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Abstract: A promising design to improve selectivity in the Nephrops-directed trawl fishery is the horizontally divided trawl codend. Previous studies have succeeded in separating the majority of fish from Nephrops; however, cod (*Gadus morhua*), juvenile roundfish and flatfish still enter the lower compartment in relative high proportions. In this study we investigated if and to which extent it is possible to improve the vertical separation of fish from Nephrops by adding active behaviour stimulators. These stimulators are designed to exploit fish avoidance behaviour and lead them into the upper compartment while Nephrops roll into the lower compartment. We tested two types of behaviour stimulators: a chain curtain at the entrance of the lower compartment at the point of separation and a set of rising float-lines inserted ahead of the point of separation. The length-dependent vertical separation of five important commercial fish species and Nephrops was analysed in comparison to the horizontally divided trawl codend with no stimulator, towed in parallel to the test trawl. The results showed that fish's vertical separation can be partially improved by the addition of stimulators, without complicating fishing operations or increasing the proportion of Nephrops that enters the upper compartment. However, the improvement was limited and none of the two active stimulators tested managed to simultaneously improve the separation of cod, juvenile roundfish and flatfish.

**Can active behaviour stimulators improve fish separation from *Nephrops*
(*Nephrops norvegicus*) in a horizontally divided trawl codend?**

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25 **Abstract**

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28 *Nephrops*; however, cod (*Gadus morhua*), juvenile roundfish and flatfish still enter the lower
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37 parallel to the test trawl. The results showed that fish's vertical separation can be partially
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42

43 **Keywords**

44 Horizontally divided codend; behavioural stimulators; vertical separation; *Nephrops*; bycatch

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48 **Introduction**

49 Reducing bycatch of unwanted species and undersized individuals in mixed-species trawl fisheries
50 represents a challenge due to the different sizes and shapes of the species caught. A well-studied
51 example is the *Nephrops*-directed mixed trawl fishery in the northeast Atlantic (Catchpole and
52 Revill, 2008). This fishery catches several commercially important fish species including roundfish
53 and flatfish. To target *Nephrops*, the fishery adopts a minimum mesh size of 70 or 90 mm
54 (depending on region). However, the poor selective properties of these mesh sizes in relation to
55 minimum conservational reference sizes (MCRS) often result in high catches of fish (Kelleher,
56 2005; Krag et al., 2008). To appropriately select out some of the commercial northeast Atlantic fish
57 species caught, a mesh size of 120 mm should be adopted (Graham and Ferro, 2004), a solution
58 not compatible with targeting *Nephrops* (Krag et al., 2008). Moreover, the majority of the bycatch
59 species are now subjected to the European Union's landing obligation (European Union, 2013)
60 whereas *Nephrops* has obtain an exemption, in some regions, due to its high survival rates
61 (European Commission, 2018). Therefore, fishermen are likely to fulfill their quota for fish before
62 that for *Nephrops*. Mandatory bycatch reduction devices, such as grids and square mesh panels,
63 have been introduced in many regions to mitigate the amount of bycatch and release undersized
64 individuals (Catchpole and Revill, 2008). Grids mechanically filter the catch according to size and
65 are relatively independent from species behaviour; however, they can be subjected to clogging
66 and cause a loss of commercial size *Nephrops* (Catchpole and Revill, 2008; Drewery et al., 2010).
67 Square mesh panels reduce the catch of roundfish without affecting the catch of *Nephrops*, but
68 their efficiency depends on species contacting the panel and, thus, varies according to species-
69 specific behaviours (Catchpole and Revill, 2008; Drewery et al., 2010).

70 A promising strategy to combine a behavioural and mechanical selection of the catch is to
71 introduce a horizontal net panel that separates the trawl into compartments leading to
72 independent codends. Ideally, if all fish species are separated from *Nephrops*, they can be more
73 appropriately select out without the risk of losing target catch. Previous studies have proved that,
74 when inside the trawl, *Nephrops* move passively towards the codend (Main and Sangster, 1985;
75 Briggs, 1992) and only few big individuals manage to rise vertically during towing (Graham and
76 Fryer, 2006; Krag et al., 2009a; Karlsen et al., 2015). Therefore, when encountering a horizontal
77 separation, the majority of *Nephrops* enter the lower compartment. On the contrary, fish
78 behaviour in the trawl is affected by several factors, and so is their separation into different
79 compartments. Fryer et al. (2017) reviewed studies that included a horizontal net panel, and
80 analysed the main factors affecting the separation of the commercial species caught by demersal
81 trawls. The height of the horizontal panel from the lower netting and the horizontal distance from
82 the groundgear to the start of the separator panel, were identified as the main factors affecting
83 the proportion of fish entering the upper compartment (Fryer et al., 2017). In particular, cod
84 separation from *Nephrops* was significantly better when the horizontal panel was inserted in the
85 aft end of the trawl (Fryer et al., 2017) and designs including a horizontally separated trawl codend
86 managed to segregate the majority of the fish in the upper compartment (Krag et al., 2009a; Melli
87 et al., 2018). However, length-dependent differences in vertical separation were observed in most
88 species, with smaller individuals entering more frequently the lower compartment (Holst et al.,
89 2009; Melli et al., 2018). Due to these differences, the horizontal separation alone might not be
90 sufficient to separate most fish from *Nephrops*.

91 Additional devices can be inserted before or at the separation to increase the proportion of fish
92 entering the upper compartment. Graham and Fryer (2006) combined a grid with a horizontally

93 divided trawl and achieved to separate the majority of fish bycatch from *Nephrops*. However, the
94 size and rigidity of the grid raised concerns for its use under commercial conditions. Other, more
95 flexible solutions might be able to achieve a similar result by exploiting fish behavioural response
96 to mechanical and visual stimuli (Graham, 2010). For example, simple frames with few vertical
97 bars at the entrance of the lower compartment succeeded in leading fish into the upper
98 compartment despite not representing a real physical obstacle to their passage (Krag et al., 2009a;
99 Karlsen et al., 2015). Stimulators tested to increase fish contact with square mesh panels may also
100 be applied to improve species separation (Herrmann et al., 2015; Krag et al., 2016). Grimaldo et al.
101 (2017) tested fluttering lines with floats to trigger fish escape responses and increased significantly
102 haddock's escape rate. Kim and Wang (2010) tested a fluttering net panel and a set of free ropes,
103 successfully stimulating the escapement of juvenile red sea bream (*Pagrus major*) in laboratory
104 conditions. These active stimulating devices rely on fish reaction to the stimulus. Thus, for the
105 stimulator to successfully improve fish separation from *Nephrops*, fish must have enough time and
106 energy to react and the reaction must be directed to the upper compartment.

107 The aim of this study was to investigate if and to which extent the separation of fish from
108 *Nephrops* in a horizontally divided trawl codend could be improved using active behaviour
109 stimulators. We tested two different stimulators : a chain curtain at the entrance of the lower
110 compartment and a set of rising float-lines, in the section forward to the separation. The first
111 stimulator aimed at maximizing the illusion of a blocked passage into the lower compartment
112 (Glass and Wardle, 1995). The second stimulator was designed to give fish with relatively poor
113 swimming capacities enough time to rise into the upper compartment, considering the towing
114 speed and possible states of fatigue. Indeed, small fish are likely to utilize most of their aerobic
115 swimming during the initial capture phase while attempting to swim ahead of the footrope

116 (Winger et al., 2010). Inside the trawl, they are assumed to depend upon anaerobic swimming
117 and, thus, any burst-swimming activity is unlikely to be at maximum speed or sustainable for
118 extended periods (Webb, 1994). Moreover, fish swimming speed, endurance and maneuverability
119 vary among species in addition to sizes (Videler and Wardle, 1991; Wardle 1993). Therefore, the
120 efficacy of the active stimulators on species vertical separation was investigated by species and
121 length class.

122 **Materials and methods**

123 Two sea trials were conducted in September 2016 and 2017 with the research vessel “Havfisken”
124 (17 m, 373 kW). The vessel was equipped for three-wire, twin-trawling with two identical Combi
125 trawls (40 m long footrope, 420 meshes circumference of the trawl mouth, 80 mm mesh size)
126 towed in parallel. The twin-rig system was spread with two Type 2 Thyborøn doors (1.78 m², 197
127 kg) and a 400 kg central roller clump. Each trawl spread was monitored throughout the haul with
128 distance sensors (Simrad PI) mounted on doors and clump. The trawls were rigged with 75 m long,
129 single wire sweeps with 4.3 cm (diameter) rubber discs. One trawl was equipped with one of the
130 active swimming stimulators while the other had no stimulator and was used as a control, which
131 we refer to as the baseline for species vertical separation. The baseline design of the horizontally
132 divided trawl codend was previously tested and described in Karlsen et al., (2015) and Melli et al.
133 (2018). We investigated if active swimming stimulators could further improve fish separation from
134 *Nephrops*.

135 The trawls were made of two net panels until the separation into the two compartments where
136 each compartment (i.e. extension and codend) was constructed of four net panels (Fig. 1 A). Both
137 compartments had 41.65 ± 1.33 mm diamond meshes (mean ± SD; dry measurement) made of 1.8

138 mm braided twine, that were turned 45 degree to obtain square meshes. In the extension section
139 of the compartments, the lower netting of the upper compartment and the upper netting of the
140 lower one were tight together. The length of the extension section was approximately 4.5 m; then,
141 the two compartments separated into two independent codends (Fig. 1 A). The total length of the
142 compartments, from the separation point, was 6 m in 2016 whereas 6 m more were added to the
143 codends sections in 2017. This modification was introduced to prevent the catch from exceeding
144 the compartments, thus invalidating the haul (Melli et al., 2018). Consequently, to sustain the
145 additional length of the codends in 2017 and prevent them from sweeping the seafloor, these
146 were lifted with ten floats each. The lift of the floats was 680 g and 800 g lift for the upper and
147 lower codends, respectively.

148 The separation point was positioned at the transition between the tapered and non-tapered
149 section of the gear (circumference 140 meshes; Fig 1 A). The entrance of the upper compartment
150 was approximately 60 cm high (based on underwater video observations) and sustained by 12
151 floats (720 g lift) outside the upper netting (Fig 1 A). The entrance and the extension of the lower
152 compartment were fixed at 30 cm high due to two frames (90 cm x 30 cm, 20 mm stainless steel
153 pipes) that secured the opening of the extension section (Fig 1 A). Moreover, the original design of
154 Karlsen et al. (2015) already involved two vertical bars (30 cm apart) in the frame at the entrance
155 of the lower compartment to visually and mechanically stimulate fish to swim into the upper
156 compartment.

157 We tested two active behaviour stimulators in 2016 and 2017, respectively:

158 1) *Chain curtain*

159 To increase the visual and physical occlusion of the entrance of the lower compartment, chains (L:
160 26.5 cm, W: 0.71 Kg/m, $\varnothing$: 5 mm thick) were added to the frame (Fig. 1 B). The chains were fixed
161 to the upper pipe of the frame with twine (nylon, 2 mm) and left free to move in the lower end. A
162 total of 12 chains was inserted in the frame, four in each of its three sections (30x30 cm)
163 approximately every 7 cm (Fig. 1 B and D). Fishing was conducted in commercial *Nephrops* and fish
164 grounds in the Skagerrak Sea, at depths between 31 m and 87 m. Experimental hauls were
165 performed at day time, at least one hour after sunrise and until one hour before sunset.

166 2) *Rising float-lines*

167 To increase the time available for rising into the upper compartment, we inserted a stimulator
168 starting 2 m in front of the separation into compartments (Fig. 1 C and E). Five lines (10 mm,
169 polypropylene) were attached to the lower netting panel with carabiner hooks (size 8 with lock, 64
170 g, 6 hooks per rope) every 40 cm (approximately 6 stretched 80 mm meshes). The line between
171 two carabiners was set to create an arc of increasing height while approaching the separation (Fig.
172 1 C). The first arc was approximately 8 cm high and each following arc was 3 cm higher, to finally
173 reach a height of approximately 20 cm in the last arc, at the separation point. In the middle of
174 each arc we inserted a float (115 g lift) blocked by twine (5 floats per rope). The five lines were
175 spaced approximately 15 cm at the frame end (i.e. entrance to the lower compartment) and
176 followed the mesh orientation in the tapered section. The two lines ending in correspondence to
177 the vertical bars of the frame were moved 20 cm forward as the bar already represented an
178 obstacle to the lower compartment entrance. Moreover, this created an alternation of floats with
179 the other lines (Fig. 1 C). Led line (0.26 Kg/m, 3.6 m long) was added outside the lower netting
180 panel to compensate for the total lift exercised by the floats. Fishing was conducted in commercial

181 *Nephrops* and fish grounds in the Skagerrak Sea, at depths between 17 and 91 m. Experimental
182 hauls were performed at day time or right before dawn.

183 During both experiments, the position of the stimulator was shifted from one trawl to the other
184 every few hauls, to compensate for systematic differences deriving from trawl-dependent vertical
185 separation efficiency. After every haul, the catch of each compartment was weighted and sorted
186 by species separately. The total length of all target fish species and the carapace length of
187 *Nephrops* were measured and rounded down to the nearest centimetre and millimetre,
188 respectively. Video footage was collected in shallow waters (15 m depth) to visualize the
189 performance and dynamic of the stimulators during fishing. A GoPro Hero 4 was attached on the
190 upper netting panel approximately 0.5 and 1.5 m before the separation in 2016 and 2017,
191 respectively.

192 **Statistical analyses**

193 The vertical separation efficiency was first estimated separately for each trawl (baseline and test)
194 and for each of the two experiments (chain curtain and rising float-lines), following the same
195 procedure described in Melli et al. (2018). All the analyses were performed using the software
196 SELNET (Herrmann et al., 2012).

197 The vertical separation efficiency $VS(l)$ was defined as the probability of finding an individual of
198 length l in the upper compartment given it was observed in either compartment. For each species
199 and each haul, $VS(l)$ was estimated using the catch data. In each haul i , nU_{li} and nL_{li} denoted the
200 number of individuals of length class l caught and length-measured in the two compartments.
201 Then, according to our definition, VS_{li} was:

$$VS_{li} = \frac{\frac{nU_{li}}{qU_i}}{\frac{nU_{li}}{qU_i} + \frac{nL_{li}}{qL_i}} \quad (1)$$

where qU_i and qL_i were the sampling factors (i.e. the proportion between the weight of the sample length-measured and the weight of the total catch of that species) in the upper and lower compartments, respectively, in haul i . A value of VS_{li} above 0.5 implies that in the haul i there was a higher probability of finding an individual of length l in the upper compartment, given an equal probability of entering either compartment. However, in this study the height of the entrance of the upper compartment accounted for 67% of the total height of the funnel section. Therefore, the probability of an individual entering the upper compartment if it was randomly distributed in the trawl section was 67% and only values of VS_{li} above or below 0.67 expressed a differential distribution of individuals. We used the term “preference” to describe this differential distribution (Melli et al., 2018).

The averaged length-dependent vertical separation efficiency, $VS(l, \nu)$, was estimated using the pooled data over hauls, assuming this to be a representative sample of how the vertical separation would perform on average under different fishing conditions. Only hauls containing at least 10 individuals of that species in the upper and lower compartments summed were included (Krag et al., 2014). Following the procedure described in Melli et al. (2018), we applied a highly flexible function, often used for paired gears data (Krag et al., 2014; 2015), and adopted recent improvements in model average estimation (Herrmann et al., 2017). The ability of the model to describe the experimental data was assessed based on the p -value, which expresses the likelihood to obtain by coincidence a discrepancy between the fitted model and the experimental data at least as big as the one observed. Therefore, poor fit statistics (p -value < 0.05; deviance >>DOF)

might indicate structural problems in describing the experimental data with the model (Wileman et al., 1996). In such cases, the deviation between the observed data and the fitted curve was examined and if no pattern was identified the result was attributed to data overdispersion and the model was accepted.

The 95% Efron confidence intervals (CIs; Efron, 1982) for the averaged vertical separation were estimated using a double bootstrap method with 1000 repetitions (Millar, 1993). The procedure accounted for uncertainty due to between-haul variation in vertical separation efficiency by selecting h hauls with replacement from the h hauls available in the experiment during each bootstrap repetition. Within-haul uncertainty in the size structure of the catch data was accounted for by randomly selecting individuals with replacement from each haul and each length class. The number of fish selected from each haul was the number of fish length-measured in that haul in respectively the upper and lower compartment.

Quantifying the effect of the stimulator

According to the method described in Melli et al. (2018), while calculating the length-based vertical separation efficiencies with 95% Efron CIs, we synchronized the hauls selected for the outer bootstrap loop for baseline and test trawls and calculated in each bootstrap the device effect $\Delta VS(l, \nu)$ on the vertical separation by:

$$\Delta VS(l, \nu) = VSB(l, \nu) - VST(l, \nu) \quad (2)$$

where $VSB(l)$ is the length-based, average vertical separation efficiency of the baseline trawl and $VST(l)$ is the length-based, average vertical separation efficiency of the test trawl. By this synchronization in the haul selection and the direct calculation of $\Delta VS(l, \nu)$ in each bootstrap we removed part of the between-haul variation in vertical separation efficiency deriving from

environmental factors and fishing dynamics, thus increasing the power of the analysis to infer the effect of the active swimming stimulator. $\Delta VS(l, \nu)$ spans between -1 and 1, where values above 0.0 imply that the stimulator increased the probability of finding an individual of length l in the upper compartment. Similarly, values below 0.0 imply a lower probability. For those length-classes in which the 95% confidence intervals for $\Delta VS(l, \nu)$ did not contain 0.0, we determined a significant effect of the stimulator in modifying the vertical separation efficiency.

Results

A total of 14 valid hauls were conducted with the chain curtain and 10 with the rising float-lines (Table 1). Additional hauls were precautionary excluded from analyses when the catch exceeded the point of separation ($n=3$) or when the entrance to the lower compartment was partially blocked by marine litter or seaweed ($n=3$). The towing time was on average 74 ± 30 min (mean $\pm$ SD) and in 2016 and 75 ± 25 min (mean $\pm$ SD) in 2017, according to the vessel eco-sounder and the observed catch levels. Hauls at low depths were conducted to target *Nephrops*, whose availability in September was limited to shallower waters, or to collect video footage of the performance of the stimulators during fishing.

In both experiments, sufficient data for analysis were collected for six commercial species (Table 2): three roundfish species, cod, haddock (*Melanogrammus aeglefinus*), and whiting (*Merlangius merlangus*); two flatfish species, plaice (*Pleuronectes platessa*) and lemon sole (*Microstomus kitt*); and *Nephrops*.

Fit statistics for each of the models are reported in Table 3. In most cases, p -values were above 0.05, implying that the deviation between the experimental data and the modelled fits could well be a coincidence. Therefore, the model could be trusted to describe the trends in the

267 experimental data. However, three models in the first experiment (chain curtain) and two models
268 in the second experiment (rising float-lines) resulted in poor fit statistics (p -value below 0.05,
269 Deviance $\gg$ DoF). These were the models for cod, plaice and *Nephrops* in the test trawl with the
270 chain curtain and the models for *Nephrops* (baseline trawl) and whiting (test trawl) in the rising
271 float-lines experiment (Table 3). The residual deviations between the data and the modelled
272 curves were investigated for each of these cases but no systematic structure was detected. Thus,
273 we attributed the poor fit-statistics of these cases to overdispersion in the data and not to
274 structural problems in describing the experimental data with the combined model (Wileman et al.,
275 1996).

276 All the separation efficiency curves described well the experimental data (Fig. 2 and 3). Where
277 fewer individuals were caught, an increasing binominal noise was observed through the increasing
278 width of the CIs.

279 1) *Stimulator at the separation point: chain curtain*

280 In the baseline trawl, cod showed a length-dependent vertical distribution, with small cod (7–18
281 cm) preferring the lower compartment and bigger cod (31–45, 69–82 cm) having a preference for
282 the upper compartment (Fig. 2). Juveniles of both haddock and whiting were distributed
283 uniformly, meaning that their vertical separation reflected the proportion between the heights of
284 the two compartments. In contrast, individuals above 17 cm showed a preference for the upper
285 compartment. The preference for the upper compartment was significant for haddock only at 17–
286 24 cm and 36–47 cm. The two flatfish species showed different vertical distributions, with plaice
287 having a preference for the lower compartment (20–39 cm) and lemon sole having a uniform

288 distribution. *Nephrops* showed a strong preference for the lower compartment for all the length
289 classes well represented in the data (20–65 mm).

290 The main changes in the vertical distribution in the test trawl equipped with the chain curtain
291 were observed in cod and plaice. Cod juveniles (7–16 cm) were significantly raised into the upper
292 compartment, losing their preference for the lower one (Fig. 2, delta). In the test trawl, cod
293 between 27 and 59 cm showed a preference for the upper compartment (Fig. 2, test trawl);
294 however, the difference respect to the vertical separation in the baseline trawl was not significant
295 for this size group according to the delta. Similarly, plaice below 35 cm lost their preference for the
296 lower compartment (Fig. 2, test trawl), although the difference was significant only for individuals
297 between 27 and 32 cm (Fig. 2, delta).

298 2) *Stimulator before the separation point: rising float-lines*

299 Respect to the experiment conducted in 2016, wider CIs were obtained for some species and size
300 groups (e.g. cod above 37 cm and haddock above 17 cm; Fig. 3). In particular, very few haddock
301 were caught in 2017, but the species was included as a significant change in vertical distribution
302 emerged for the few length classes represented. In the baseline trawl, species vertical
303 distributions were consistent with those observed in 2016, with the exception of lemon sole.
304 Haddock (15–26 cm) and whiting (16–37 cm) showed a preference for the upper compartment;
305 small cod (9–15 cm) showed a preference for the lower compartment and a uniform distribution
306 for the bigger length classes. Plaice showed a preference for the lower compartment (11–31 cm),
307 although a stronger length-dependency emerged respect to 2016. Lemon sole also distributed
308 similarly to plaice, with small individuals (14–20 cm) having a preference for the lower

309 compartment and bigger individuals distributing uniformly. *Nephrops* maintained a strong
310 preference for the lower compartment.

311 In the test trawl equipped with the rising float-lines, the vertical separation of juvenile haddock
312 and whiting were affected by the stimulator. Small haddock were raised into the upper
313 compartment in greater numbers, eliminating the length-dependency in vertical distribution.
314 However, the effect was significant for few length classes (13–16 cm). A stronger preference for
315 the upper compartment was shown by whiting of all the main length classes represented (14–40
316 cm; Fig. 3, test trawl), which resulted significant for individuals between 17 and 30 cm (Fig. 3,
317 delta). A preference for the upper compartment emerged also in cod between 22 and 54 cm (Fig.
318 3, test trawl); however, the difference respect to the vertical separation in the baseline trawl was
319 not significant statistically (Fig. 3, delta). No difference in vertical distribution was observed in
320 either flatfish species. Small *Nephrops* (17–27 mm) entered in significant higher numbers the
321 lower compartment, with almost no individual of these length classes caught in the upper
322 compartment.

323 Discussion

324 The results obtained in this study reiterate the efficiency of the design used as baseline, originally
325 developed by Karlsen et al. (2015) and partially modified in Melli et al. (2018), in separating fish
326 from *Nephrops*. In previous studies, as well as in the baseline trawl of this study, cod and often
327 whiting showed a strongly length-dependent distribution, with small individuals showing a
328 significant preference for the lower compartment (Valdemarsen et al., 1985; Ferro et al., 2007;
329 Krag et al., 2009a). However, in this study and in Melli et al. (2018) the length-dependent
330 preference for the lower compartment of cod was limited to individuals below 18 cm and most

331 whiting above 17 cm had a strong preference for the upper compartment. Similarly, plaice and
332 lemon sole were described to have a preference for the lower compartment (Krag et al., 2009a)
333 but in this study (in 2016) and in the baseline trawl of Melli et al. (2018), lemon sole showed a
334 uniform distribution. These differences in vertical separation between studies are difficult to
335 interpret and may be associated to many environmental and technical factors such as current
336 direction and intensity, water flow intensity in the trawl, circumference of the tapered section of
337 the trawl before the separation, etc.

338 Active behaviour stimulators could play a role in stabilizing the vertical separation efficiency, thus
339 reducing the described variability across experiments. According to our results, only few species
340 and length-groups needed to be further stimulated to rise into the upper compartment: small
341 haddock and whiting, cod and flatfish. These groups showed either a random distribution or a
342 preference for the lower compartment. Although roundfish below 15 cm are likely to be selected
343 out in a lower compartment made of 90 mm diamond mesh size, i.e. the commercial mesh size in
344 the Skagerrak Sea, separating them from shellfish can reduce physical damages to the individuals
345 (Karlsen et al., 2015), enhancing their survival. The results of the current study proved that the
346 vertical separation of all these groups can be partially improved by adding simple behaviour
347 stimulators, without complicating the fishing operation or increasing the amount of *Nephrops* that
348 enters the upper compartment. However, of the two stimulators tested in this study, none
349 managed to improve simultaneously the separation of all these three groups. Furthermore, the
350 improvement was so limited that it would unlikely be considered by the legislation or the
351 fishermen.

352 The chain curtain was significantly effective in raising small cod (7–16 cm) and, for a limited length
353 range, plaice (27–32 cm). Both species lost their preference for the lower compartment in favour
354 of a more uniform distribution. As cod and flatfish are, among the species considered, those
355 showing the strongest tendency to swim in close proximity to the lower netting panel (Fryer et al.,
356 2017), we believe that the chain curtain was successful in stimulating fish avoidance behaviour.
357 Fish that are forced to encounter an obstacle or to pass through a dark area have been observed
358 to speed up and attempt to keep position ahead of it (Glass and Wardle, 1995; He et al., 2008;
359 Krag et al., 2009b). This eventually has led them to rise into the upper compartment (Glass and
360 Wardle, 1995). However, considering the strong mechanical stimulus represented by the moving
361 chains we expected a stronger effect. The lack of a strong response to the stimulation can be
362 explained by both physiological constraints and behaviour. On one hand, fish could be too
363 exhausted to react to the stimulator when this is located at the separation point. Fish in the trawl
364 extension are assumed to rely on anaerobic swimming which allows short bursts but not
365 continuous extended swimming (Webb, 1994). Moreover, studies in laboratory conditions proved
366 that the maximum swimming speed is often length-dependent (He, 1993; Winger et al., 1999). On
367 the other hand, video observations in shallow water revealed that the chains were bending
368 backwards due to the strong water flow. Therefore, smaller individuals might have found a
369 preferred path below the chains, similarly to what described as a response to the footrope before
370 fish enter the trawl (Winger et al., 2010).

371 In contrast, the rising float-lines significantly affected small haddock (13–16 cm) and whiting (18–
372 27 cm), although the improvement in vertical separation was minimal due to the already good
373 separation achieved in the baseline trawl for these species. Moreover, the low number of haddock
374 caught during the survey caused wide CIs, which prevented any conclusion about the effect on

375 bigger length classes. No effect was detected on the two flatfish species analysed, despite the
376 substantial obstacle represented by the ropes and floats on the lower netting panel. In contrast,
377 undersized *Nephrops* (17–27 cm) were affected by the rising float-lines and entered almost
378 exclusively the lowest compartment. The difference, although significant, is minimal due to the
379 already strong preference for the lower compartment of this species. Even though few individuals
380 in this length-range would be retained with the mesh sizes used commercially, this result is of
381 interest as *Nephrops*, and especially the smaller individuals, are usually considered to be passive in
382 this section of the trawl (Main and Sangster, 1985). It is unclear what might have caused this
383 effect, but it is likely a consequence of the contact between *Nephrops* and the components of the
384 stimulator (i.e. floats and lines).

385 Contrary to our expectations, moving the stimulator ahead of the separation to increase the time
386 available to fish to react to the stimulus did not improve considerably the vertical separation. One
387 possible explanation is that the distance covered by the stimulator was not sufficient to trigger a
388 response in time to affect the separation. However, in Melli et al. (2018) a visual stimulation (LED
389 lights) was similarly applied ahead of the separation (2 m) and for most species it did modify the
390 vertical separation, although increasing the proportion of individuals entering the lower
391 compartment. Another possibility is that the type of stimulation did not cause a response.
392 Previous studies using fluttering ropes and floats were relatively successful in stimulating fish
393 escape through a square mesh panel (Herrmann et al., 2015; Krag et al., 2016; Grimaldo et al.,
394 2017). However, these studies applied the stimulators in bigger section of the trawls respect to the
395 one used in this study. Possibly, in a narrower section fish are overstimulated or stressed for this
396 type of stimulation to be effective.

397 In conclusion, despite applying relatively strong stimuli and in different position respect to the
398 point of separation we were not able to substantially improve the separation of fish from
399 *Nephrops*. The baseline design of the horizontally divided trawl codend offers already an efficient
400 separation, and could be at present adopted by the industry. Perhaps, the Northeast Atlantic
401 *Nephrops*-directed trawl fishery, which is characterized by narrow trawl sections and muddy
402 bottoms, does not represent the right application for this type of active swimming stimulators.
403 However, the responses to the stimulators identified in this study could be applied to other trawl
404 fisheries that could benefit from species separation. Finally, active swimming stimulators are more
405 likely to be effective at an earlier stage in the capture process, when fish are more responsive and
406 their level of stress and exhaustion is lower.

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412 **References**

413 Akaike, H. 1974. A new look at the statistical model identification. IEEE Trans. Automat. Contr.
414 19(6), 716–723. <https://doi.org/10.1109/TAC.1974.1100705>

415 Briggs, R.P. 1992. An assessment of nets with a square mesh panel as a whiting conservation tool
416 in the Irish Sea *Nephrops* fishery. Fish. Res. 13, 133–152. [https://doi.org/10.1016/0165-](https://doi.org/10.1016/0165-7836(92)90023-M)
417 7836(92)90023-M

418 Burnham, K.P., and Anderson, D.R. 2002. Model selection and multimodel inference: a practical
 419 information-theoretic approach. 2nd ed. Springer, New York.

420 Catchpole, T.L., and Revill, A.S. 2008. Gear technology in *Nephrops* trawl fisheries. Rev. Fish Biol.
 421 Fish. 18, 17–31. <https://doi.org/10.1007/s11160-007-9061-y>.

422 Drewery, J., Bova, D., Kynoch, R.J., Edridge, A., Fryer, R.J., and O'Neill, F.G. 2010. The selectivity of
 423 the Swedish grid and 120 mm square mesh panels in the Scottish *Nephrops* trawl fishery. Fish.
 424 Res. 106(3), 454–459. <https://doi.org/10.1016/j.fishres.2010.09.020>

425 Efron, B. 1982. The jackknife, the bootstrap and other resampling plans. SIAM Monograph No. 38,
 426 CBMS-NSF.

427 European Commission 2018. Commission Delegated Regulation (EU) 2018/45 of 20 October 2017
 428 establishing a discard plan for certain demersal fisheries in the North Sea and in Union waters of
 429 ICES Division IIa for the year 2018. Official Journal of the European Communities, L7: 6–12.

430 European Union 2013. Regulation (EU) No 1380/2013 of the European Parliament and of the
 431 Council of 11 December 2013 on the Common Fisheries Policy, amending Council Regulations (EC)
 432 No 1954/2003 and (EC) No 1224/2009 and repealing Council Regulations (EC) No 2371/2002 and
 433 (EC) No 639/2004 and Council Decision 2004/585/EC. Official Journal of the European
 434 Communities, L354: 22–61.

435 Ferro, R.S.T., Jones, E.G., Kynoch, R.J., Fryer, R.J., Buckett, B.E. 2007. Separating species using a
 436 horizontal panel in the Scottish North Sea whitefish trawl fishery. ICES J. Mar. Sci. 64, 1543–1550.
 437 <https://doi.org/10.1093/icesjms/fsm099>

438 Fryer, R.J., Summerbell, K., and O'Neill, F.G. 2017. A meta-analysis of vertical stratification in
 439 demersal trawl gears. *Can. J. Fish. Aquat. Sci.* 999, 1–8. <https://doi.org/10.1139/cjfas-2016-0391>

440 Glass, C.W., and Wardle, C.S. 1995. Studies on the use of visual stimuli to control fish escape from
 441 codends. II. The effect of a black tunnel on the reaction behaviour of fish in otter trawl
 442 codends. *Fish. Res.* 23(1–2), 165–174. . [https://doi.org/10.1016/0165-7836\(94\)00331-P](https://doi.org/10.1016/0165-7836(94)00331-P)

443 Graham, N. 2010. Technical measures to reduce bycatch and discards in trawl fisheries. *In* He, P.
 444 (Ed.), *Behavior of Marine Fishes: Capture Processes and Conservation Challenges*, pp. 237–264.
 445 Wiley-Blackwell, Arnes, IA.

446 Graham, N., and Ferro, R.S.T. 2004. The Nephrops fisheries of the Northeast Atlantic and
 447 Mediterranean: a review and assessment of fishing gear design. *ICES Coop. Res. Rep.* 270.

448 Graham, N., and Fryer, R.J. 2006. Separation of fish from *Nephrops norvegicus* into a two-tier cod-
 449 end using a selection grid. *Fish. Res.* 82, 111–118 <https://doi.org/10.1016/j.fishres.2006.08.011>

450 Grimaldo, E., Sistiaga, M., Herrmann, B., Larsen, R.B., Brinkhof, J., and Tatone, I., 2017. Improving
 451 release efficiency of cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) in the
 452 Barents Sea demersal trawl fishery by stimulating escape behaviour. *Can. J. Fish. Aquat. Sci.* 75(3),
 453 402–416. <https://doi.org/10.1139/cjfas-2017-0002>

454 He, P. 1993. Swimming speeds of marine fish in relation to fishing gears. *In* *ICES Mar. Sci. Symp.*
 455 196, 183–189.

456 He, P., Smith, T., and Bouchard, C. 2008. Fish behavior and species separation for the Gulf of Main
 457 multispecies trawls. *J. Ocean. Tech.* 3, 60–77.

458 Herrmann, B., Sistiaga, M.B., Nielsen, K.N., and Larsen, R.B. 2012. Understanding the size
 459 selectivity of redfish (*Sebastes* spp.) in North Atlantic trawl codends. J. Northw. Atl. Fish. Sci. 44, 1–
 460 13. <https://doi.org/10.2960/J.v44.m680>

461 Herrmann, B., Wienbeck, H., Karlsen, J.D., Stepputtis, D., Dahm, E., and Moderhak, W. 2015.
 462 Understanding the release efficiency of Atlantic cod (*Gadus morhua*) from trawls with a square
 463 mesh panel: effects of panel area, panel position, and stimulation of escape response. ICES J. Mar.
 464 Sci. 72(2), 686–696. <https://doi.org/10.1093/icesjms/fsu124>

465 Herrmann, B., Sistiaga, M., Rindahl, L., and Tatone, I. 2017. Estimation of the effect of gear design
 466 changes on catch efficiency: Methodology and a case study for a Spanish longline fishery targeting
 467 hake (*Merluccius merluccius*). Fish. Res. 185, 153–160.
 468 <http://doi.org/10.1016/j.fishres.2016.09.013>

469 Holst, R., Ferro, R.S., Krag, L.A., Kynoch, R.J., and Madsen, N. 2009. Quantification of species
 470 selectivity by using separating devices at different locations in two whitefish demersal trawls. Can.
 471 J. Fish. Aquat. Sci. 66(12), 2052–2061. <https://doi.org/10.1139/F09-145>

472 Karlsen, J.D., Krag, L.A., Albertsen, C.M., and Frandsen, R.P. 2015. From fishing to fish processing:
 473 separation of fish from crustaceans in the Norway lobster-directed multispecies trawl fishery
 474 improves seafood quality. PLOS ONE 10(11), e0140864.
 475 <https://doi.org/10.1371/journal.pone.0140864>

476 Katsanevakis, S. 2006. Modeling fish growth: model selection, multi-model inference and model
 477 selection uncertainty. Fish. Res. 81, 229–235. <https://doi.org/10.1016/j.fishres.2006.07.002>

478 Kelleher, K. 2005. Discards in the world's marine fisheries: an update. FAO Fisheries Technical
 479 Paper No. 470. Food and Agriculture Organization of the United Nations, Rome, Italy.

480 Kim, Y.H., and Whang, D.S. 2010. An actively stimulating net panel and rope array inside a model
 481 cod-end to increase juvenile red seabream escapement. Fish. Res. 106(1), 71–75. .
 482 <https://doi.org/10.1016/j.fishres.2010.07.005>

483 Krag, L.A., Frandsen, R.P., and Madsen, N. 2008. Evaluation of a simple means to reduce discard in
 484 the Kattegat-Skagerrak *Nephrops* (*Nephrops norvegicus*) fishery: Commercial testing of different
 485 codends and square-mesh panels. Fish. Res. 91(2-3), 175–186.
 486 <https://doi.org/10.1016/j.fishres.2007.11.022>

487 Krag, L.A., Holst, R., and Madsen, N. 2009a. The vertical separation of fish in the aft end of a
 488 demersal trawl. ICES J. Mar. Sci. 66(4), 772–777. <https://doi.org/10.1093/icesjms/fsp034>

489 Krag, L.A., Madsen, N., and Karlsen, J.D. 2009b. A study of fish behaviour in the extension of a
 490 demersal trawl using a multi-compartment separator frame and SIT camera system. Fish. Res.
 491 98(1–3), 62–66. <https://doi.org/10.1016/j.fishres.2009.03.012>

492 Krag, L.A., Herrmann, B., and Karlsen, J.D. 2014. Inferring fish escape behaviour in trawls based on
 493 catch comparison data: model development and evaluation based on data from Skagerrak,
 494 Denmark. PLOS ONE 9(2), e88819. <https://doi.org/10.1371/journal.pone.0088819>

495 Krag, L.A., Herrmann, B., Karlsen, J.D., and Mieske, B. 2015. Species selectivity in different sized
 496 topless trawl designs: Does size matter? Fish. Res. 172, 243–249.
 497 <https://doi.org/10.1016/j.fishres.2015.07.010>

498 Krag, L.A., Herrmann, B., Feekings, J., Lund, H.S., and Karlsen, J.D. 2016. Improving escape panel
 499 selectivity in *Nephrops*-directed fisheries by actively stimulating fish behavior. Can. J. Fish. Aquat.
 500 Sci. 74(4), 486–493. <https://doi.org/10.1139/cjfas-2015-0568>

501 Main, J., and Sangster, G.I. 1985. The behaviour of the Norway Lobster, *Nephrops norvegicus* (L.),
 502 during trawling. Scot. Fish. Res. Rep. No. 34. Department of Agriculture and Fisheries for Scotland.
 503 Aberdeen. pp. 23

504 Melli, V., Krag, L.A., Herrmann, B., and Karlsen, J.D. 2018. Investigating fish behavioural responses
 505 to LED lights in trawls and potential applications for bycatch reduction in the *Nephrops*-directed
 506 fishery. ICES J. Mar. Sci. <https://doi.org/10.1093/icesjms/fsy048>

507 Millar, R.B. 1993. Incorporation of between-haul variation using bootstrapping and nonparametric
 508 estimation of selection curves. Fish. Bullet. 91, 564–572.

509 Valdemarsen, J.W., Engas, A., and Isaksen, B. 1985. Vertical entrance into a trawl of Barents Sea
 510 gadoids as studied with a two-level fish trawl. ICES CM 1985/ B:46.

511 Videler, J.J., and Wardle, C.S. 1991. Fish swimming stride by stride: speed limits and
 512 endurance. Rev. Fish Biol. Fisher. 1(1), 23–40. <https://doi.org/10.1007/BF00042660>

513 Wardle, C.S. 1993. Fish behaviour and fishing gear. In Pitcher, TJ (Ed.) Behaviour of teleost fishes.
 514 2nd ed. Chapman & Hall, London. pp. 609–643.

515 Webb, P.W. 1994. Exercise performance of fish. In Jones, JH (Ed.) Advances in Veterinary Science
 516 and Comparative Medicine, Comparative Vertebrate Exercise Physiology: Phyletic Adaptations,
 517 38(B), 1–49.

518
519 Wileman, D., Ferro, R.S.T., Fonteyne, R., and Millar, R.B. 1996. Manual of methods of measuring
520 the selectivity of towed fishing gears. ICES Coop. Res. Rep. 215.

521 Winger, P.D., He, P., and Walsh, S.J. 1999. Swimming endurance of American plaice
522 (*Hippoglossoides platessoides*) and its role in fish capture. ICES J. Mar. Sci. 56(3), 252–265.
523 <https://doi.org/10.1006/jmsc.1999.0441>

524 Winger, P.D., Eayrs, S., and Glass, C.W. 2010. Fish behaviour near bottom trawls. *In* He, P. (Ed.),
525 Behavior of marine fishes: capture processes and conservation challenges, pp. 67–102. Wiley-
526 Blackwell, Arnes, IA.

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537 **Figures labels**

538 **Figure 1.** Schematic illustration of the baseline trawl and of the active behaviour stimulators tested in 2016 and 2017.

539 A) Baseline design of the horizontally divided trawl codend. Full grey lines represent selvedges. Each compartment
540 includes an extension (4.5 m) and a codend. The length of the codends varied between experiments: (1) length of
541 codends in 2016, (2) length of codends in 2017. Floats on the codends (dashed) were added only in 2017. Underwater
542 pictures are oriented towards the point of separation, viewing the two compartments. D) and E), the position of the
543 stimulator is indicated by a white arrow.

544 **Figure 2.** Length-based vertical separation efficiency of the six species analysed during the chain curtain experiment.

545 Lengths are in cm for fish species and mm for *Nephrops*. In the first two columns, the curve (solid line) represents the
546 modelled vertical separation fitted to the experimental points (dots) in the baseline and test trawls. The grey bands
547 represent the 95% Efron CIs and the dash-dot line is the length distribution of the data. The dashed horizontal line,
548 located at 0.67, describes an equal preference for entering either compartment. In the third column, the solid line
549 represents the difference (Delta) in vertical separation between the baseline and test trawls, accounting for
550 synchronized hauls. The grey bands are the 95% Efron CIs and the dashed line represents no difference in vertical
551 separation.

552

553 **Figure 3.** Length-based vertical distribution efficiency of the six species analysed during the rising float-lines

554 experiment. Lengths are in cm for fish species and mm for *Nephrops*. In the first two columns, the curve (solid line)
555 represents the modelled vertical distribution fitted to the experimental points (dots) in the baseline and test trawls.
556 The grey bands represent the 95% Efron CIs and the dash-dot line is the length distribution of the data. The dashed
557 horizontal line, located at 0.67, describes an equal preference for entering either compartment. In the third column,
558 the solid line represents the difference (Delta) in VS between the baseline and test trawls, accounting for synchronized
559 hauls. The grey bands are the 95% Efron CIs and the dashed line represents no difference in vertical distribution.

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563 **Tables**

564

565 **Table 1**

566 Overview of the experimental hauls, showing the technical and environmental parameters and total catch (kg) per
 567 each of the four compartments. BU = baseline upper compartment; BL = baseline lower compartment; TU = test upper
 568 compartment; TL = test lower compartment. Hauls were separated by stimulator (Stim.), i.e. chain curtain (C) and
 569 rising float-lines (F). The position of the stimulator was shifted from the Starboard trawl (S) to the Port trawl (P).

Haul No.	Year	Stim.	Test trawl	Start time (hh:mm)	Towing time (hh:mm)	Depth (m)	Wind (m/s)	Speed (kn)	BU (kg)	BL (kg)	TU (kg)	TL (kg)
1	2016	C	P	13:20	01:00	120	6	2.7	326	132	448	138
2	2016	C	P	16:00	01:00	105	7	2.6	271	130	75	120
3	2016	C	P	08:15	02:00	63	8	2.6	100	175	125	170
4	2016	C	S	15:20	02:00	61	-	2.6	95	157	120	135
5	2016	C	S	08:10	01:00	31	3	2.6	154	218	197	163
6	2016	C	P	10:50	01:30	38	3	2.6	144	180	133	213
7	2016	C	P	14:45	01:00	86	3	2.6	176	79	375	230
8	2016	C	P	16:55	01:05	87	3	2.7	136	158	550	182
9	2016	C	P	07:25	01:10	78	3	2.6	721	380	1179	360
10	2016	C	P	12:40	00:50	85	8	2.6	643	190	330	161
11	2016	C	P	16:30	00:40	87	9	2.6	298	240	238	143
12	2016	C	P	07:20	00:45	84	9	2.6	420	183	288	114
13	2016	C	S	09:45	01:00	61	9	2.6	33	18	53	25
14	2016	C	S	12:45	02:15	62	8	2.6	70	32	149	50
1	2017	F	S	10:00	00:30	17	8	2.7	73	153	166	128
2	2017	F	S	15:30	01:30	70	8	2.7	487	209	725	226
3	2017	F	S	07:40	01:00	85	12	2.7	260	136	420	140
4	2017	F	S	11:35	01:00	87	10	2.7	210	102	375	114
5	2017	F	S	14:55	01:10	87	10	2.7	260	130	605	250
6	2017	F	S	12:00	01:20	42	5	2.7	65	62	40	40
7	2017	F	P	05:30	02:00	39	4	2.7	101	144	170	180
8	2017	F	P	12:30	01:30	91	6	2.7	513	232	660	200
9	2017	F	P	06:00	01:00	38	10	2.7	87	163	66	118
10	2017	F	P	11:10	01:30	76	10	2.7	315	330	230	91

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572 **Table 2.** Number of hauls and number of individuals per species per compartment included in the two experiments. U
573 = upper compartment; L = lower compartment. Species that were subsampled are indicated with the raised total
574 number and the actual number of individuals measured (in brackets).

Experiment	Species	No. of hauls	Baseline trawl		Test trawl	
			nU	nL	nU	nL
Chain curtain	Cod	11	640	502	1002	322
	Haddock	8	1714	518	1160	250
	Whiting	11	5111 (4123)	670	5479 (3650)	485
	Plaice	11	1490 (870)	1505	2823 (1635)	2116
	Lemon sole	8	432	173	562	154
	<i>Nephrops</i>	6	1731	5380 (2750)	1801	5642 (2794)
Rising float-lines	Cod	9	2803	1081	4234	1473
	Haddock	6	473	189	547	110
	Whiting	10	8462 (8025)	1376	12640 (11636)	838
	Plaice	10	1063	1270	1205	1584
	Lemon sole	8	382	411	671	580
	<i>Nephrops</i>	4	799	6215 (4136)	615	7756 (4327)

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585 **Table 3.** Fit statistics for the modelled vertical separation efficiencies of the two experiments. DoF denotes the degree
586 of freedom and was calculated by subtracting the number of model parameters from the number of length classes in
587 the dataset. Significant p -values ($p < 0.05$; indicated by *) express that the residual variation between the models fit
588 and the experimental data required further investigation.

Experiment	Species	Baseline trawl			Test trawl		
		p -value	Deviance	DoF	p -value	Deviance	DoF
Chain curtain	Cod	0.54	59.28	61	0.03*	89.73	66
	Haddock	0.08	45.17	33	0.64	26.60	30
	Whiting	0.09	37.27	27	0.50	30.34	31
	Plaice	0.06	39.02	27	0.02*	41.70	25
	Lemon sole	0.09	26.35	18	0.45	19.08	19
	<i>Nephrops</i>	0.22	44.33	38	0.03*	57.10	39
Rising float-lines	Cod	0.66	48.30	53	0.09	68.57	54
	Haddock	0.32	23.43	21	0.18	27.86	22
	Whiting	0.06	45.38	32	<0.01*	55.70	32
	Plaice	0.20	40.75	34	0.47	32.86	33
	Lemon sole	0.25	22.62	19	0.26	21.30	18
	<i>Nephrops</i>	<0.01*	74.28	41	0.45	43.46	43

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Figure

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