *Nephrops* had a significant
354 preference for the lower compartment for the size interval (26, 70) mm during the day and for individuals < 68
355 mm during the night.

357 Discussion

358 We were studying the effect of a horizontally divided codend design on the separation of different species and
359 body sizes. As the vertical separation of fish can be affected with changes in total height and/or the relative
360 height of the compartments (Fryer et al. 2017), we standardized the results across four other studies on divided
361 codends to enable comparisons (Table 5). Most studies on horizontally divided gears have presented their results
362 as an overall proportion of a species that enters a compartment. We use overall preferences, i.e. when the
363 proportion of a species that enters a compartment is larger than the relative height of that compartment, as a
364 standard measure and thus account for the relative height of the compartment at the leading edge of the separator
365 panel using the available information in the literature. Comparisons of ‘proportions’ and ‘preferences’ reveal that
366 even though the highest proportion of a species is caught in one compartment, it may prefer the other
367 compartment. This appear as conflicting information if proportions erroneously are interpreted as the overall
368 vertical distribution in the gear. To disentangle the effect of size distribution of the fished population and
369 changes in vertical distribution caused by changes in the behaviour of the species, we compared the preferences
370 of length-classes with that of the two other studies that did length-based analysis (Graham and Fryer 2006; Holst
371 et al. 2009). For other studies, interpretations are made based on information given on the size distribution of the
372 fished population.

373 Vertical distribution

374 We demonstrated that most fish could be separated from the majority of *Nephrops* in a horizontally divided
375 codend in which the upper compartment covered two-thirds of the total height and using a simple frame with two

376 vertical bars in the transition between the tapered section of the trawl and the codend. However, the overall
377 vertical distribution of fish was uniform (65.2%, CI: 60.0–69.1), i.e. the proportion of the fish caught in each
378 compartment corresponded to the proportion of the height of each compartment suggesting an improvement
379 potential of the gear. The separation efficiency was tested in the commercial demersal mixed trawl fishery in
380 Skagerrak, where eight commercial fish species were caught together with *Nephrops*. The divided codend was
381 designed to encourage fish to choose the most open path in the gear on its way to the catch accumulation in the
382 aft end. Krag et al. (2009a) suggested that fish holding in front of a frame lining the sides of the codend entrance
383 reacted to the visual stimuli created by it. Both roundfish and flatfish can be encouraged to rise from the bottom
384 due to the presence of vertical guiding bars, so the proportion that enters the upper compartment increases
385 compared with that when using a frame without vertical bars (Krag et al. 2009b). However, similar to that
386 described by Krag et al. (2009b), the separation of flatfish in the current study was not as good as that for
387 roundfish. I.e. two vertical bars spaced by 30 cm on a separator frame was not sufficient to encourage a
388 preference of flatfish for the upper compartment. This is not surprising because flatfish are strongly associated
389 with the seabed and they stay close to the bottom panel inside the trawl (Ryer 2008).

390

391 **Three separation patterns**

392 *Length-dependent vertical distribution (cod and whiting)*

393 Overall, we found that a higher proportion of cod entered the upper compartment. This is similar to that found
394 for cod in other horizontally divided codend designs (Table 5; see also He et al. 2008; Krag et al. 2009a, 2009b).
395 However, when we took the height of the compartment relative to the total height of the gear into account, we
396 found that cod had an overall preference for the small mesh lower compartment, indicating a low vertical
397 distribution in the gear. This puts a limitation to how effectively cod can be selected out and contrasted that of
398 the other studies that mostly found a preference for the upper compartment, except for one experiment that
399 resulted in a uniform distribution (Table 5). Krag et al. (2009a, 2009b) used a three compartment codend design
400 with a frame at the entrance. The upper compartment constituted 50% of the total height of the gear. He et al.
401 (2008) used a codend divided in half, but with the possibility for the fish to change compartments after the point
402 of separation. Our length-based analysis showed a strong length dependency in the separation efficiency for cod.
403 Small cod had a significant preference for the lower compartment whereas individuals measuring greater than 44
404 cm had no significant preference for any compartment. From this, an increase in the separation of small

405 individuals is necessary to select them out of the larger meshes in the upper compartment in a commercial
406 fishery. In their length-dependent analysis, Holst et al. (2009) found a preference for the upper compartment for
407 all the size groups. A visual inspection of the size distribution given in some of the studies does not suggest that
408 differences in fished populations can explain the differences in the separation of cod between studies using
409 divided codend designs. However, the frequency distribution of the size classes is not easily determined by
410 visual inspection, and so this has to be analysed further to conclude whether the differences in separation is in
411 fact due to differences in the vertical distribution of cod resulting from differences in gear design, or if it is
412 confounded by differences in fish size distributions.

413
414 Similar to cod, we found that a larger proportion of whiting entered the upper than the lower compartment while
415 it had an overall preference for the lower compartment (Table 5). In their three-compartment codend design Krag
416 et al. (2009a, 2009b) also found that most whiting entered the upper compartment, but contrary to our study, they
417 found a preference for the upper compartment that covered 50% of the total height of their gear (Table 5). Our
418 length-based analysis showed that small (≤ 19 cm) whiting had a preference for the lower compartment, while
419 larger ones had a uniform distribution. This indicates that the frame with the two vertical guiding bars were not
420 sufficient to encourage small whiting to enter the upper compartment. Holst et al. (2009) did a length-dependent
421 analysis of the data presented in Krag et al. (2009a, 2009b) using a simple frame without vertical bars (see Trial
422 1 and 2). They also found a length-dependent separation, but with a uniform distribution for small individuals ($<$
423 17 cm) and significant preference for the upper compartment for larger whiting (see Trial 2). From the length-
424 distribution it appears that the proportion of individuals <22 cm were higher in our study compared to that in
425 Holst et al. (2009) and this may have caused the stronger length-dependency observed for this size range in our
426 study. Similarly, the fished population was centred around 30 cm in Holst et al. (2009), which was higher than
427 the mean length of 24 cm (SD: ± 4.8 cm) in our study and so a higher proportion of large individuals may have
428 caused the significant preference for the upper compartment. In another similar study, however, Holst et al.
429 (2009) found no length-dependent separation (see Trial 1). This may be explained by the rather narrow size
430 range for the fished population obtained for that trial with no individuals smaller than ca. 17 cm and few
431 individuals larger than ca. 30 cm.

432

433 *Preference for the upper compartment (haddock and saithe)*

434 As expected, the largest proportion of haddock entered and had an overall preference for the upper compartment.
435 This is in line with the finding of other studies of divided codend designs (Graham and Fryer 2006; He et al.
436 2008; Krag et al. 2009a, 2009b). Despite this overall preference for the upper compartment, our length-
437 dependent analysis only showed a significant preference for this compartment for a limited size range (23-30
438 cm), while the rest of the population had a uniform distribution with a tendency of smaller individuals entering
439 the lower compartment more often. Both Graham and Fryer (2006) and Holst et al. (2009) found that most
440 classes of haddock significantly preferred the upper compartment, however the two studies report opposite size-
441 dependent separation patterns. Graham and Fryer (2006) report of few individuals > 16 cm in the catches and the
442 presence of a grid could have encouraged fish to enter the upper compartment leading to the observed positive
443 separation pattern with length.

444
445 In agreement with our findings, saithe have been found to mostly enter the upper compartment of divided
446 codends and to have a preference for this compartment (Krag et al. 2009a; Holst et al. 2009). We found that
447 individuals larger than the MCRS of 30 cm had a significant preference for the upper compartment. The
448 separation efficiency was slightly dependent on length where a lower proportion of smaller individuals entered
449 the upper compartment. Holst et al. (2009) also found that saithe significantly preferred the upper compartment,
450 but detected no length-dependent separation in the two trials using a simple separator frame. This could be due to
451 the limited size range present in the data. In the first trial, individuals measured less than 25 cm, whereas in the
452 second trial, the saithe were mainly in the size range of 40–55 cm.

453

454 *Preference for the lower compartment (hake, plaice, witch flounder, lemon sole, and Nephrops)*

455 We found that the largest proportion of hake entered the lower compartment. This compartment was also highly
456 preferred when considering its relative height. Our length-based analysis showed that the preference for the
457 lower compartment decreased with size for individuals <35 cm. In the three-compartment gear used by Krag et
458 al. (2009a) hake had a preference for the middle compartment when the relative height of the different
459 compartments was considered. However, the structure of the fished population was not given, thus it could not
460 be evaluated if the differences in vertical distribution was caused by differences in the size of the fish caught.

461 Our results suggest that to select hake out of a larger meshed upper compartment, a stronger stimulus than a
462 separator frame with two guiding bars is needed.

463
464 Plaice (mean 29 cm, SD: ± 4.3 cm) showed a significant preference for the lower compartment for most size
465 classes (15-40 cm) for which we had data. Similar size-independent separation was found in the size range of
466 10–45 cm (most individuals measured around 30 cm) when using a simple frame with two horizontal bars to
467 divide the codend into three compartments (Holst et al. 2009). The proportion of plaice entering the upper
468 compartment in our study was higher than that found for the simple frame without vertical bars in Krag et al.
469 (2009b). Although it was not sufficient to change the preference of plaice for the lower compartment as it did for
470 Krag et al. (2009b, Table 5), it suggests that plaice can be stimulated to swim into the upper panel by using
471 simple visual stimuli such as a few vertical bars in a frame. This should be investigated further to separate plaice
472 from *Nephrops* and being able to select small plaice out through the netting in the upper compartment.

473
474 Witch flounder was caught in greatest numbers in the lower compartment and also had a preference for this
475 compartment. In contrast to our study, Krag et al. (2009a) found that witch flounder were mostly caught in the
476 upper compartment, leading to an almost uniform distribution in the upper, middle, and lower compartments
477 when the height of each compartment relative to the total codend height at the point of separation was
478 considered. However, the length distribution of the fished population was not given, and thus the results cannot
479 be compared with our study.

480
481 Like the two other flatfish species, the largest overall proportion of lemon sole entered the lowest compartment
482 and was found to prefer the lower compartment. Despite the two vertical bars in the only 30 cm high frame, the
483 preference for the lower compartment was much stronger than for the 37.5 cm high lower compartment in the
484 separator frame without vertical bars in Krag et al. (2009a, 2009b). This may be caused by the differences in
485 total height of the gear at the position of the frame (90 cm in this study and 150 cm in Krag et al. 2009a, 2009b).
486 Although the presence of vertical bars do not change the preference of lemon sole, they encourage a higher
487 proportion to enter the upper compartment (Table 5). The structure of the fished population in our study were
488 similar to those in Krag et al. (2009b) (range: 10-40 cm, peak ca. 25 cm). Thus, even though it was not
489 demonstrated in our study, lemon sole, like plaice, can be stimulated to swim into the upper panel by using

490 vertical bars. Simple visual stimuli should be investigated further to identify devices that can successfully
491 separate lemon sole from *Nephrops*.

492
493 *Nephrops* showed a strong preference of *Nephrops* for the lower compartment. This agrees with reported video
494 observations of *Nephrops* entering the trawl at a low level and move passively along the bottom of the net on
495 their way to the codend (Main and Sangster 1985b; Briggs 1992). Overall, preference for the lower compartment
496 was also observed by Graham and Fryer (2006) although not as strong as in our study (Table 5) as the presence
497 of the grid seems to have encouraged *Nephrops* to enter the upper compartment. According to their length-based
498 results, as many as 40–70% of the individuals with a carapace length of 50 mm entered the upper compartment
499 and would have been lost in a commercial fishery. The length-dependent pattern found in our study was much
500 weaker and would lead to a lesser loss of valuable *Nephrops* through the net in the upper compartment in a
501 commercial fishery (11%, CI: 7.7–14.0%).

503 **Diel effects on vertical distribution**

504 Surprisingly, the observed separation of fish from *Nephrops* was similar during the day and night. We only
505 detected a significant difference for a limited size range in plaice. Fish are thought to react to the gear mainly
506 using vision (Glass and Wardle 1989; Walsh and Hickey 1993), although some studies suggest that other senses
507 may have a role when the light intensity is low (Engås and Ona 1990; Krag et al. 2010). Thus, we expected that
508 the species would not exhibit their distinct escape behaviour in the night, so there would be diel differences in
509 the vertical distribution. For example, cod and plaice, which prefer the lower compartment, have been found to
510 enter the upper compartment in significantly larger proportions in the night compared with the day (Ferro et al.
511 2007). Based on our data set, we cannot conclude whether the lack of behavioural differences between day and
512 night was explained by fish employing different types of sensory information when inside the trawl, or if the
513 light intensity was comparable throughout the diel cycle. Our study was conducted in September when there was
514 a strong contrast between day and night in terms of the light intensity. However, the fishery was conducted in
515 relatively deep waters (ca. 110–170 m, except for one shallower haul) in muddy *Nephrops* areas, which may
516 have reduced the differences in light intensity between day and night. Thus, the visual cues provided by the gear
517 may have had little effect on the behaviour of fish, which may explain the lack of diel variations.

518 **Management implications**

519 *Nephrops*-directed mixed species trawl fisheries are among the most economically important fisheries in EU
520 waters and they are known to generate one of the highest discard levels (e.g., Evans et al. 1994; Bergmann et al.
521 2002). Several different mesh sizes and selective devices have been tested and show improvements in both
522 species and size selectivity, but the proportion of unwanted catch is still relative large. (e.g. Revill et al. 2007;
523 Krag et al. 2008; Frandsen et al. 2011; Krag et al. 2015; Krag et al. 2017). The divided codend design presented
524 here separates the majority of fish from the majority of *Nephrops* and thereby enable that these, morphological
525 very different groups, can be provided with more suitable mesh sizes and subsequent size selectivity aiding
526 fishermen in complying with the European Landing Obligation. Furthermore, less damage as well as
527 improvements in the catch quality and fish welfare can be obtained (Karlsen et al. 2015). The 10% of *Nephrops*
528 that we analysed measuring greater than or equal to the MCRS in the upper compartment would probably be lost
529 in a commercial fishery if a large mesh netting is used to optimize the selection of fish. However, this loss may
530 be compensated for by reducing the loss of *Nephrops* with a carapace length greater than or equal to 32 mm by
531 using a small mesh lower compartment. The possibility of having small meshes in parts of the gear challenges
532 the current technical legislation, which imposes a lower limit on the mesh size (EU 2016). The reduction from 40
533 mm MLS to 32 mm MCRS for *Nephrops* in Skagerrak makes this even more important because the number of
534 valuable individuals that may be lost using a 90 mm diamond mesh codend is increased.

535
536 We assumed that our averaged length-based vertical separation curves were based on representative samples to
537 determine how the vertical separation would perform on average in a commercial fishery, and we used them to
538 identify and evaluate the separation efficiency for different size classes of various fish species. Based on our
539 results, large reductions of undersized haddock, saithe and whiting can be obtained in the *Nephrops* directed
540 fisheries. The undersized cod and hake, whiting, plaice, and lemon sole as well as witch flounder below the
541 marketable size were caught in the lower compartment more than be expected if their vertical distribution was
542 uniform. The proportions of these species lost in the codend selection depend on the mesh size used in the lower
543 compartment. Due to the flexible design of the horizontally divided codend used in our study, the codends can be
544 changed between hauls and adjusted according to the actual conditions in the fishing grounds as well as the catch
545 profile observed in the last haul. The size range of undersized fish that cannot escape through the meshes in the
546 lower compartment must be considered further in order to stimulate them to swim into the upper compartment to
547 escape through larger meshes. Fish react to light and colour, or contrast stimuli (Glass et al. 1995; He et al.

548 2008). A recent study using a similar codend design to that in our study confirms that fish react to light stimuli
 549 inside the gear, but the separation of fish and *Nephrops* was not improved (Melli et al. 2018). Thus, a better
 550 understanding of how stimuli that affect the behaviour of fish inside a trawl is needed to improve the vertical
 551 separation further. A horizontally divided codend is simple to use under commercial conditions and can improve
 552 the species and size selectivity in *Nephrops*-directed mixed species fisheries and probably in other fisheries.

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672 **Tables**

673 Table 1 Operational conditions. hh: hours, mm: minutes.

Haul	Day (D)/ Night (N)	Towing time (hh:mm)	Wind speed (m/s)	Wave height (m)	Towing speed (knots)	Fishing depth (m)	Trawl door distance (m)	Wire Length (m)
1	N	02:50	5	0–1.0	2.5	56	83	235
3	D	02:23	8	0–1.0	2.6	113	100	377
5	N	02:15	3	0–0.5	2.6	132	95	471
7	D	02:30	4	0–0.5	2.6	141	100	424
8	N	03:30	5	0–1.0	2.6	122	100	424
10	D	01:15	3	0–0.5	2.6	132	100	424
11	N	03:15	2	0	2.7	132	100	424
13	D	02:23	4	0–0.5	2.7	141	100	471
14	N	02:45	4	0–0.5	2.6	141	100	471
16	D	03:00	4	0–0.5	2.7	141	100	471
17	N	02:45	5	0–0.5	2.6	141	97	424
20	D	02:35	5	0–0.5	2.7	141	100	471
21	N	02:30	8	0–0.5	2.6	169	90	518
24	N	02:40	8	0–0.5	2.6	160	100	471

674

676 Table 2. Fit statistics.

Species	All hauls			Day-hauls			Night-hauls		
	<i>p</i> -value	Deviance	DOF	<i>p</i> -value	Deviance	DOF	<i>p</i> -value	Deviance	DOF
Cod	0.0451	100.35	78	0.1121	90.15	75	0.0269	85.22	62
Whiting	0.1916	33.17	27	NA	NA	NA	NA	NA	NA
Haddock	0.4779	44.86	45	0.8364	34.85	44	0.1477	36.94	29
Saithe	0.0065	61.75	37	0.1912	42.08	35	0.0342	52.92	36
Hake	0.7711	29.47	36	0.7564	39.04	46	0.2882	30.59	27
Plaice	0.1708	31.57	25	0.0294	38.70	24	0.0853	27.91	19
Witch flounder	0.2456	27.25	23	0.0624	34.20	23	0.5766	17.20	19
Lemon sole	0.5134	18.14	19	0.3023	19.47	17	0.4297	15.30	15
Nephrops	0.1705	53.90	45	0.1511	46.96	38	0.3784	44.21	42

677

678

679 Table 3. Numbers of individuals in the upper and lower compartments in each haul. D: day haul; N: night haul.

Haul	D/N	Cod		Whiting		Haddock		Saithe		Hake		Plaice		Witch flounder		Lemon sole		<i>Nephrops</i>	
		Upper	Lower	Upper	Lower	Upper	Lower	Upper	Lower	Upper	Lower	Upper	Lower	Upper	Lower	Upper	Lower	Upper	Lower
1	N	83	88	168	101	50	11	0	0	3	18	171	83	6	1	19	10	115	1157
3	D	256	248	209	171	45	53	139	44	2	12	23	20	9	9	6	4	16	163
5	N	75	63	0	0	4	3	456	185	1	0	14	12	20	28	1	2	2	6
7	D	131	122	21	15	20	11	76	28	5	16	37	62	37	46	11	17	12	130
8	N	249	134	2	0	33	7	783	544	14	9	42	23	20	22	7	2	13	26
10	D	94	97	9	18	63	58	221	102	11	17	44	78	17	22	13	36	2	33
11	N	126	106	0	0	49	17	1446	263	3	5	91	107	50	84	20	36	2	5
13	D	232	205	23	6	279	46	1100	173	12	34	38	104	33	56	11	20	6	156
14	N	125	69	2	0	54	17	691	172	10	6	38	34	35	52	2	9	1	11
16	D	239	235	27	5	212	37	832	186	14	34	44	94	15	52	6	20	18	171
17	N	81	88	1	0	7	3	719	195	1	2	37	62	19	40	2	1	0	1
20	D	163	164	15	5	215	30	140	27	17	44	28	56	30	61	11	23	37	304
21	N	42	55	0	0	0	0	160	118	4	6	5	3	71	86	1	1	5	16
24	N	58	60	1	1	3	1	218	94	0	2	7	8	24	46	4	3	0	3
Total		1954	1734	478	322	1034	294	6981	2131	97	205	619	746	386	605	114	184	229	2182
Analysed		1954	1734	472 _l	321 _l	1027	290	6981	2131	92 _l	196 _l	614	743	380	604	99 _l	175 _l	225	2167

680 _lBootstrap was based on only 7–10 of the 14 hauls because hauls containing <10 individuals summed over the upper and lower compartments were not included.

681 Table 4. Proportions (%) of fish and *Nephrops* entering the upper compartment of the horizontally divided
 682 codend. SD: standard deviation. CI: Efron 95% confidence limits. MCRS: minimum conservation reference size
 683 for Skagerrak. *Market: no MCRS for the given species and sizes under the given limit have no market. Fish
 684 lengths: cm; *Nephrops* lengths: mm.

Species	All lengths		MCRS (*Market)	<MCRS/*Market	
	Mean length (±SD, range)	% upper (CI range)		Mean length (±SD, range)	% upper (CI range)
All fish	35 (±10.1; 9–104)	65.2 (60.0–69.1)	NA	NA	NA
Roundfish	38 (±16.8; 9–104)	69.3 (63.0–73.9)	NA	NA	NA
Flatfish	29 (±4.8; 11–49)	41.8 (35.8–49.2)	NA	NA	NA
Cod	39 (±12.5; 9–96)	53.0 (50.3–56.2)	30	25 (±14.0; 9–29)	39.2 (29.5–48.9)
Whiting	24 (±4.8; 10–47)	59.5 (54.7–70.7)	23	20 (±5.3; 10–22)	54.9 (41.5–64.0)
Haddock	31 (±8.0; 11–64)	78.0 (64.9–84.6)	27	22 (±10.5; 11–26)	70.9 (57.1–85.1)
Saithe	36 (±9.3; 20–62)	76.6 (69.3–82.2)	30	25 (±11.7; 20–29)	71.6 (61.3–81.8)
Hake	36 (±10.0; 14–104)	31.9 (25.3–41.2)	27	23 (±13.3; 14–26)	20.8 (9.3–41.4)
Plaice	29 (±4.3; 15–49)	45.2 (36.4–54.5)	27	24 (±4.8; 15–26)	46.5 (33.4–57.8)
Witch flounder	32 (±4.6; 19–46)	38.6 (34.7–42.0)	28,	26 (±5.9; 19–27)	35.5 (25.4–45.8)
Lemon sole	26 (±4.4; 11–39)	36.1 (29.4–45.1)	26	22 (±4.1; 11–25)	44.1 (25.5–58.9)
<i>Nephrops</i>	43 (±9.0; 21–72)	9.4 (7.9–12.1)	32	44 (±8.6; 32–72)*	9.6 (7.8–11.8)*
<i>Day</i>					
All fish	34 (±10.4; 9–104)	63.4 (54.2–69.1)	NA	NA	NA
Roundfish	35 (±10.9; 9–104)	68.3 (57.9–74.4)	NA	NA	NA
Flatfish	30 (±4.8; 12–49)	34.6 (30.3–40.4)	NA	NA	NA
Cod	40 (±12.8; 9–93)	51.0 (50.1–52.0)	30	26 (±14.3; 9–29)	33.5 (21.8–43.5)
Haddock	32 (±6.0; 11–64)	78.0 (62.1–85.9)	27	22 (±10.5; 11–26)	66.4 (48.5–84.5)
Saithe	35 (±9.6; 20–62)	81.7 (72.0–85.1)	30	25 (±9.6; 20–29)	79.7 (66.9–84.8)
Hake	37 (±10.4; 16–104)	28.0 (24.2–31.8)	27	24 (±12.6; 16–26)	22.2 (7.1–47.8)
Plaice	29 (±4.3; 15–49)	34.1 (29.9–40.5)	27	24 (±5.3; 15–26)	34.5 (26.4–45.6)
Witch flounder	32 (±4.6; 19–46)	36.4 (30.6–43.0)	28*	26 (±6.6; 19–27)	28.9 (17.2–46.3)
Lemon sole	26 (±4.0; 12–39)	32.6 (27.9–40.0)	26	23 (±3.7; 19–25)	33.8 (15.9–51.9)
<i>Nephrops</i>	48 (±9.2; 28–71)	8.7 (5.8–10.2)	32	49 (±8.8; 32–71)*	9.0 (6.2–11.0)*
<i>Night</i>					
All fish	36 (±9.7; 10–96)	66.8 (60.8–71.3)	NA	NA	NA
Roundfish	37 (±10.0; 10–104)	70.1 (62.7–76.5)	NA	NA	NA
Flatfish	29 (±4.8; 11–45)	47.8 (39.3–57.3)	NA	NA	NA
Cod	37 (±12.0; 10–96)	55.9 (49.1–60.9)	30	25 (±13.4; 10–29)	46.8 (32.7–56.8)
Haddock	28 (±7.6; 13–64)	77.8 (74.4–81.6)	27	21 (±9.4; 13–26)	83.5 (72.5–96.4)
Saithe	38 (±8.9; 20–60)	74.0 (63.8–81.2)	30	25 (±12.7; 20–29)	65.3 (58.8–78.4)
Hake	35 (±9.7; 14–52)	44.3 (22.6–61.5)	27	21 (±14.5; 14–26)	17.6 (3.3–100.0)
Plaice	28 (±4.2; 17–41)	54.9 (43.6–64.3)	27	24 (±4.4; 17–26)	53.1 (33.3–66.4)
Witch flounder	31 (±4.5; 20–45)	40.0 (36.3–43.5)	28*	26 (±5.5; 20–27)	38.7 (26.6–50.4)
Lemon sole	24 (±4.8; 11–33)	42.7 (18.2–65.5)	26	21 (±4.6; 11–25)	60.0 (42.0–77.8)
<i>Nephrops</i>	39 (±6.5; 21–72)	10.0 (9.0–31.0)	32	40 (±6.1; 32–72)*	10.2 (8.4–34.0)*

685 ₁Analysis of individuals \geq MCRS.

686 Table 5. Species specific preference (proportion, %) observed in different studies. Preference for a compartment:

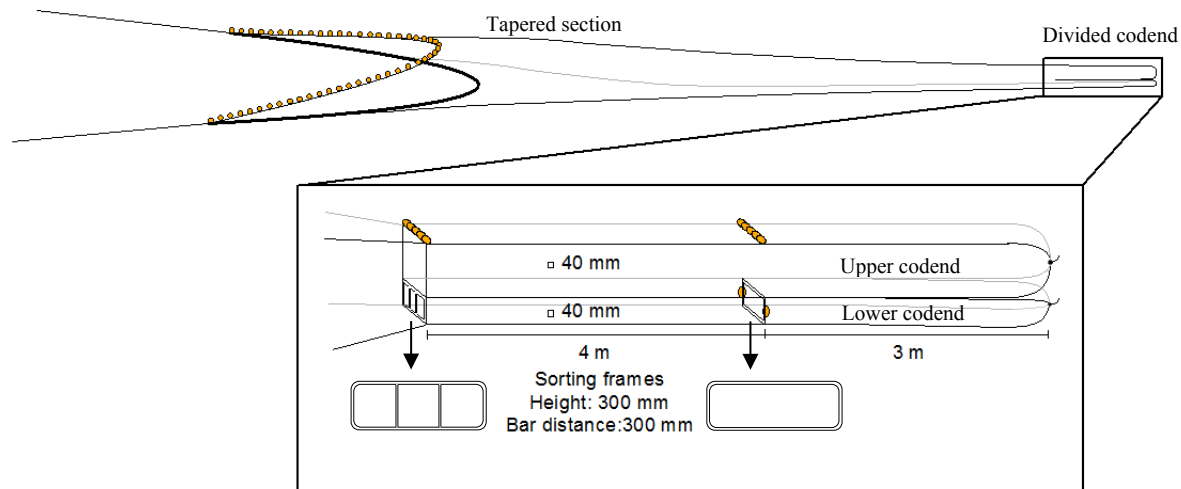
687 >1. Uniform distribution = 1.

Species	Upper	Middle	Lower	Main population	Divided codend design	Reference
Cod	0.79 (53%)	NA	1.39 (46%)	10-16 cm, 20-58 cm	Frame, two vertical bars	This study
	1.14 (57%)	1.20 (30%)	0.52 (13%)	22-55 cm	Simple frame ₇	Holst et al. (2009) ₂
	1.08 (54%)	1.12 (28%)	0.72 (18%)	18-30 cm	Simple frame ₇	Krag et al. (2009b)
	1.34 (67%)	0.76 (19%)	0.56 (14%)	15-33 cm	Complex frame ₃	Krag et al. (2009b)
	1.28 (64%)	NA	0.92 (46%)	Not given	Separation panel ₄	He et al. (2008)
	1.00 (50%)	NA	1.00 (50%)	Not given	Ropes ₅	He et al. (2008)
Whiting	0.89 (60%)	NA	1.23 (37%)	18-33 cm	Frame, two vertical bars	This study
	1.54 (77%)	0.64 (16%)	0.28 (7%)	22-38 cm	Simple frame ₇	Holst et al. (2009) ₂
	1.82 (91%)	0.32 (8%)	0.04 (1%)	16-27 cm	Simple frame ₇	Krag et al. (2009b)
	1.90 (65%)	0.16 (4%)	0.04 (1%)	16-25 cm	Complex frame ₃	Krag et al. (2009b)
Haddock	1.16 (78%)	NA	0.67 (22%)	12-16 cm, 23-50 cm	Frame, two vertical bars	This study
	1.46 (73%)	0.88 (22%)	0.20 (5%)	12-20 cm, 30-42 cm	Simple frame ₇	Krag et al. (2009a)
	1.74 (87%)	0.32 (8%)	0.16 (4%)	18-30 cm	Simple frame ₇	Krag et al. (2009b)
	1.56 (78%)	0.60 (15%)	0.28 (7%)	18-32 cm	Complex frame ₃	Krag et al. (2009b)
	0.94-1.90 (47-95%)	NA	0.10-1.06 (5-53%)	Few > 16 cm	Grid 25/150	Graham and Fryer (2006)
	1.10-1.90 (55-95%)	NA	0.10-0.90 (5-45%)	Few > 16 cm	Grid 30/150	Graham and Fryer (2006)
	1.14-1.86 (57-93%)	NA	0.14-0.86 (7-43%)	Few > 16 cm	Grid 30/200	Graham and Fryer (2006)
	1.80 (90%)	NA	0.20 (10%)	Not given	Separation panel ₄	He et al. (2008)
Saithe	1.84 (92%)	NA	0.16 (8%)	Not given	Ropes ₅	He et al. (2008)
	1.14 (77%)	NA	0.71 (23%)	22-30 cm, 35-52 cm	Frame, two vertical bars	This study
	1.64 (82%)	0.48 (12%)	0.20 (5%)	40-55 cm	Simple frame ₇	Holst et al. (2009) ₂
Hake	1.74 (87%)	0.36 (9%)	0.20 (5%)	18-27 cm	Simple frame ₇	Holst et al. (2009)
	0.48 (32%)	NA	2.06 (68%)	20-55 cm	Frame, two vertical bars	This study
Plaice	0.80 (40%)	1.48 (37%)	0.92 (23%)	Not given	Simple frame ₇	Krag et al. (2009a)
	0.67 (45%)	NA	1.66 (55%)	18-38 cm	Frame, two vertical bars	This study
	0.54 (27%)	1.08 (27%)	1.88 (47%)	20-40 cm	Simple frame ₇	Krag et al. (2009b)
Witch flounder	1.08 (54%)	0.84 (21%)	1.00 (25%)	21-37 cm	Complex frame ₃	Krag et al. (2009b)
	0.58 (39%)	NA	1.86 (61%)	23-40 cm	Frame, two vertical bars	This study
	0.90 (45%)	1.08 (27%)	1.16 (29%)	Not given	Simple frame ₇	Krag et al. (2009a)
Lemon sole	0.54 (36%)	NA	1.94 (64%)	13-33 cm	Frame, two vertical bars	This study
	0.78 (39%)	1.40 (35%)	1.04 (26%)	Not given	Simple frame ₇	Krag et al. (2009a)
	0.66 (33%)	1.56 (39%)	1.16 (29%)	15-32 cm	Simple frame ₇	Krag et al. (2009b)
	1.00 (50%)	1.24 (31%)	0.76 (19%)	15-34 cm	Complex frame ₃	Krag et al. (2009b)
<i>Nephrops</i>	0.14 (9%)	NA	2.75 (91%)	27-65 mm	Frame,	This study

0.32 (16%)	NA	1.68 (84%)	Not given	two vertical bars Grid 25/150	Graham and Fryer (2006)
0.28 (14%)	NA	1.72 (86%)	Not given	Grid 30/150	Graham and Fryer (2006)
0.26 (13%)	NA	1.74 (87%)	Not given	Grid 30/200	Graham and Fryer (2006)

688 ₁Simple frame: Frame with two horizontal bars
689 ₂Holst et al. (2009) made a length-based analysis of the data reported by Krag et al. (2009a).
690 ₃Complex frame: Frame with two horizontal and two vertical bars
691 ₄Separation panel: Black and netting separation panels, opening, black tunnel, separation panel
692 ₅Ropes: Black separation panel, ropes, opening, black tunnel, separation panel
693

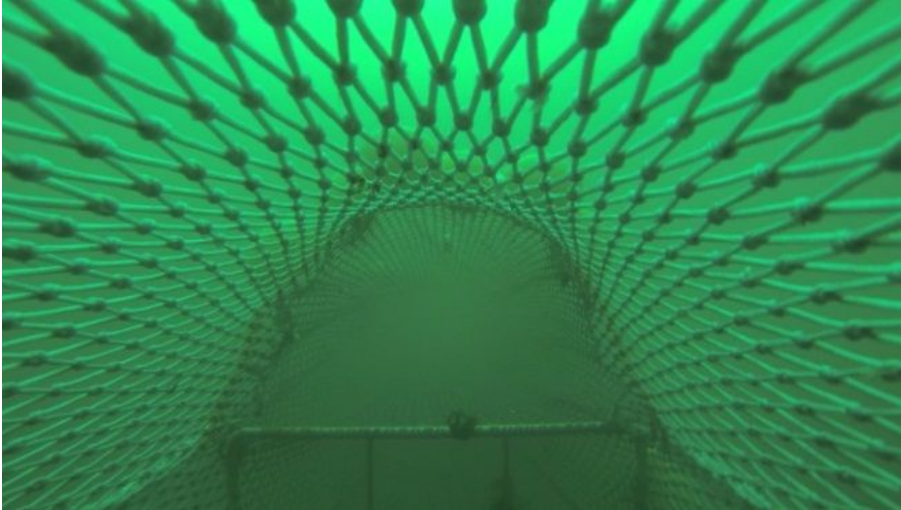
694 **Figures**



695

696 Fig. 1. Schematic illustrations of the trawl gear. The enlarged section shows the upper and lower compartments
 697 of the non-selective horizontally divided codend (40 mm mesh size), and the two frames used to separate fish
 698 from *Nephrops* (frame with vertical bars) and to keep the lower compartment open (both frames).

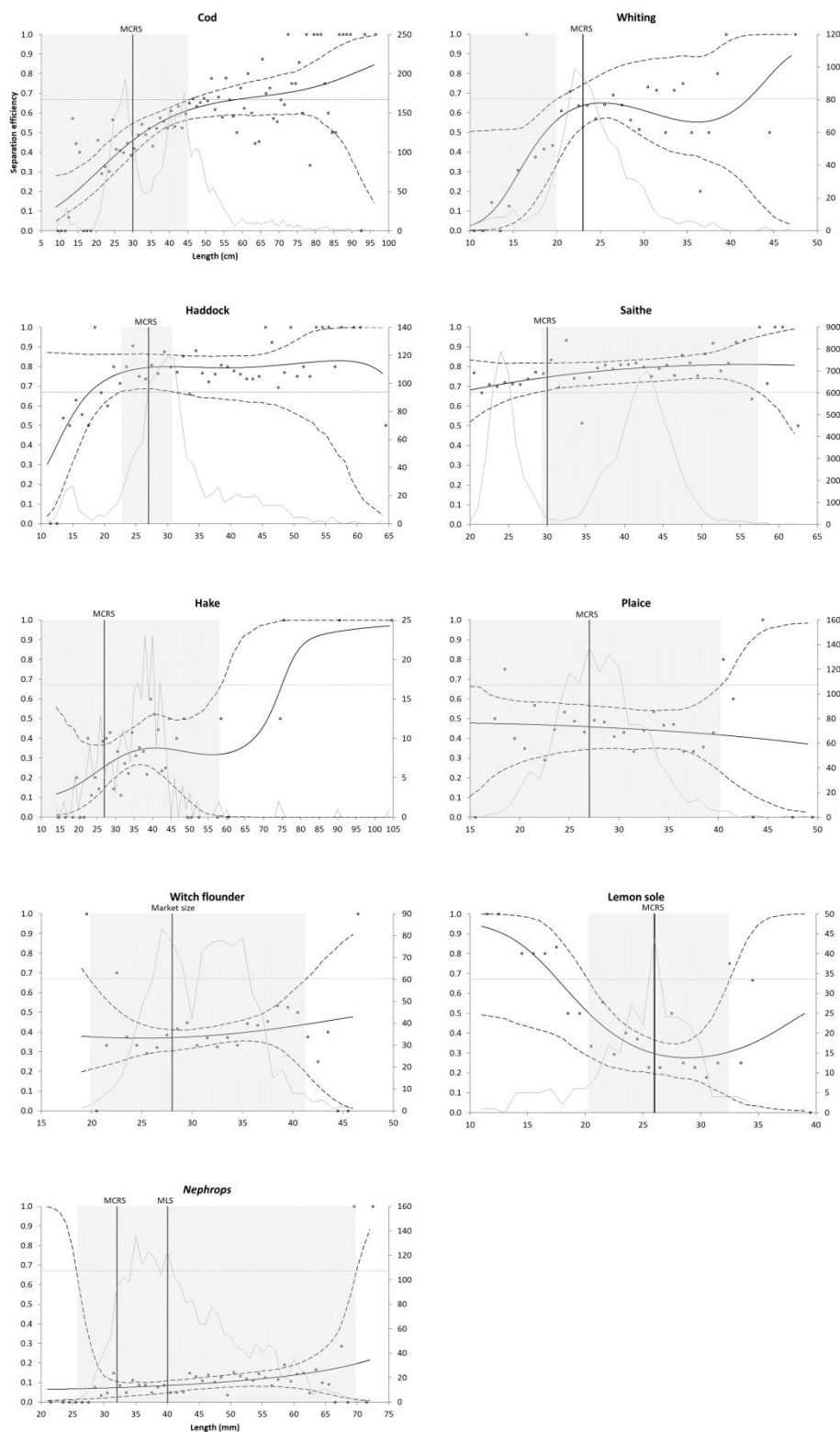
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701 Fig. 2. The opening of the entrance of the upper compartment of the vertically divided codend used in the
702 fishery. The steel frame defining the opening into the lower compartment comprised about one-third of the total
703 height at the codend entrance, whereas the opening into the upper compartment comprised the remaining two-
704 thirds. Note the square mesh orientation in the codend section.

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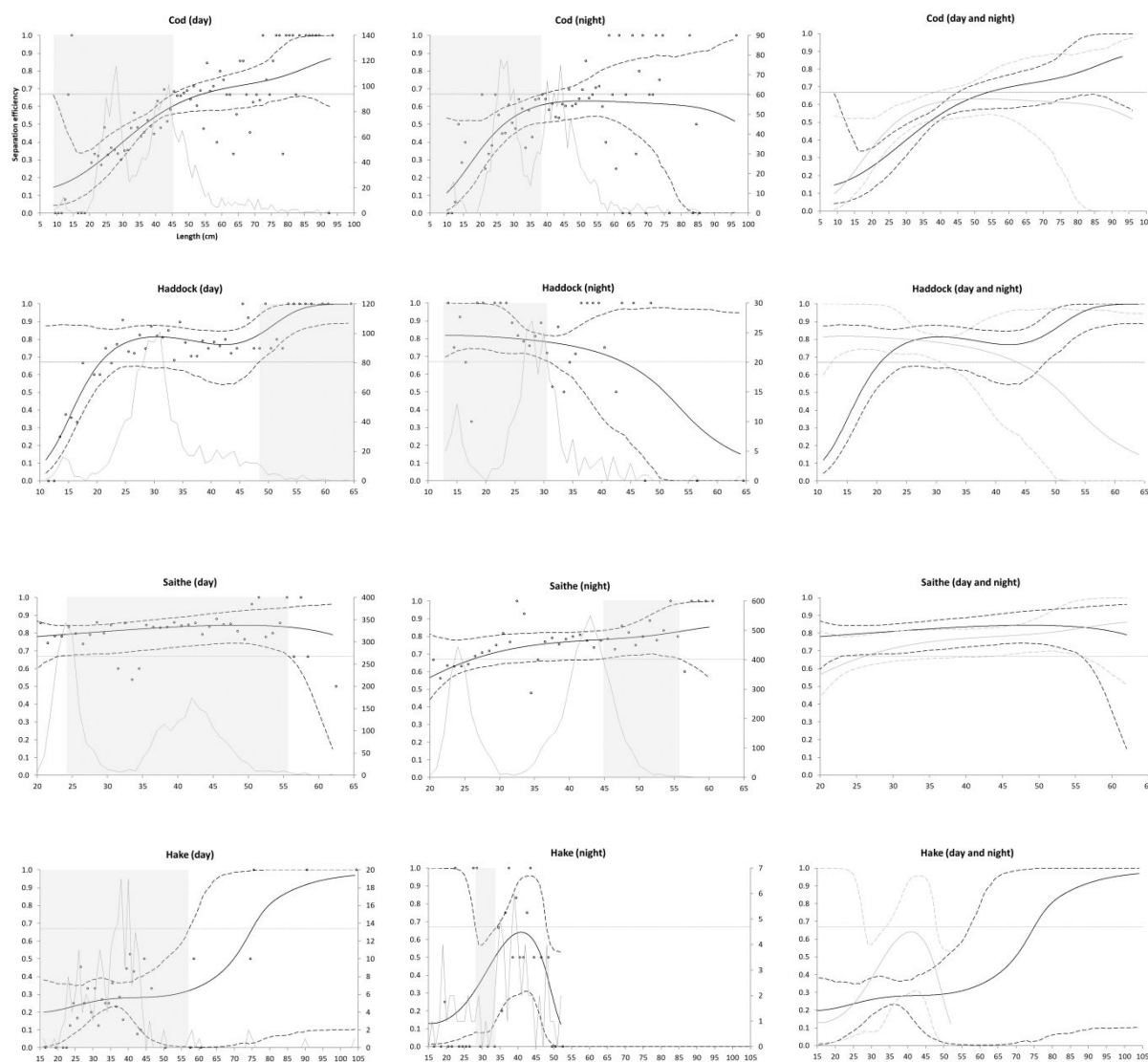
711 Fig. 3. Length-dependent vertical separation of the nine commercial species observed in the separated codend.

712 Solid line: estimated catch proportion for the species in the upper compartment (Model 3). Broken lines: 95%

713 confidence limits. Circles: observed values. Horizontal grey line: separation efficiency of 0.67; both confidence

714 limits >0.67 or <0.67 indicate that the vertical separation differed significant from that expected based on a

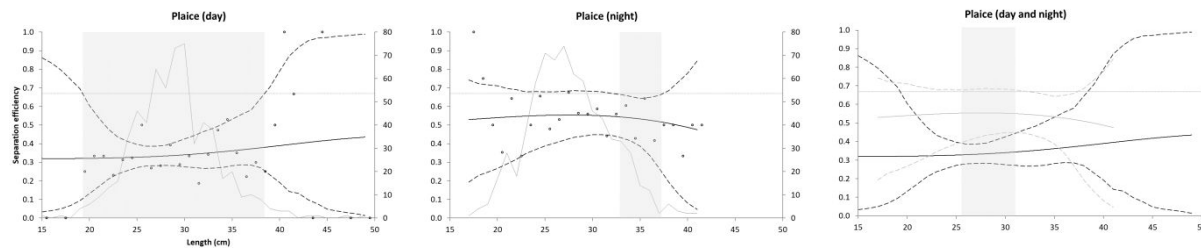
715 uniformly vertical distribution at the point of the separator frame in the gear. Grey line: population. Grey area:
716 length range with a significant preference for a compartment. MCRS: minimum conservation reference size.
717



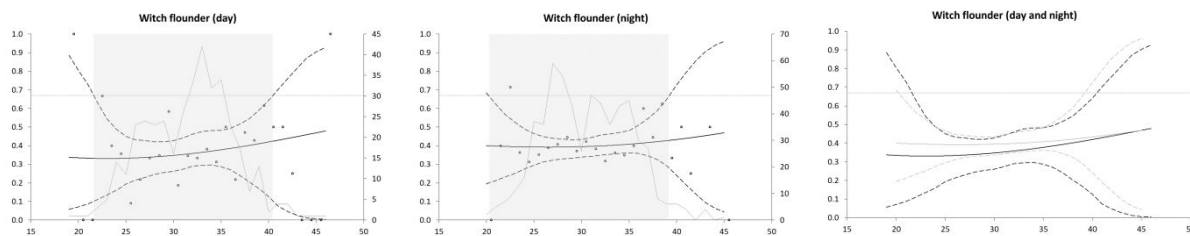
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722 Fig. 4. Length-dependent vertical separation of roundfish. Solid line: estimated catch proportion for species in
723 the lower compartment (Model 3). Broken lines: 95% confidence limits. Circles: observed values. Grey line:
724 population. Horizontal grey line: separation efficiency of 0.67; confidence limits >0.67 or <0.67 (grey areas)
725 indicate that the vertical separation differed significantly from that expected based on a uniformly vertical
726 distribution at the point of the separator frame in the gear.

727

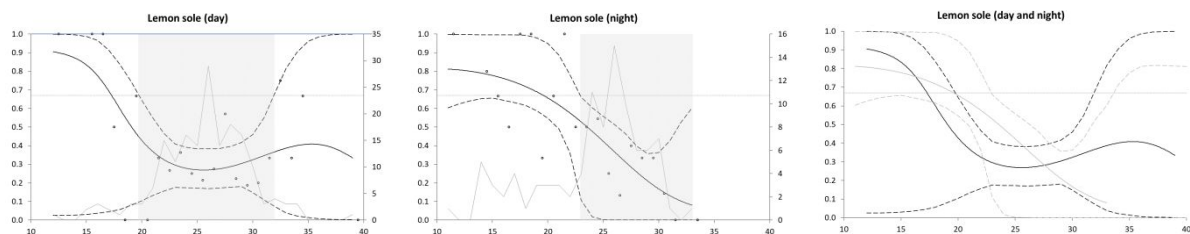
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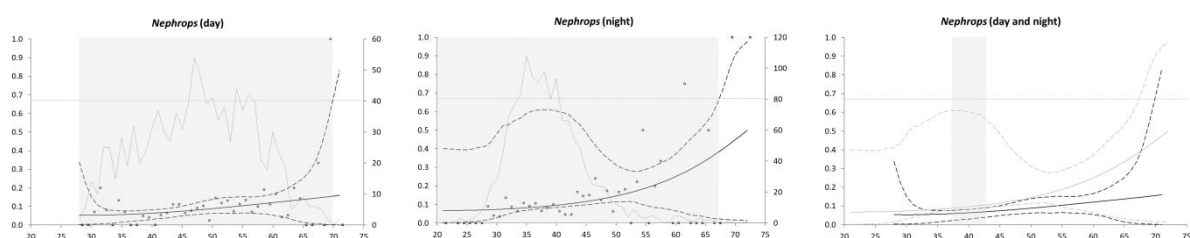
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731



732 Fig. 5. Length-dependent vertical separation of flatfish and *Nephrops*. Solid line: estimated catch proportion for
 733 species in the lower compartment (Model 3). Broken lines: 95% confidence limits. Circles: observed values.
 734 Grey line: population. Horizontal grey line: separation efficiency of 0.67; confidence limits >0.67 or <0.67
 735 indicate that the vertical separation differed significantly from that expected based on a uniformly vertical
 736 distribution at the point of the separator frame in the gear. Grey area: length range with a significant preference
 737 for the upper or lower compartment (left and middle columns), or significant difference between day and night
 738 (right columns).

739

1 **Appendix 1**

2 Table A1. Values (confidence interval) for the mean estimated length-dependent separation given as proportion of individuals that enters the upper compartment from all
 3 hauls pooled. The size groups are given in 5-cm increments. Bold values are size groups covered by the experimental data obtained from the cruise.

Length	Cod	Whiting	Haddock	Saithe	Hake	Plaice	Witch flounder	Lemon sole	<i>Nephrops</i>
10	0.13 (0.06–0.28)	0.03 (0.00–0.51)	0.25 (0.02–0.88)	0.59 (0.10–0.90)	0.10 (0.01–0.62)	0.48 (0.01–0.73)	0.42 (0.15–0.97)	0.95 (0.50–1.00)	0.08 (0.01–1.00)
15	0.21 (0.13–0.32)	0.25 (0.04–0.52)	0.55 (0.31–0.86)	0.64 (0.23–0.88)	0.12 (0.01–0.53)	0.48 (0.11–0.66)	0.40 (0.16–0.93)	0.82 (0.43–0.98)	0.07 (0.01–1.00)
20	0.29 (0.20–0.39)	0.56 (0.34–0.67)	0.73 (0.61–0.86)	0.68 (0.52–0.83)	0.17 (0.04–0.40)	0.47 (0.28–0.59)	0.38 (0.21–0.66)	0.52 (0.29–0.69)	0.07 (0.01–1.00)
25	0.38 (0.29–0.48)	0.65 (0.57–0.79)	0.79 (0.68–0.86)	0.72 (0.63–0.82)	0.23 (0.11–0.37)	0.46 (0.33–0.57)	0.37 (0.28–0.44)	0.32 (0.21–0.39)	0.07 (0.01–0.79)
30	0.46 (0.39–0.55)	0.61 (0.48–0.87)	0.80 (0.68–0.86)	0.75 (0.68–0.82)	0.29 (0.20–0.40)	0.45 (0.35–0.55)	0.38 (0.32–0.41)	0.28 (0.15–0.40)	0.07 (0.02–0.13)
35	0.52 (0.47–0.59)	0.56 (0.38–0.89)	0.80 (0.64–0.85)	0.77 (0.70–0.82)	0.33 (0.26–0.46)	0.44 (0.35–0.54)	0.40 (0.36–0.46)	0.36 (0.03–0.95)	0.08 (0.03–0.10)
40	0.58 (0.53–0.63)	0.60 (0.30–0.97)	0.79 (0.63–0.85)	0.79 (0.72–0.83)	0.35 (0.25–0.52)	0.42 (0.24–0.65)	0.43 (0.26–0.61)	0.53 (0.01–1.00)	0.08 (0.05–0.11)
45	0.61 (0.57–0.67)	0.81 (0.07–1.00)	0.80 (0.62–0.86)	0.80 (0.73–0.84)	0.34 (0.17–0.50)	0.39 (0.08–0.96)	0.47 (0.03–0.86)	0.58 (0.00–1.00)	0.09 (0.07–0.12)
50	0.64 (0.58–0.70)	0.94 (0.01–1.00)	0.81 (0.56–0.93)	0.81 (0.74–0.86)	0.33 (0.08–0.50)	0.37 (0.02–0.99)	0.51 (0.00–0.97)	0.56 (0.00–1.00)	0.11 (0.08–0.14)
55	0.66 (0.59–0.72)	0.90 (0.00–1.00)	0.83 (0.46–0.99)	0.81 (0.72–0.92)	0.32 (0.02–0.57)	0.34 (0.00–0.99)	0.56 (0.00–0.99)	0.56 (0.00–1.00)	0.12 (0.08–0.16)
60	0.67 (0.59–0.75)	0.81 (0.00–1.00)	0.82 (0.17–1.00)	0.81 (0.58–0.98)	0.32 (0.00–0.74)	0.30 (0.00–0.99)	0.61 (0.00–0.99)	0.56 (0.00–1.00)	0.14 (0.07–0.19)
65	0.68 (0.59–0.77)	0.80 (0.00–1.00)	0.73 (0.02–1.00)	0.80 (0.29–1.00)	0.36 (0.00–0.92)	0.28 (0.00–0.99)	0.65 (0.00–0.99)	0.56 (0.00–1.00)	0.16 (0.04–0.28)
70	0.70 (0.59–0.79)	0.80 (0.00–1.00)	0.49 (0.00–1.00)	0.78 (0.09–1.00)	0.46 (0.00–0.98)	0.26 (0.00–0.99)	0.69 (0.00–0.99)	0.56 (0.00–1.00)	0.20 (0.01–0.68)
75	0.71 (0.60–0.81)	0.80 (0.01–1.00)	0.41 (0.00–1.00)	0.75 (0.04–1.00)	0.67 (0.00–1.00)	0.24 (0.00–0.99)	0.71 (0.00–0.99)	0.56 (0.00–1.00)	0.25 (0.00–0.99)
80	0.73 (0.58–0.87)	0.80 (0.01–1.00)	0.40 (0.00–1.00)	0.70 (0.02–1.00)	0.86 (0.00–1.00)	0.22 (0.00–0.99)	0.72 (0.00–0.99)	0.56 (0.00–1.00)	0.32 (0.00–1.00)
85	0.76 (0.50–0.93)	0.80 (0.01–1.00)	0.39 (0.00–1.00)	0.64 (0.01–1.00)	0.92 (0.00–1.00)	0.21 (0.00–0.98)	0.73 (0.00–0.99)	0.56 (0.00–1.00)	0.40 (0.00–1.00)
90	0.80 (0.36–0.97)	0.80 (0.01–1.00)	0.39 (0.00–1.00)	0.57 (0.00–1.00)	0.94 (0.00–1.00)	0.21 (0.00–0.98)	0.74 (0.00–0.99)	0.56 (0.00–1.00)	0.47 (0.00–1.00)
95	0.84 (0.18–0.99)	0.80 (0.02–1.00)	0.39 (0.00–1.00)	0.51 (0.00–1.00)	0.95 (0.00–1.00)	0.20 (0.00–0.98)	0.74 (0.00–0.99)	0.56 (0.00–1.00)	0.53 (0.00–1.00)
100	0.87 (0.05–1.00)	0.80 (0.02–1.00)	0.39 (0.00–1.00)	0.46 (0.00–1.00)	0.96 (0.00–1.00)	0.20 (0.00–0.98)	0.75 (0.00–0.99)	0.56 (0.00–1.00)	0.59 (0.00–1.00)

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