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Published in:
Canadian Journal of Fisheries and Aquatic Sciences

Link to article, DOI:
10.1139/cjfas-2018-0313

Publication date:
2019

Document Version
Peer reviewed version

Citation (APA):
Karlsen, J. D., Krag, L. A., Herrmann, B., & Lund, H. S. (2019). Using vertical distribution to separate fish from crustaceans in a mixed species trawl fishery. *Canadian Journal of Fisheries and Aquatic Sciences*, *76*(10), 1781-1794. https://doi.org/10.1139/cjfas-2018-0313

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

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Abstract

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

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

Introduction

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

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

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

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

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

Materials and methods

Gear design and sea trials

The experiment used a codend made of four net panels. The diamond mesh netting (40 mm mesh made of 1.8 mm polyethylene twine) was turned 45 degrees and mounted as square meshes to the tapered section to obtain more stable mesh geometry and to maximize the water flow through the small meshes. The codend was divided into upper and lower compartments by a horizontal net panel. In the aft end, the codend was split to give separate collecting bags for the two compartments that eased handling during hauling (Fig. 1, enlarged section). The entrance of the upper compartment was about 60 cm high and comprised two-thirds of the total height of the gear. The height of the lower compartment was fixed to 30 cm by a frame made from 20 mm stainless steel pipes mounted at its entrance, and comprised the remaining one-third of the total height. The frame had two vertical guide bars placed 30 cm apart to encourage fish to swim into the upper compartment. A similar frame without the vertical bars was mounted 4 m aft of the compartment entrance to aid full opening in the lower compartment. Five 1-L floats were attached across the top panel above both frames to ensure good opening in the upper compartment and to compensate for the weight of the frames (Fig. 1). To further optimize the catch separation, the foremost frame was placed in the transition between the tapered and non-tapered section of the gear, where the inclination of the bottom netting of the trawl ended (Fig. 1). At this point, we expected *Nephrops* to be closer to the bottom netting panel in the trawl than the untapered codend section. Measurements of the codend mesh size were conducted using dry netting before sea trials with OMEGA mesh gauge (Fonteyne et al., 2005).

The experiment was conducted aboard the commercial trawler FN-136 Tove Kajgaard (162 BT, 22 m, 299 kW) using a three-wire towing rig. The codend was attached to the vessel's commercial trawl used in the mixed species *Nephrops*-directed fishery. The trawl had a 47.5 m floatline and the groundgear measured 54.5 m. The circumference comprised 500 meshes (80 mm diamond) and the headline height was ca. 2 m. Fishing was conducted during day and night hours from 23 September to 1 October, 2013, in commercial fishing grounds in Skagerrak. To separate the day and night tows, the day tows were performed in the time interval between one hour after sunrise to one hour before sunset, and night tows from one hour after sunset until one hour before sunrise. The overall geometry of the towing rig was monitored continuously using double spread sensors (Marport) and the values were recorded every 15 min. The geometry of the entrance of the upper compartment was monitored by underwater video recordings. The camera (GoPro Hero 3+) was attached to the top panel about 1.5 m in front of the entrance of the upper compartment facing towards the entrance of the divided codend. The haul time was less than that normally used in the commercial fishery to avoid the risk of large catches reaching the separation point of the small mesh non-selective codend, thereby mixing the catches in the two compartments. The catches from the two compartments were kept separate during handling and measurements. The total lengths of cod, whiting (*Merlangius merlangus*), haddock (*Melanogrammus aeglefinus*), saithe (*Pollachius virens*), hake (*Merluccius merluccius*), plaice (*Pleuronectes platessa*), witch flounder (*Glyptocephalus cynoglossus*), and lemon sole (*Microstomus kitt*) were measured to the nearest centimetre below, and the carapace length of *Nephrops* was measured to the nearest millimetre below. In the subsequent analysis, 0.5 cm was added for fish and 0.5 mm for *Nephrops* (Krag et al. 2014). All individuals from each species were measured in each haul, except for saithe, which was subsampled in the upper compartment in one haul due to a large catch size, where 25% of the saithe were measured in this haul.

Data analysis

The mean body length (± standard deviation, SD) and mean proportions of individuals (with confidence interval, CI) caught in the upper compartment was calculated separately for all fish, roundfish, flatfish and each species, and separately for those caught during the day and during the night, and for fish smaller than MCRS. To evaluate the length-dependent vertical separation efficiency for each species separately, and separately for the day and 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 mesh compartments (u: upper, d: lower) in each haul i. We defined the experimental vertical separation efficiency VS_{li} as the proportion of fish with length l caught in the upper compartment compared with the total in a haul i, as follows.

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

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

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

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

$$VS(l,\boldsymbol{v}) = \frac{\exp\left(f(l,\boldsymbol{v})\right)}{1.0 + \exp\left(f(l,\boldsymbol{v})\right)} \quad , \qquad (3)$$

where f is a polynomial of order k with coefficients $v_0, \ldots, v_k$ so $\boldsymbol{v} = (v_0, \ldots, v_k)$. We considered f up to an order of 4 with parameters $v0$, $v1$, $v2$, $v3$, and $v4$. $VS(l,\boldsymbol{v})$ expresses the probability of finding a fish of length l in the upper compartment given that it was observed in the upper or lower compartment. We used $f\,(l,\boldsymbol{v})$ in the following formula.

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

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

Confidence intervals (CI) were estimated for the length-dependent vertical separation efficiency using a double bootstrap method with the software SELNET released by 08.03.2017 (Millar 1993; Herrmann et al. 2012). The procedure accounted for uncertainty due to between-haul variation in the vertical separation efficiency by selecting h hauls with replacement from the h hauls available from the pool of hauls in the three specific cases investigated (i.e., all, day, or night hauls) during each bootstrap repetition. The within-haul uncertainty in the size structure of the catch data for the upper and lower compartments was accounted for by randomly selecting fish with replacement from each of the selected hauls from the upper and lower compartments. The number of fish selected from each haul was the number of fish with length measurements in that haul in the upper and lower compartments. The data were then combined as described above and the vertical separation efficiency was estimated. Only hauls containing at least 10 individuals in the summed upper and lower compartments were investigated for a given species. In total, 1000 bootstrap replicates were performed and the Efron 95% CI (Efron 1982) was calculated for the vertical separation curve. Incorporating the combined model approach described above in each of the bootstrap replicates allowed us to consider additional uncertainty regarding the vertical separation efficiency due to uncertainty in model selection (Krag et al. 2015).

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

Results

Fishing gear and fishing operation

The average mesh size (± SD) was 44.03 mm (± 1.35 mm) for the upper codend compartment (n = 30) and 43.63 mm (± 1.27 mm) for the lower codend compartment (n = 30). Fourteen valid hauls were conducted during good fishing conditions in commercial fishing grounds (Table 1). The duration of the hauls varied between 1.25 and 3.50 h (mean: 2.63 h). Underwater video recordings showed that the net was open and stable at the entrance of the divided codend (Fig. 2). There were no problems handling the two frames in the lower compartment during the fishing process and the two vertical bars in the foremost frame did not collect any objects.

Ability of the model to describe the data

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

Vertical distribution

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

Length-dependent vertical distribution

Cod

The mean length of the cod (n = 3688) was 39 cm (range: 9–96 cm) (Table 3–4). Overall, the individuals entered the upper compartment less than expected if their vertical distribution was uniform (Table 4). There was a strong length dependency in terms of the vertical distribution by cod, with a mean vertical separation efficiency of 0.22 for individuals measuring less than the MCRS of 30 cm, and 0.68 for individuals measuring greater than or equal to the MCRS (Fig. 3). Of the total cod analysed, 32% measured less than the MCRS and they had a mean size of 25 cm (SD: ± 14.0). The preference for the lower compartment was significant for cod < 45 cm. Cod ≥ 45 cm showed a uniform vertical distribution (Fig. 3).

Whiting

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

Preference for the upper compartment

Haddock

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

Saithe

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

Preference for the lower compartment

Hake

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

Plaice

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

Witch flounder

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

Lemon sole

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

Nephrops

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

Day/night effects

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

During the day, cod in the size interval [9, 45) cm had a significant preference for the lower compartment. At night this preference was significant for individuals ≤ 37 cm (Fig. 4). The significant preference for the upper compartment in haddock during the day was limited to individuals ≥ 49 cm. This shifted to the size interval (12, 31) cm at night. For saithe, the preference for upper compartment during the day was significant for the size interval (24, 56) cm. During the night, this significant preference was limited to the size interval (46, 56) cm. Hake ≤57 cm had a significant preference for the lower compartment during the day while only those in the size interval (28, 34) cm had the same preference during the night. Similarly, the preference of plaice for the lower compartment that was significant for the size interval (19, 39) cm during the day, was reduced to the size interval [33, 38) cm at night (Fig. 5). The size interval for which witch flounder had a significant preference for the lower compartment was similar during the day and night ((21, 41) cm and (20, 39] cm, respectively). This was also the case for lemon sole ((19, 32) cm during the day and [23, 34) cm during the night). *Nephrops* had a significant preference for the lower compartment for the size interval (26, 70) mm during the day and for individuals <68 mm during the night.

Discussion

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

Vertical distribution

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

Three separation patterns

Length-dependent vertical distribution (cod and whiting)

Overall, we found that a higher proportion of cod entered the upper compartment. This is similar to that found for cod in other horizontally divided codend designs (Table 5; see also He et al. 2008; Krag et al. 2009a, 2009b). However, when we took the height of the compartment relative to the total height of the gear into account, we found that cod had an overall preference for the small mesh lower compartment, indicating a low vertical distribution in the gear. This puts a limitation to how effectively cod can be selected out and contrasted that of the other studies that mostly found a preference for the upper compartment, except for one experiment that resulted in a uniform distribution (Table 5). Krag et al. (2009a, 2009b) used a three compartment codend design with a frame at the entrance. The upper compartment constituted 50% of the total height of the gear. He et al. (2008) used a codend divided in half, but with the possibility for the fish to change compartments after the point of separation. Our length-based analysis showed a strong length dependency in the separation efficiency for cod. Small cod had a significant preference for the lower compartment whereas individuals measuring greater than 44 cm had no significant preference for any compartment. From this, an increase in the separation of small individuals is necessary to select them out of the larger meshes in the upper compartment in a commercial fishery. In their length-dependent analysis, Holst et al. (2009) found a preference for the upper compartment for all the size groups. A visual inspection of the size distribution given in some of the studies does not suggest that differences in fished populations can explain the differences in the separation of cod between studies using divided codend designs. However, the frequency distribution of the size classes is not easily determined by visual inspection, and so this has to be analysed further to conclude whether the differences in separation is in fact due to differences in the vertical distribution of cod resulting from differences in gear design, or if it is confounded by differences in fish size distributions.

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

Preference for the upper compartment (haddock and saithe)

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

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

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

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

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

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

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

Like the two other flatfish species, the largest overall proportion of lemon sole entered the lowest compartment and was found to prefer the lower compartment. Despite the two vertical bars in the only 30 cm high frame, the preference for the lower compartment was much stronger than for the 37.5 cm high lower compartment in the separator frame without vertical bars in Krag et al. (2009a, 2009b). This may be caused by the differences in 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). Although the presence of vertical bars do not change the preference of lemon sole, they encourage a higher proportion to enter the upper compartment (Table 5). The structure of the fished population in our study were similar to those in Krag et al. (2009b) (range: 10-40 cm, peak ca. 25 cm). Thus, even though it was not demonstrated in our study, lemon sole, like plaice, can be stimulated to swim into the upper panel by using vertical bars. Simple visual stimuli should be investigated further to identify devices that can successfully separate lemon sole from *Nephrops*.

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

Diel effects on vertical distribution

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

Management implications

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

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

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

Acknowledgement

This study was part of the FishValue (VærdiFisk) project, which received funding from the Ministry of Food, Agriculture, and Fisheries of Denmark, and the EU through the European Maritime and Fisheries Fund (EMFF, grant no. 33113-I-16-015), as well as the DiscardLess project, which received funding from the EU Horizon 2020 Programme (grant no. 633680). Special thanks go to skipper Lars Kajgaard, the crew on FN-436 Tove Kajgaard, and chairman Claus Hjørne Petersen from the Fisherman's Association of Strandby. Special thanks also go to an anonymous reviewer whose comments greatly improved this paper.

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Tables

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

676 Table 2. Fit statistics.

	All hauls			**Day-hauls**			**Night-hauls**		
Species	***p*-value**	**Deviance**	**DOF**	***p*-value**	**Deviance**	**DOF**	***p*-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

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**		***Nephrops***	
		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[1]	321[1]	1027	290	6981	2131	92[1]	196[1]	614	743	380	604	99[1]	175[1]	225	2167

[1] Bootstrap 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.

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

Species	**All lengths** **Mean length (±SD, range)**	**% upper (CI range)**	**MCRS (*Market)**	**<MCRS/*Market** **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[1]	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)
Nephrops	43 (±9.0; 21–72)	9.4 (7.9–12.1)	32	44 (±8.6; 32–72)*	9.6 (7.8–11.8)*
Day					
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)
Nephrops	48 (±9.2; 28–71)	8.7 (5.8–10.2)	32	49 (±8.8; 32–71)*	9.0 (6.2–11.0)*
Night					
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)
Nephrops	39 (±6.5; 21–72)	10.0 (9.0–31.0)	32	40 (±6.1; 32–72)*	10.2 (8.4–34.0)*

[1] Analysis of individuals ≥MCRS.

Table 5. Species specific preference (proportion, %) observed in different studies. Preference for a compartment: >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[1]	Holst et al. (2009)[2]
	1.08 (54%)	1.12 (28%)	0.72 (18%)	18-30 cm	Simple frame[1]	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[1]	Holst et al. (2009)[2]
	1.82 (91%)	0.32 (8%)	0.04 (1%)	16-27 cm	Simple frame[1]	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[1]	Krag et al. (2009a)
	1.74 (87%)	0.32 (8%)	0.16 (4%)	18-30 cm	Simple frame[1]	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)
	1.84 (92%)	NA	0.16 (8%)	Not given	Ropes[5]	He et al. (2008)
Saithe	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[1]	Holst et al. (2009)[2]
	1.74 (87%)	0.36 (9%)	0.20 (5%)	18-27 cm	Simple frame[1]	Holst et al. (2009)
Hake	0.48 (32%)	NA	2.06 (68%)	20-55 cm	Frame, two vertical bars	This study
	0.80 (40%)	1.48 (37%)	0.92 (23%)	Not given	Simple frame[1]	Krag et al. (2009a)
Plaice	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[1]	Krag et al. (2009b)
	1.08 (54%)	0.84 (21%)	1.00 (25%)	21-37 cm	Complex frame[3]	Krag et al. (2009b)
Witch flounder	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[1]	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[1]	Krag et al. (2009a)
	0.66 (33%)	1.56 (39%)	1.16 (29%)	15-32 cm	Simple frame[1]	Krag et al (2009b)
	1.00 (50%)	1.24 (31%)	0.76 (19%)	15-34 cm	Complex frame[3]	Krag et al (2009b)
Nephrops	0.14 (9%)	NA	2.75 (91%)	27-65 mm	Frame,	This study

				two vertical bars	
0.32 (16%)	NA	1.68 (84%)	Not given	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)

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[1] Simple frame: Frame with two horizontal bars

[2] Holst et al. (2009) made a length-based analysis of the data reported by Krag et al. (2009a).

[3] Complex frame: Frame with two horizontal and two vertical bars

[4] Separation panel: Black and netting separation panels, opening, black tunnel, separation panel

[5] Ropes: Black separation panel, ropes, opening, black tunnel, separation panel

Figures

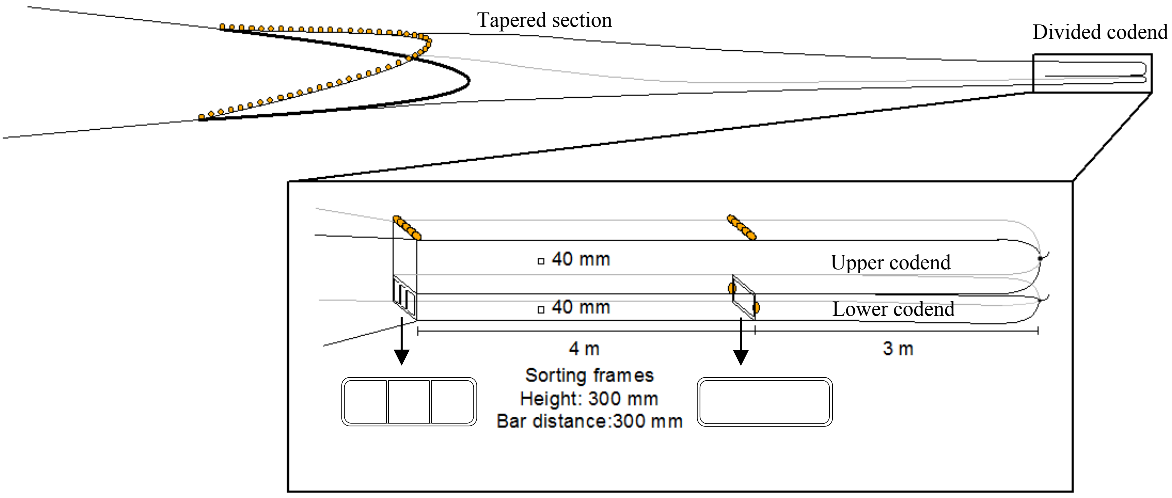

Fig. 1. Schematic illustrations of the trawl gear. The enlarged section shows the upper and lower compartments of the non-selective horizontally divided codend (40 mm mesh size), and the two frames used to separate fish from *Nephrops* (frame with vertical bars) and to keep the lower compartment open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

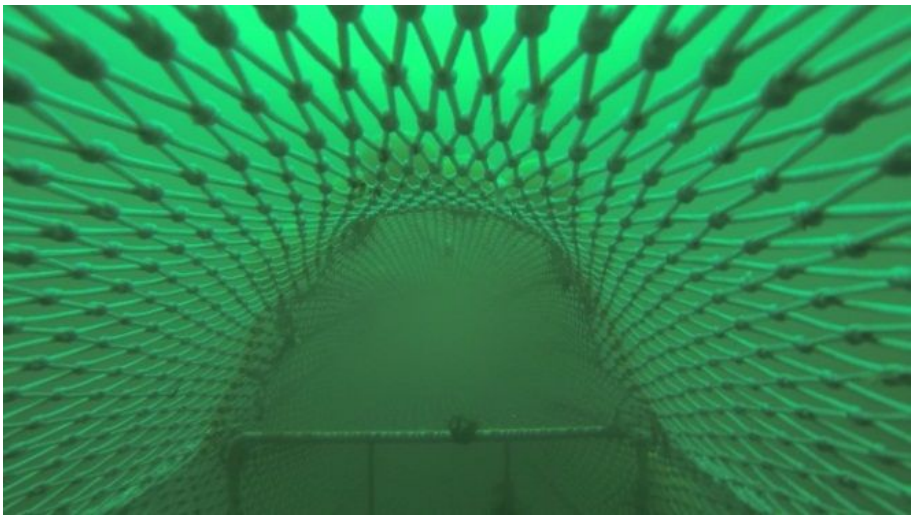

Fig. 2. The opening of the entrance of the upper compartment of the vertically divided codend used in the fishery. The steel frame defining the opening into the lower compartment comprised about one-third of the total height at the codend entrance, whereas the opening into the upper compartment comprised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

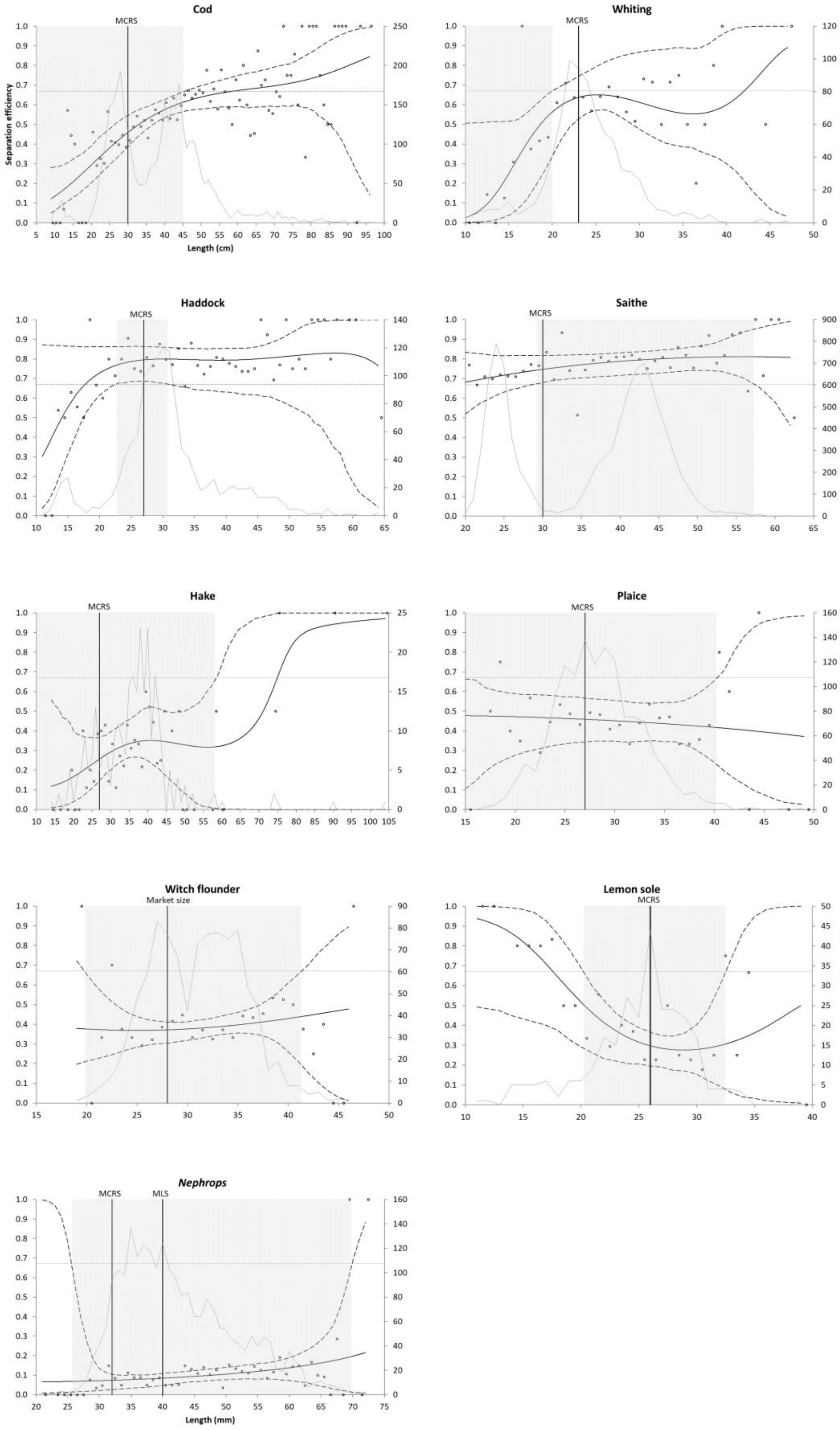

Fig. 3. Length-dependent vertical separation of the nine commercial species observed in the separated codend. Solid line: estimated catch proportion for the species in the upper compartment (Model 3). Broken lines: 95% confidence limits. Circles: observed values. Horizontal grey line: separation efficiency of 0.67; both confidence limits >0.67 or <0.67 indicate that the vertical separation differed significant from that expected based on a

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

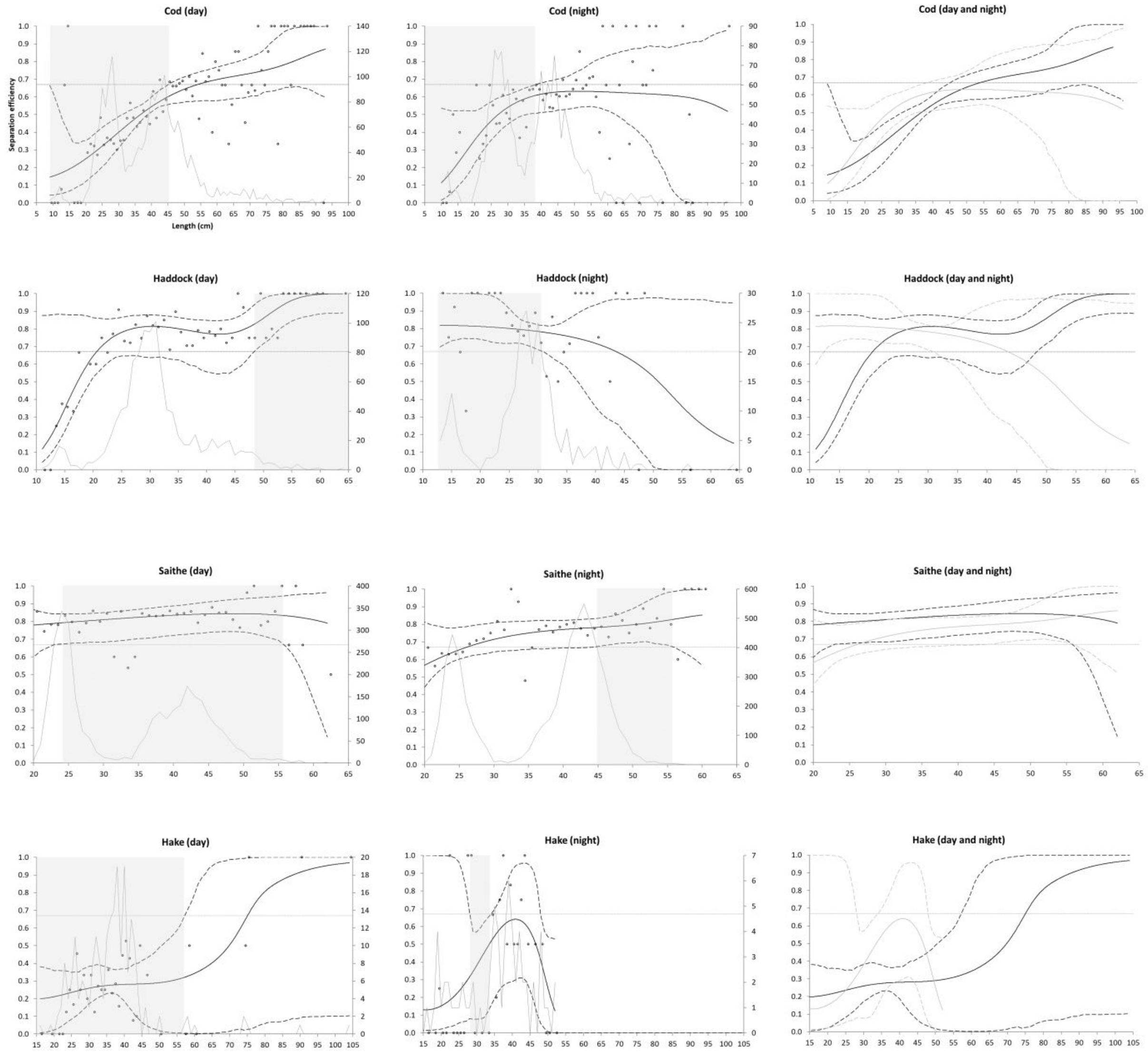

Fig. 4. Length-dependent vertical separation of roundfish. Solid line: estimated catch proportion for species in the lower compartment (Model 3). Broken lines: 95% confidence limits. Circles: observed values. Grey line: population. Horizontal grey line: separation efficiency of 0.67; confidence limits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

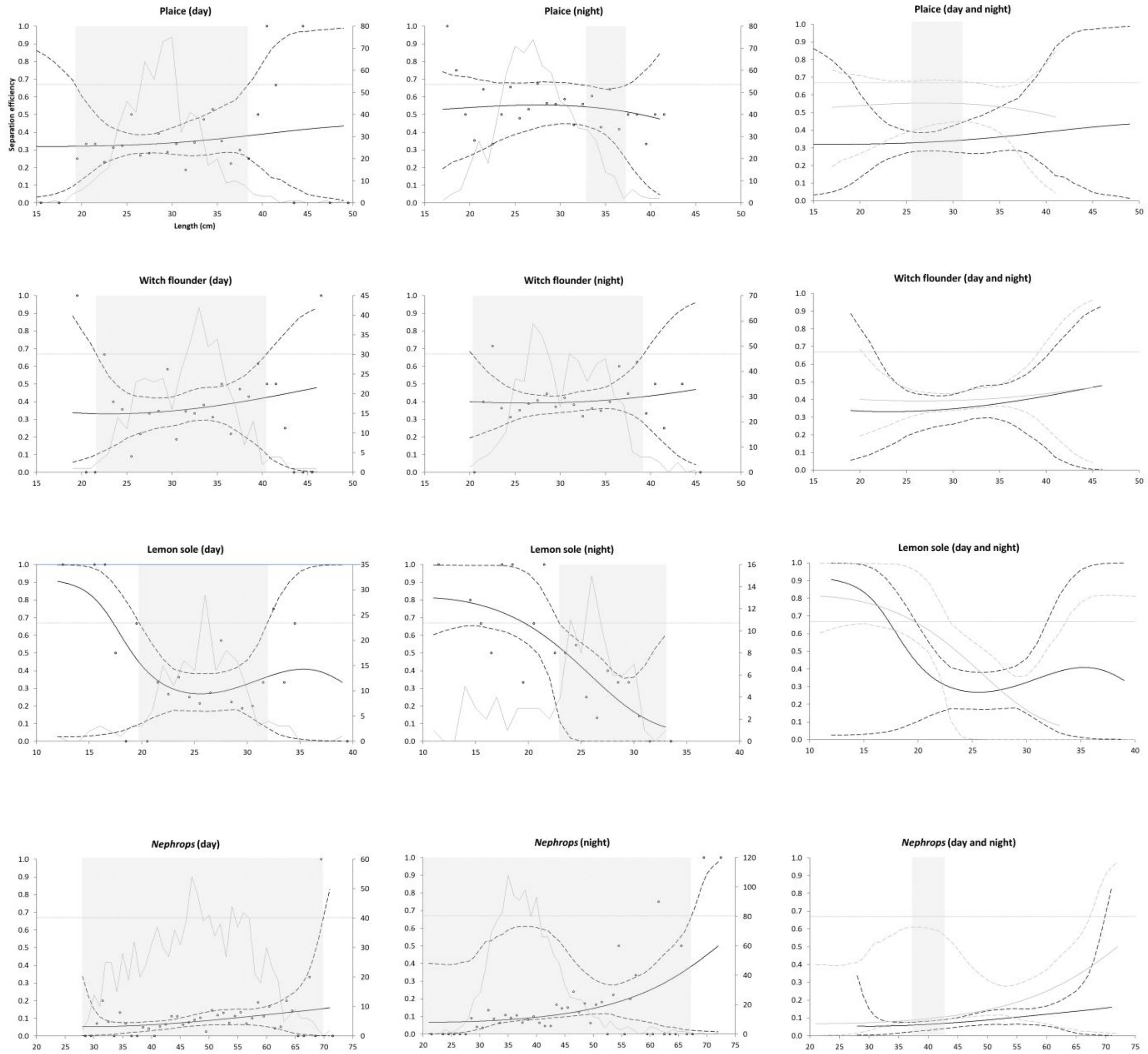

Fig. 5. Length-dependent vertical separation of flatfish and *Nephrops*. Solid line: estimated catch proportion for species in the lower compartment (Model 3). Broken lines: 95% confidence limits. Circles: observed values. Grey line: population. Horizontal grey line: separation efficiency of 0.67; confidence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

Appendix 1

Table A1. Values (confidence interval) for the mean estimated length-dependent separation given as proportion of individuals that enters the upper compartment from all 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	*Nephrops*
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)