1	Investigating fish behavioural responses to LED lights in trawls and
2	potential applications for bycatch reduction in the Nephrops-directed
3	fishery.
4	V. Melli ¹ *, L.A. Krag ¹ , B. Herrmann ^{2,3} , J.D. Karlsen ¹
5	
6	¹ DTU Aqua, National Institute of Aquatic Resources, North Sea Science Park, DK-9850, Hirtshals, Denmark
7	² SINTEF Fisheries and Aquaculture, Willemoesvej 2, DK-9850 Hirtshals, Denmark
8	³ University of Tromsø, Breivika, N-9037 Tromsø, Norway
9	
10	Email addresses: VM – <u>vmel@aqua.dtu.dk</u> ; LAK – <u>lak@aqua.dtu.dk;</u> BH –
11	<u>Bent.Herrmann@sintef.no</u> ; JDK – juka@aqua.dtu.dk
12	
13	Correspondence: Valentina Melli, DTU Aqua, National Institute of Aquatic Resources, North Sea
14	Science Park, DK-9850, Hirtshals, Denmark.
15	Telephone: +45 35883270; e-mail: <u>vmel@aqua.dtu.dk</u>
16	
17	
18	
19	
20	
21	
22	
23	
24	
25	
26	
27	
28	
29	
30	
31	

32

33 Abstract

Light Emitting Diodes (LED) have been tested in trawl fisheries to reduce the bycatch of 34 unwanted species through behavioural stimulation. Previous studies used LED lights to 35 either highlight escaping routes or increase the contact rate with square mesh panels. 36 37 However, phototactic responses (moving towards or away from light sources) to LED lights 38 could also be exploited to separate species during the catching process. We investigated 39 if either positive or negative phototaxis can be triggered in fish to modify their vertical 40 distribution in the aft section of a horizontally separated trawl codend. The aim was to separate fish into the upper compartment and Nephrops (Nephrops norvegicus) into the 41 lower compartment. We conducted two different experiments in front of the separation 42 43 into compartments, inserting green LED lights in the upper and lower netting panel, respectively. Species vertical separation was analysed and compared in two identical 44 45 trawls towed in parallel, one equipped with lights and one without. Significant differences 46 in species vertical distribution were observed; however, most effects resulted in increased number of individuals entering the lower compartment. No clear species-specific 47 phototactic response was identified and the results highlighted the challenges of inferring 48 behavioural responses in trawls. Future steps required to improve the understanding of 49 50 fish reactions to artificial lights are discussed.

51

52 Keywords

53 LED lights; phototaxis; vertical separation; *Nephrops*; bycatch reduction

54

56

- 57
- 58

59 **1. Introduction**

60 Artificial light affects the behaviour of many species, both terrestrial and marine. Most 61 species are known to respond to light by either positive or negative phototaxis, i.e. moving 62 respectively towards or away from the light source (Pascoe, 1990; Marchesan et al., 2005). 63 In the marine environment phototaxis has been observed in both invertebrates and teleost fish (Verheijen, 1960) and described as the consequence of several behavioural 64 responses. Positive phototaxis can result from e.g. searching for species-specific preferred 65 66 light levels, disorientation or prey availability in proximity of the light source (Verheijen, 1960; Marchesan et al., 2005; Arimoto et al., 2010). Negative phototaxis has also been 67 68 related to light level preferences, as well as to anti-predator avoidance behaviours 69 (Marchesan et al., 2005; Ryer et al., 2009). An approaching light can be visually interpreted 70 as the increasing proximity of an unknown danger, which frequently triggers anti-predator responses (Domenici, 2002). In general, when a phototactic response occurs, whether it 71 72 is positive or negative phototaxis, it is species-specific and depends on environmental 73 factors and the physical characteristics of the light source (Marchesan et al., 2005).

Species response to artificial lights found an early application in fisheries. Positive phototaxis has been used for centuries in night fishing to catch cephalopods and schooling fish (Ben-Yami, 1976; Inada and Arimoto, 2007; Arimoto et al., 2010). Over time, the use of lights as lures has been adopted by a variety of fisheries, both artisanal and industrial, such as purse seines, gillnets, longlines, and pots (Ben-Yami, 1976; Bryhn et al., 2014;

Nguyen et al., 2015; Nguyen et al., 2017). The lights used in fisheries have also developed 79 accordingly, growing in intensity and endurance, and becoming cheaper and more 80 available for individuals and whole industries. Recently, artificial lights have aroused 81 82 interest from researchers in gear technologies as a potential stimulus to improve gear 83 selectivity and reduce the bycatch of unwanted species. For example, lights attached to a 84 partially raised footrope in a shrimp trawl allowed fish to escape below it, resulting in a 85 reduction of fish bycatch (Hannah et al., 2015). Inside a midwater trawl targeting Pacific 86 hake (Merluccius productus) escape windows with lights were preferred by Chinook salmon (Oncorhynchus tshawytscha; Lomeli and Wakefield, 2014). Artificial lights used as 87 visual deterrents in gillnets have significantly reduced the bycatch of sea turtles, without 88 89 affecting the catch of the target fish species (Wang et al., 2010).

90 Despite these successes, species-specific behavioural responses to light stimuli are still 91 not fully understood and the application of light in trawls often produces unexpected results. Hannah et al. (2015) attached lights to a grid in a shrimp trawl to visually stimulate 92 93 fish to follow the grid to an escape opening. As a result, most fish, which previously tried 94 to avoid the grid, swam through it and were caught. Similar results were obtained by 95 Larsen et al. (2017), who used lights to highlight the escape opening in a Nordmøre grid. 96 Grimaldo et al. (2017) tested lights on free moving ropes in a square mesh section to increase the contact probability of cod (Gadus morhua) and haddock (Melanogrammus 97 98 aeglefinus) with the netting; thus, enhancing their escape rate. Video observations throughout the experiment highlighted different behaviours in the two gadoids, with 99 neither of them being useful to improve their escape rate. Haddock showed a panic 100 101 reaction to the moving lights, which prevented individuals from approaching the meshes

at the correct angle to escape. In contrast, cod remained stationary in front of the lights 102 103 and seemed to be unaffected by them. These examples suggest that the complexity of stimuli received by fish inside a trawl, such as visual and mechanical obstacles (e.g. a grid) 104 and the background illuminated (e.g. netting), might overcome potential phototactic 105 106 responses. All of these studies have applied lights directly in the area providing an escape 107 route (i.e. open window, square mesh panel, etc.) where an immediate response is 108 necessary for fish to escape. It is not known if lights can be used to gradually influence 109 species position before the point of interest.

110 In this study we investigated if: i) phototaxis can be exploited to modify fish vertical distribution before a separation into two stacked compartments; and ii) either positive or 111 112 negative phototaxis is efficient in leading fish into the upper compartment. We used the 113 Nephrops (Nephrops norvegicus) directed trawl fishery as a case study, as the horizontally 114 divided design has proved to have a great potential for reducing bycatch in this fishery 115 (Main and Sangster, 1985a; Krag et al., 2009; Karlsen et al., 2015). Separating fish from 116 Nephrops has two major advantages: i) fish in the upper compartment can be selected out with a larger mesh size or released, in accordance with quota availability (Krag et al., 117 2008; Frandsen et al., 2010), and ii) the quality of the fish bycatch can benefit from less 118 119 interaction with shellfish; hence, reducing internal and external damage (Karlsen et al., 2015). Due to the small mesh sizes used to retain the target species, the fish bycatch in 120 121 this fishery includes commercial and undersized individuals of several species (Kelleher, 2005). Because *Nephrops* is relatively passive inside the trawl, with most individuals rolling 122 along the bottom panel towards the codend (Main and Sangster, 1985b), actively 123 124 swimming fish species can be vertically separated from it. Nevertheless, this separation

depends on the vertical distribution of fish in the funnel and on their swimming capacity; 125 thus, it varies among species and length classes (Main and Sangster, 1985a; Ferro et al., 126 2007; Krag et al., 2009; Rosen et al., 2012). Species that have a tendency to stay close to 127 128 the bottom panel, e.g. cod and flatfish, need to be stimulated to rise or they will most 129 likely enter the lower compartment together with the crustaceans. Thus, visual and 130 mechanical stimulations have been tested to modify species vertical separation. For 131 example, the heights of the entrance to each compartment have been optimized to make 132 the upper compartment appear like the clearest path (Glass et al., 1993; Krag et al., 2009). Visual stimuli, such as a black tunnel (He et al., 2008) at the entrance of the lower 133 134 compartment have successfully changed the vertical preference of cod. Similarly, mechanical stimuli such as frames and grids, which obstruct the entrance to the lower 135 compartment, have succeeded in separating most fish from Nephrops (Karlsen et al., 136 137 2015). However, to the best of our knowledge, nobody has previously attempted to use 138 artificial light phototaxis to influence species vertical separation.

139

2. Materials and methods

140 2.1 Baseline trawl

The horizontally separated trawl used in this study was an adaptation of a trawl tested by Karlsen et al. (2015). We used two identical Combi trawls (40 m long footrope, 420 meshes fish circle, 80 mm mesh size) made of two net panels before the separation and four net panels after the separation into an upper and lower compartment by a horizontal net panel. Both the compartments had nominal 40 mm meshes (41.65 ± 1.33 dry; 1.8 mm twine) diamond that were turned 45 degrees to obtain square meshes. The vertical separation was positioned in the transition between the tapered and non-tapered

sections of the gear, where the inclination of the lower netting of the trawl ends (Fig. 1). 148 149 Respect to the design tested by Karlsen et al. (2015), part of the tapered section was cut out to increase the circumference before the separation from 100 to 140 meshes, which 150 extended the vertical space available to fish in this part of the gear. The entrance of the 151 152 upper compartment was approximately 60 cm high (based on underwater video 153 observations) and sustained by 12 floats (720 g lift) inserted outside the upper netting 154 (Fig. 1). The entrance of the lower compartment was fixed by two frames, 30 cm high and 155 90 cm wide (\emptyset 20 mm stainless steel pipes) which prevented the lower compartment from collapsing (Fig. 1). The frame at the entrance of the lower compartment included two 156 157 vertical bars (30 cm apart) to visually and mechanically stimulate fish to swim into the 158 upper compartment, following Krag et al. (2009).

159 FIGURE 1

160 2.2 Experimental design

Phototactic responses were stimulated in the trawl funnel, before the point of vertical 161 162 separation, using green Electralume® LED lights (Lindgren-Pitman, Pompano Beach, FL, USA; 0.5-2.0 lx). These lights have been used in other studies (Hannah et al., 2015; 163 Grimaldo et al., 2017; Nguyen et al., 2017) because they are compact, inexpensive, 164 165 pressure resistant, and with a battery life of approximately 350 hours. The green colour of these lights (centred at 540 nm) is considered ideal for sea water in coastal temperate 166 areas, because it is less easily absorbed, and thus penetrates deeper. Moreover, some of 167 168 the target species of the study, like cod, have been proven to have a primary sensitivity peak that occurs at 490 nm (blue/green light; Anthony and Hawkins, 1983). 169

To investigate potential phototactic responses, we conducted two experiments. In 170 Experiment 1 we attached 10 Electralume[®] LED lights to the lower netting panel in the aft 171 part of the tapered section and in Experiment 2 we placed them in the corresponding 172 upper netting panel (Fig. 1). In both experiments the 10 lights were attached to two 5 m 173 174 long polypropylene ropes (8 mm diameter, 3 strands), which were fixed respectively to 175 the lower or upper netting panel with cable ties. The lights were blocked in continuous mode and directed towards the forward part of the trawl. Electralume® LED lights emit 176 177 light in all directions except for the rear, with the intensity being higher laterally at about 45 degrees respect to the central axis (V. Melli, personal observations). The distance 178 179 between the last three lights of each rope was reduced to increase the strength of the 180 stimulus while approaching the vertical separation (Fig. 1).

181 2.3 Sea trial

182 The sea trial was conducted on 5-20 September 2016 with the research vessel "Havfisken" (17 m, 373 kW). We used three-wire, twin trawls towed in parallel, with one trawl working 183 184 as the baseline for species separation and the other as the test equipped with the lights. Using this setup, it would normally be assumed that the two trawls encountered the same 185 fish population. However, due to a second experiment located in the forward part of the 186 trawl (Melli et al., 2017), the population entering the baseline and test trawls differed and 187 the two gears were thus analysed separately. To avoid any trawl-dependent effect on the 188 189 vertical separation of the species, the position of the light treatment was shifted from one trawl to the other approximately every sixth haul. Two Type 2 Thyborøn doors (1.78 m², 190 197 kg), with an additional weight of 25 kg, and a 400-kg triangular central clump were 191 192 used to spread the twin trawl-rig. Doors and clump were equipped with distance sensors

193 (Simrad PI) to monitor each trawl spread in the twin-rig. The trawls were rigged with 75 194 m long single wire sweeps with 4.3 cm (diameter) rubber discs. The distance between the 195 two trawls' mouths was estimated to be approximately 50 m. Fishing was conducted in 196 commercial Nephrops and fish grounds in the Skagerrak Sea, at depths between 45 and 197 86 m. According to the optical classification of this area (coastal waters type 1; Aarup et al., 1996), the range of depths was out of the Eutrophic zone (i.e. where less than 1% of 198 the surface light reaches). To be representative of commercial fishing conditions, 199 200 experimental hauls were performed at both day time, between 1h after sunrise and 1h before sunset and night time, between 1h after sunset and 1h before sunrise. The catch 201 in each compartment was weighted and sorted by species. The total length of all 202 203 commercial fish species and the carapace length of Nephrops were measured and rounded down to the nearest cm and mm, respectively. 204

205 2.4 Estimation of the vertical separation efficiency

The aim of the study was to separate fish from *Nephrops*; therefore, we defined the vertical separation efficiency *VS(I)* as the probability of finding a fish of length *I* in the upper compartment, given that it was observed in the upper or lower compartment. For each experiment (1 and 2) and each species, *VS(I)* was estimated for the baseline and test trawls separately based on the catch data summed over all hauls following the method described below.

Let nU_{li} and nL_{li} denote the number of individuals of length class *l* caught and measured in each of the two compartments in each haul *i*, respectively. Then, VS_{li} is the proportion of fish of length *l* caught in the upper compartment compared to the total in a haul *i*:

215
$$VS_{li} = \frac{\frac{nU_{li}}{qU_i}}{\frac{nU_{li}}{qU_i} + \frac{nL_{li}}{qL_i}}$$
 (1)

where qU_i and qL_i are 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*.

219 Assuming that the vertical separation summed over the hauls is representative of how the vertical separation would perform on average, an estimation of the average vertical 220 221 separation can be obtained by pooling the data from the different hauls. A parametric model for VS(l) is defined by VS(l, v), where v is a vector consisting of the parameters of 222 the model. The analysis is therefore reduced to a maximization problem, to estimate the 223 224 values of the parameters \boldsymbol{v} which make the observed experimental data averaged over 225 hauls most likely, assuming that the model is able to describe the data sufficiently well. 226 Thus, the maximum likelihood function for binomial data (2) is minimized with respect to 227 \boldsymbol{v} , which is equivalent to maximizing the probability for the observed data.

228
$$g(\boldsymbol{\nu}) = -\sum_{l} \sum_{i=1}^{h} \left\{ \frac{nU_{il}}{qU_{i}} \times ln(VS(l,\boldsymbol{\nu})) + \frac{nL_{il}}{qL_{i}} \times ln(1.0 - VS(l,\boldsymbol{\nu})) \right\}$$
(2)

where the summations are made over length classes *l* and the *h* hauls belonging to the case analyzed. To find a model for VS(l, v) that is sufficiently flexible to account for the trends in the experimental data we adapted a model often applied in catch comparison studies to determine the efficiency and selectivity of fishing gears (Krag et al. 2014, 2015):

233
$$VS(l, v) = \frac{\exp(f(l, v))}{1.0 + \exp(f(l, v))}$$
 (3)

where *f* is a polynomial of order *k* with coefficients $v_{0},...,v_{k}$ so $\mathbf{v} = (v_{0},...,v_{k})$. $f(l,\mathbf{v})$ is determined as follows:

236
$$f(l, \boldsymbol{\nu}) = \sum_{i=0}^{4} v_i \times \left(\frac{l}{100}\right)^i = v_0 + v_1 \times \frac{l}{100} + v_2 \times \frac{l^2}{100^2} + \dots + v_4 \times \frac{l^4}{100^4}$$
 (4)

Leaving out one or more of the parameters $v_0...v_4$ in (4) provided 31 additional models 237 that were considered as potential models to describe VS(1, v). Based on these models, 238 239 model averaging was applied to describe VS(*l*, *v*) according to how likely the individual 240 models were when compared to each other (Burnham and Anderson, 2002). We called 241 the resulting model the combined model. In the combined model the individual models 242 were ranked and weighted according to their Akaike information criterion (AIC) values (Akaike, 1974; Burnham and Anderson, 2002). Models with AIC values within +10 of the 243 value of the model with the lowest AIC were considered to contribute to VS(1, v) based on 244 the procedure described by Katsanevakis (2006) and Herrmann et al. (2017). The ability 245 of the combined model to describe the experimental data was assessed based on the p-246 247 value and the model deviance respect to the degrees of freedom (DoF). The *p*-value in this 248 analysis expresses the likelihood of obtaining at least as big a discrepancy as that observed 249 between the fitted model and the experimental data by coincidence. Therefore, for the 250 combined model to be a candidate model, the *p*-value should not be below 0.05 and the 251 deviance should be in the same order of the DoF (Wileman et al., 1996). In case of poor 252 fit statistics (p-value <0.05; deviance >>DoF), the model curve plots and the residuals were 253 examined to determine whether there were structural problems in describing the 254 experimental data with the combined model or if it was a case of data overdispersion (Wileman et al., 1996). The value of VS(l, v) for the combined model represents the 255 probability of finding a fish of length / in the upper compartment. A value above 0.5 256 257 indicated a higher probability of finding the individual in the upper compartment. 258 However, to indicate that the proportion of a species entering a given compartment is higher than the height of the opening of that compartment relative to the total section at the point of separation, we adopted the term "preference". Considering that the upper compartment accounted for 67% of the total section, only values of VS(l, v) above 0.67 were consider to represent a significant difference in vertical distribution between the two compartments. Similarly, a value significantly below 0.67 would imply a preference for the lower compartment.

265 Confidence intervals (CIs) for the length-dependent vertical separation efficiency were 266 estimated using a double bootstrap method (Millar, 1993). The procedure accounted for the uncertainty due to between-haul variation in the vertical separation efficiency by 267 selecting h hauls with replacement from the h hauls available for the specific case 268 investigated during each bootstrap repetition. Within-haul uncertainty in the size 269 270 structure of the catch data was accounted for by randomly selecting individuals with replacement from each haul and each compartment separately. The number of fish 271 272 selected from each haul was the number of fish length-measured in that haul in each 273 compartment. For each species, only hauls containing at least 10 individuals in the upper 274 and lower compartments summed were included, following Krag et al. (2014). A total of 1,000 bootstrap repetitions were performed and Efron 95% CIs (Efron, 1982) were 275 276 calculated for the vertical separation curve. By incorporating the combined model approach in each of the bootstrap repetitions we accounted for the additional uncertainty 277 278 on the vertical separation efficiency due to uncertainty in model selection (Herrmann et 279 al., 2017). All the analyses were performed using the software SELNET (Herrmann et al., 2012). 280

281 2.5 Quantifying the effect of the treatment

The length-based, average vertical separation efficiency of the baseline trawl, VSB(I), and 282 test trawl, VST(*I*), for each experiment (1 and 2) was estimated with 95% CIs according to 283 the procedure described in the previous section. In principle, we could have inferred 284 whether the treatment had any significant effect on the vertical separation by overlapping 285 286 the CIs obtained for VSB(I) and VST(I). However, this approach does not take full 287 advantage of our experimental design, in which the baseline and test trawl are fished 288 simultaneously in parallel and are therefore subjected to the same varying fishing 289 conditions between hauls. Therefore, instead of applying the analysis separately for the baseline and test trawl, as described in the previous section, we synchronized the hauls 290 291 selected for the outer bootstrap loop for the baseline and test trawls and for each 292 bootstrap we calculated the treatment effect $\Delta VS(l, \nu)$ on the vertical separation by:

293
$$\Delta VS(l, \mathbf{v}) = VSB(l, \mathbf{v}) - VST(l, \mathbf{v})$$
(5)

294 Through this synchronization in the haul selection and the direct calculation of $\Delta VS(l, \mathbf{v})$ in 295 each bootstrap we removed part of the between-haul variation in vertical separation efficiency and increased the power of the analysis to infer the treatment effect. $\Delta VS(l, v)$ 296 297 can span between -1 and 1, where positive values mean that more individuals of length / 298 are entering the upper compartment in response to the lights. In contrast, negative values 299 mean more individuals are entering the lower compartment. For those length-classes in 300 which the 95% CIs for $\Delta VS(l, v)$ did not contain 0.0, we determined a significant effect of 301 the light treatment.

302 **3. Results**

A total of 18 hauls were conducted, ten hauls for Experiment 1 and eight hauls for Experiment 2 (Table 1). The towing time varied between 30 and 120 min according to the

catch observed with the vessel's eco-sounder, as it was imperative for a correct
interpretation of the vertical separation efficiency that no fish were found ahead of the
separation into two compartments when hauling the catch.

308 TABLE 1

Sufficient data for analysis were collected for six commercial species (Table 2): the target species, *Nephrops*; three roundfish species, cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), and whiting (*Merlangius merlangus*); and two flatfish species, plaice (*Pleuronectes platessa*) and lemon sole (*Microstomus kitt*). Due to the period of the study, very few fish were encountered while fishing in *Nephrops* grounds. Therefore, because the strongest reactions to the lights were expected from fish, only a few hauls during Experiment 1 were used to verify the effect on *Nephrops* (Table 2).

316 TABLE 2

317 Fit statistics for each of the models are reported in Table 3. In most cases, p-values were above 0.05, indicating that the model could be trusted to describe the experimental data. 318 Four models in each experiment had poor fit statistics (p < 0.05, deviance >> DoF): in 319 320 Experiment 1 the models for the baseline trawl of haddock and whiting and for the test trawl for cod and *Nephrops*; and in Experiment 2 the models for haddock and whiting in 321 322 both the baseline and test trawls (Table 3). For these cases the residual deviations between the data and the modelled curves were investigated. No systematic structure 323 was detected. We considered the low *p*-values to be a consequence of overdispersion in 324 325 the data caused by the sub-sampling (e.g. whiting and *Nephrops*) and the high dispersion 326 in those length classes with relative low frequency. Such cases are frequent and have been

reported before (e.g. Larsen et al., 2017). Therefore, we were confident that all the models could be used to describe the vertical separation efficiency. The results for both experiments are hereafter presented by species to facilitate the interpretation of changes in vertical separation efficiency.

331 TABLE 3

332 Nephrops

The separation efficiency curves of both the baseline and test trawls described overall the 333 334 experimental data well (Fig. 2). Where fewer individuals were caught, an increasing binominal noise is observed through the increasing size of the CIs. In both trawls, 335 336 Nephrops showed a strong, significant preference for the lower compartment, with CIs 337 well below 0.67 for all length classes represented (18-62 mm; Fig. 2). The difference in separation efficiency (ΔVS) indicated a significant effect of the light treatment (Fig. 2, 338 Delta). When lights were inserted in the lower panel, *Nephrops* between 40 and 55 mm 339 were found in greater numbers in the lower compartment. 340

341 FIGURE 2

342 **Cod**

The separation efficiency curves for cod described the main trends in the data relatively well in both experiments (Fig. 3). Few individuals above 40 cm were caught; thus, the CIs were broad for the biggest length classes. For cod, there was a length dependency in vertical preference, with smaller individuals more frequently entering the lower compartment. In the baseline trawl, cod of 25-59 cm and 30-43 cm in Experiment 1 and 2, respectively, showed a preference for the upper compartment. However, this

preference disappeared in the test trawl with the light treatment in either position. LED lights in the lower panel (Experiment 1) significantly and negatively affected cod of length 11-18 cm and 28-43 cm (Fig. 3, Delta), corresponding to the two main bulks of length classes caught during the trial. Lights in the upper panel (Experiment 2) did not cause a significant change in vertical distribution, with the exception of, the 30-cm length class which entered more frequently the lower compartment.

355 FIGURE 3

356 Haddock

The separation efficiency curves for haddock represent the experimental data reasonably 357 358 well, without systematic deviations between the experimental points and the modelled 359 curves (Fig. 4). Few individuals above 40 cm were caught; thus, the CIs were broad for the 360 biggest length classes. A large proportion of haddock entered the upper compartment, but a significant preference for this compartment was detected only for few length 361 classes, 18-26 cm and 25-32 cm in the baseline trawl of Experiment 1 and 2, respectively. 362 363 Lights in the lower panel (Experiment 1) did not cause any change in haddock's vertical distribution lights inserted in the upper panel (Experiment 2) significantly and positively 364 affected individuals of 33-42 cm (Fig. 4, Delta). 365

366 FIGURE 4

367 Whiting

The separation efficiency curves for whiting described the main trends in the data very well, with relatively small CIs for length classes with strong data (20-27 cm) (Fig. 5). Whiting generally had a strong length-dependency in its vertical separation. In the

371 baseline trawl, small individuals (5-15 cm) entered the lower compartment in greater 372 numbers, although the result was only significant in Experiment 1. In contrast, whiting belonging to the main bulk of data (20-30 cm) had a strong preference for the upper 373 compartment in the baseline trawl of both experiments. The light treatment did not 374 375 improve the vertical separation of whiting in either experiment. With the lights in the lower panel (Experiment 1), whiting had a more uniform distribution, with no preference 376 for the upper compartment, and the difference was significant for individuals of 20-23 cm 377 378 (Fig. 5, Delta). In Experiment 2, the lights in the upper panel negatively affected individuals between 16 and 22 cm, which were caught significantly more in the lower compartment. 379

380 FIGURE 5

381 Plaice

382 The separation efficiency curves of both the baseline and test trawls described the experimental data for plaice belonging to the main interval of the length classes relatively 383 well (20-40 cm; Fig. 6). A relatively large proportion of plaice were caught in the upper 384 385 compartment, but overall there was a uniform vertical distribution, with the CIs for all 386 length-classes overlapping the horizontal line representing an equal preference for either compartment (Fig. 6). LED lights in the lower compartment (Experiment 1) significantly 387 388 and negatively affected plaice of 23-32 cm (Fig. 6, Delta). Lights in the upper compartment 389 did not cause significant changes in the vertical separation efficiency.

390 FIGURE 6

391 Lemon sole

392 Few lemon sole were caught during the experiments; however, the separation efficiency 393 curves represented the experimental data well (Fig. 7) and the fit statistics indicated that the models could be trusted. In the baseline trawl, lemon sole had a uniform distribution, 394 and thus, according to the size of the entrances of the compartments, entered the upper 395 396 compartment in greater numbers. No change in the vertical separation efficiency was 397 observed when lights were attached to the lower netting panel (Experiment 1), whereas 398 small lemon sole of 17-21 cm were significantly affected by lights in the upper netting 399 panel (Experiment 2), resulting in a preference for the lower compartment (Fig. 7, Delta).

400 FIGURE 7

401 **4. Discussion**

Several stimuli contribute in determining species vertical distribution in the trawl 402 extension. Sound, vibrations, intra- and inter-species interactions, visible background and 403 404 state of fatigue due to the first part of the catching process, as well as individual physical 405 constrains, have been described to influence species separation (Winger et al., 2010; Fryer et al., 2017). When testing lights, these confounding factors often complicate the 406 407 interpretation of results and limit the inference of species-specific behavioural responses. 408 The methodology applied in this study accounted for the variability introduced by other 409 factors than the device tested by towing the baseline and test trawls in parallel. Unfortunately, we could not account for interactions between the light treatment and 410 411 other factors or determine which of the parameters of the light (e.g. intensity, colour, 412 orientation) was the main driver of the response. In this study, we aimed at investigating 413 if phototaxis could be exploited to modify fish vertical distribution and if either positive 414 or negative phototaxis could be efficient in leading fish into the upper compartment.We

found that LED lights in the trawl extension had significant effects on the vertical
distribution of the species investigated. However, we could not conclude these changes
were caused by phototactic responses, i.e. movements directed towards or away from
the lights.

LED lights in the lower panel increased small cod (11-18 cm) preference for the lower 419 420 compartment, while medium-sized cod (28-43 cm) lost the preference for the upper 421 compartment observed in the baseline trawl. Similarly, whiting (20-23 cm) shifted from a clear preference for the upper compartment in the baseline trawl to a uniform 422 423 distribution with LED lights in the lower panel. Small plaice (23-32 cm) were uniformly 424 distributed in the baseline trawl, whereas showed a preference for the lower 425 compartment in the test trawl. Surprisingly, Nephrops between 40 and 55 mm showed a significant increased preference for the lower compartment in the test trawl. This species 426 427 usually has a weakly length-dependent vertical separation, with a higher percentage of individuals above 50 mm (carapace length) entering the upper compartment (Karlsen et 428 429 al., 2015; Graham and Fryer, 2006). Because these individuals would be lost in a compartment with large meshes, i.e. the upper compartment, the potential positive 430 phototaxis observed in this study might be of interest to reduce the loss of the target 431 432 species.

These responses, despite being apparently directed towards the lights, should not be interpreted as positive phototaxis. When testing the lights in the opposite position (upper netting panel) we did not obtain inverted effects respect to those observed in Experiment 1. On the contrary, some species still entered in higher numbers the lower compartment. For example, small whiting (16-22 cm) and small lemon sole (15-21 cm) were both found

in higher numbers in the lower compartment in the test trawl. However, small whiting
were only slightly affected by the lights, partly losing their preference for the upper
compartment, whereas small lemon sole had a strong preference for the lower
compartment when exposed to lights in the upper panel. In contrast, haddock between
33 and 42 cm developed a strong preference for the upper compartment in response to
the lights.. Unfortunately, no data were collected for *Nephrops* in Experiment 2, and thus
any influence of lights in the upper panel on large individuals remains unknown.

According to the results, species-specific phototactic responses were not clearly 445 446 identified. Each species seemed to react mainly to one treatment position, showing only a tendency or no response to the other. Most of the significant changes in vertical 447 448 distribution could be attributed to an increased awareness of the surroundings, panic or species-specific escape behaviours. For example, many demersal species have a tendency 449 450 to move towards the seafloor when threatened (Winger et al., 2010; Gibson, 2014). Unfortunately, the lack of understanding of which parameters of the lights are the main 451 452 drivers of species responses limit the inferential power of this type of study. For example, we cannot exclude that the lack of response to one of the light treatment position was 453 determined by a difference in intensity of the stimulus between the two experiments, 454 455 considering that when attached to the lower panel the lights were partly obscured by the sediment resuspension. The actual light intensity during towing might have strong 456 457 consequences on the type of reaction obtained as species adapted to low light levels are likely to be blinded or disoriented by artificial lights. Moreover, with lights such as the 458 Electralume, which don't emit light in all directions, the orientation of the lights may affect 459 460 species perception of the stimulus. Fish's swimming direction in the trawl funnel, either

towards the codend or in the towing direction, varies because of fatigue, interaction with
other individuals, and panic (Winger et al., 2010). Accordingly, smaller individuals might
be more frequently oriented towards the codend, because their limited swimming
capacity would lead to physical exhaustion (He, 1993; Winger et al., 2010). Furthermore,
species-specific preferred orientations have been described, in particular among flatfish
(Winger et al., 2010)

467 The results obtained in this study indicate that the reaction of selected species to artificial 468 lights and the factors involved in determining the type and strength of the reaction require 469 further study. In particular, the physical parameters of the light such as intensity, colour, 470 orientation, and position should be tested systematically under controlled laboratory 471 conditions before attempting further applications inside a trawl. Without understanding the drivers of the behaviour, even positive results might be inconsistent over time and 472 473 space since commercial fisheries operate in highly variable conditions. Despite the success obtained with lights in static fisheries (Nguyen et al., 2017; Wang et al., 2010) and in the 474 475 forward part of the trawl (Hannah et al., 2015), their attempted application inside trawls have mostly failed to achieve the expected results. In our study, as well as in previous 476 studies (Grimaldo et al., 2017; Larsen at al., 2017; Hannah et al., 2015), green LED lights 477 478 were not only useless as a bycatch reduction measure, but had a negative effect on the vertical distribution of fish, increasing the amount of fish entering the lower compartment 479 480 together with *Nephrops*. Therefore, these lights do not currently represent a solution to improve fish separation from *Nephrops* in the *Nephrops*-directed mixed trawl fishery. 481 Mechanical stimulations might be more efficient in rising flatfish and small roundfish, 482 483 which according to the results of this study are the two groups whose separation still needs to be improved. Nonetheless, artificial lights as a behavioural stimulation during
the fishing process shows great potential for future application, once a more mechanistic
understanding of light and behaviour is acquired. In this study, all species investigated
responded to the lights, even the juveniles, which are known to have a limited swimming
capacity. These behavioural responses might be applicable to reduce bycatch in fisheries
elsewhere.

490 5. Acknowledgements

This study has received funding from the European Maritime and Fisheries Fund (<u>https://ec.europa.eu/fisheries/cfp/emff_en</u>) and the Ministry of Environment and Food of Denmark. Project: Vision - Development of an optimal and flexible selective system for trawl by use of new technology and underexploited fish behaviour (Grant Agreement No 33113-I-16-015).

496 **6. References**

Akaike, H., 1974. A new look at the statistical model identification. IEEE Transactions on Automatic
Control, 19: 716–722. doi:10.1109/TAC.1974.1100705

499 Anthony, P. D., and Hawkins, A. D., 1983. Spectral sensitivity of the cod, *Gadus morhua* L. Marine

500 & Freshwater Behaviour & Phy, 10(2): 145-166. doi:10.1080/10236248309378614

Arimoto, T., Glass, C., and Zhang, X., 2010. Fish vision and its role in fish capture. In: Behaviour of

502 marine fishes: Capture process and conservation challenges. Edited by P. He. Blackwell Publishing

503 Ltd. Iowa, USA. pp 25–40. ISBN: 978-0-8138-1536-7

504 Ben-Yami, M., 1976. Fishing with light. In: FAO of the United Nations. Fishing News Books, Oxford.

- 505 Bryhn, A. C., Königson, S. J., Lunneryd, S., and Bergenius, M. A. J., 2014. Green lamps as visual
- stimuli affect the catch efficiency of floating cod (*Gadus morhua*) pots in the Baltic Sea. Fisheries
- 507 Research, 157: 187-192. doi: 10.1016/j.fishres.2014.04.012
- 508 Burnham, K.P., and Anderson, D.R., 2002. Model Selection and Multimodel Inference: A Practical
- 509 Information-theoretic Approach, 2nd ed. Springer, New York.
- 510 Domenici, P., 2002. The visually mediated escape response in fish: predicting prey responsiveness
- 511 and the locomotor behaviour of predators and prey. Marine and Freshwater Behaviour and
- 512 Physiology, 35(1-2): 87-110. doi: 10.1080/10236240290025635
- 513 Efron, B., 1982. The jackknife, the bootstrap and other resampling plans. *In* Society for industrial
- and applied mathematics (SIAM) Monograph No. 38, CBSM-NSF.
- 515 Ferro, R.S.T., Jones, E.G., Kynoch, R.J., Fryer, R.J., and Buckett, B.E., 2007. Separating species using
- a horizontal panel in the Scottish North Sea whitefish trawl fishery. ICES Journal of Marine Science,
- 517 64: 1543–1550. doi: 10.1093/icesjms/fsm099
- 518 Frandsen, R.P., Madsen, N., and Krag, L.A., 2010. Selectivity and escapement behaviour of five
- 519 commercial fishery species in standard square- and diamond-mesh codends. ICES Journal of
- 520 Marine Science, 67: 1721–1731. doi: 10.1093/icesjms/fsq050
- 521 Gibson, R. N., Nash, R. D., Geffen, A. J., and Van der Veer, H. W., 2014. Flatfishes: biology and 522 exploitation. Eds. John Wiley & Sons.
- 523 Glass, C.W., Wardle, C.S., and Gosden, S.J., 1993. Behavioural studies of the principles underlying
- mesh penetration by fish. *In* ICES Marine Science Symposia, 196: 92–97.
- 525 Graham, N., and Fryer, R.J., 2006. Separation of fish from Nephrops norvegicus into a two-tier cod-
- 526 end using a selection grid. Fisheries Research, 82: 111–118. doi: 10.1016/j.fishres.2006.08.011

527 Grimaldo, E., Sistiaga, M., Herrmann, B., Larsen, R. B., Brinkhof, J., and Tatone, I., 2017. Improving 528 release efficiency of cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) in the 529 Barents Sea demersal trawl fishery by stimulating escape behaviour. Canadian Journal of Fisheries 530 and Aquatic Sciences, (ja). doi: 10.1139/cjfas-2017-0002

- Hannah, R. W., Lomeli, M. J. M., and Jones, S. A., 2015. Tests of artificial light for bycatch reduction
- in an ocean shrimp (*Pandalus jordani*) trawl: Strong but opposite effects at the footrope and near
- the bycatch reduction device. Fisheries Research, 170: 60-67. doi: 10.1016/j.fishres.2015.05.010
- He, P., 1993. Swimming speeds of marine fish in relation to fishing gears. *In* ICES Marine Science
 Symposia, 196: 183-189.
- He, P., Smith, T., and Bouchard, C., 2008. Fish behavior and species separation for the Gulf of Main
 multispecies trawls. Journal of Ocean Technology, 3: 60–77.
- Herrmann, B., Sistiaga, M.B., Nielsen, K.N., and Larsen, R.B. 2012. Understanding the size
 selectivity of redfish (*Sebastes* spp.) in North Atlantic trawl codends. Journal of Northwest Atlantic
 Fishery Science, 44: 1–13. doi: 10.2960/J.v44.m680
- Herrmann, B., Sistiaga, M., Rindahl, L., and Tatone, I., 2017. Estimation of the effect of gear design
 changes on catch efficiency: Methodology and a case study for a Spanish longline fishery targeting
 hake (*Merluccius merluccius*). Fisheries Research, 185: 153-160.
 doi:10.1016/j.fishres.2016.09.013
- Inada, H., and Arimoto, T. (2007). Trends on research and development of fishing light in
 Japan. Journal of the Illuminating Engineering Institute of Japan, 91(4): 199-209.
- 547 Karlsen, J. D., Krag, L. A., Albertsen, C. M., and Frandsen, R. P., 2015. From fishing to fish 548 processing: separation of fish from crustaceans in the Norway lobster-directed multispecies trawl

549 fishery improves seafood quality. PLOS ONE 10(11), e0140864.

- 550 doi:10.1371/journal.pone.0140864
- 551 Katsanevakis, S., 2006. Modeling fish growth: Model selection, multi-model inference and model
- selection uncertainty. Fisheries Research, 81: 229–235. doi:10.1016/j.fishres.2006.07.002
- 553 Kelleher, K., 2005. Discards in the world's marine fisheries: an update. FAO Fisheries Technical
- 554 Paper No. 470. Food and Agriculture Organization of the United Nations, Rome, Italy.
- 555 Krag, L.A., Frandsen, R.P., and Madsen, N., 2008. Evaluation of a simple means to reduce discard

556 in the Kattegat-Skagerrak *Nephrops* (*Nephrops norvegicus*) fishery: commercial testing of different

- 557 codends and square-mesh panels. Fisheries Research, 91: 175–186. 558 doi:10.1016/j.fishres.2007.11.022
- 559 Krag, L.A., Holst, R., and Madsen, N., 2009. The vertical separation of fish in the aft end of a 560 demersal trawl. ICES Journal of Marine Science, 66(4): 772-777. doi:10.1093/icesjms/fsp034
- 561 Krag, L.A., Herrmann, B., and Karlsen, J.D., 2014. Inferring fish escape behaviour in trawls based
- on catch comparison data: model development and evaluation based on data from Skagerrak,

563 Denmark. PLOS ONE 9(2), e88819. doi:10.1371/journal.pone.0088819

- Krag, L.A., Herrmann, B., Karlsen, J.D., and Mieske, B. 2015. Species selectivity in different sized
 topless trawl designs: Does size matter? Fisheries Research, 172: 243-249.
 doi:10.1016/j.fishres.2015.07.010
- Larsen, R. B., Herrmann, B., Sistiaga, M., Brinkhof, J., Tatone, I., and Langård, L., 2017. Performance
- 568 of the Nordmøre Grid in Shrimp Trawling and Potential Effects of Guiding Funnel Length and Light
- 569 Stimulation. Marine and Costal Fisheries, 9(1). doi: 10.1080/19425120.2017.1360421

Lomeli, M. J., and Wakefield, W. W., 2014. Examining the potential use of artificial illumination to
enhance Chinook salmon escapement out a bycatch reduction device in a Pacific hake midwater
trawl. NMFS Northwest Fisheries Science Center Report.

573 Main, J., and Sangster, G.I., 1985a. Trawling experiments with a two-level net to minimise the 574 undersized gadoid bycatch in a *Nephrops* fishery. Fisheries Research, 3: 131–145. doi: 575 10.1016/0165-7836(85)90014-1

- 576 Main, J., and Sangster, G.I., 1985b. The behaviour of the Norway Lobster, *Nephrops norvegicus*577 (L.), during trawling. Scottish Fishery Research Report No. 34. Department of Agriculture and
 578 Fisheries for Scotland. Aberdeen. pp. 23.
- Marchesan, M., Spoto, M., Verginella, L., and Ferrero, E. A. (2005). Behavioural effects of artificial
 light on fish species of commercial interest. Fisheries Research, 73(1): 171-185. doi:
 10.1016/j.fishres.2004.12.009
- 582 Melli, V., Karlsen, J. D., Feekings, J. P., Herrmann, B., & Krag, L. A., 2017. FLEXSELECT: counter-583 herding device to reduce bycatch in crustacean trawl fisheries. Canadian Journal of Fisheries and 584 Aquatic Sciences, (ja). doi: 10.1139/cjfas-2017-0226
- 585 Millar, R.B., 1993. Incorporation of between-haul variation using bootstrapping and 586 nonparametric estimation of selection curves. Fishery Bulletin, 91: 564–572.
- Nguyen, K. Q., and Tran, P. D., 2015. Benefits of using LED light for purse seine fisheries: A case
 study in Ninh Thuan Province, Vietnam. Fish for the People, 13(1): 30-36.
- Nguyen, K. Q., Winger, P. D., Morris, C., and Grant, S. M., 2017. Artificial lights improve the
 catchability of snow crab (*Chionoecetes opilio*) traps. Aquaculture and Fisheries. doi:
 10.1016/j.aaf.2017.05.001

- 592 Pascoe, P.L., 1990. Light and the capture of marine animals. In: Herring, P.J. (Ed.), Light and Life in
- the Sea. Cambridge University Press, Cambridge, UK, pp. 229–244.
- Ryer, C. H., Stoner, A. W., Iseri, P. J., and Spencer, M. L., 2009. Effects of simulated underwater
 vehicle lighting on fish behavior. Marine Ecology Progress Series, 391: 97-106. doi:
 10.3354/meps08168
- 597 Rosen, S., Engås, A., Fernö, A., and Jörgensen, T., 2012. The reactions of shoaling adult cod to a
- 598 pelagic trawl: implications for commercial trawling. ICES journal of marine science, 69(2): 303-312.
- 599 doi: 10.1093/icesjms/fsr199
- 600 Verheijen, F. J., 1960. The mechanisms of the trapping effect of artificial light sources upon
 601 animals. Archives Néerlandaises de Zoologie, 13(1): 1-107.
- Wang, J. H., Fisler, S., and Swimmer, Y., 2010. Developing visual deterrents to reduce sea turtle
 bycatch in gill net fisheries. Marine Ecology Progress Series, 408: 241-250. doi:
 10.3354/meps08577
- Wileman, D. A., Ferro, R. S. T., Fonteyne, R., and Millar, R. B., 1996. Manual of Methods of
 Measuring the Selectivity of Towed Fishing Gears. ICES Cooperative Research Report No. 215, ICES,
 Copenhagen, Denmark.
- Winger, P.D., Eayrs, S., and Glass, C.W., 2010. Fish behaviour near bottom trawls. In He, P. (Ed.),
 Behavior of marine fishes: capture processes and conservation challenges, pp. 67–102. WileyBlackwell, Arnes, IA.
- 611

612

614				
615				
616				
617				
618				
619				
620				
621				
622	Figures			

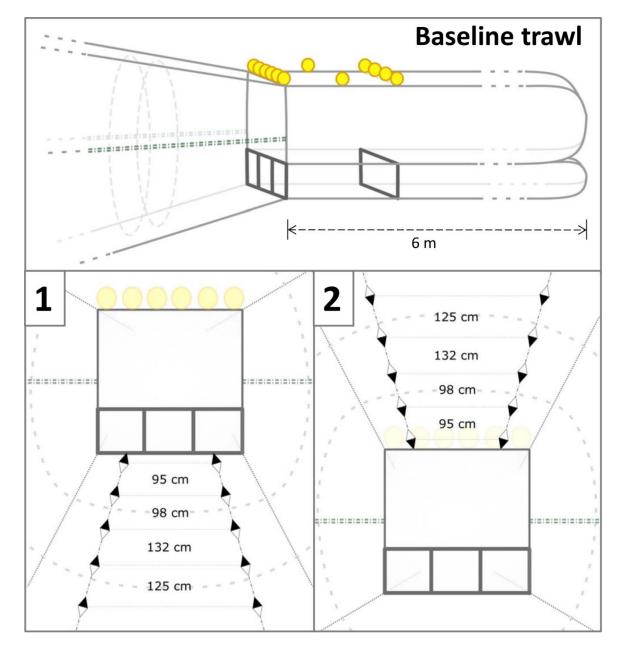


Figure 1. Schematic illustration of the baseline trawl and the position of the lights in experiment 1 and 2.
The dot-dash double lines represent the selvages. LED lights are represented with the white triangle
indicating the direction of the light emitted. To facilitate the identification of all the components the
proportions shown are not accurate.

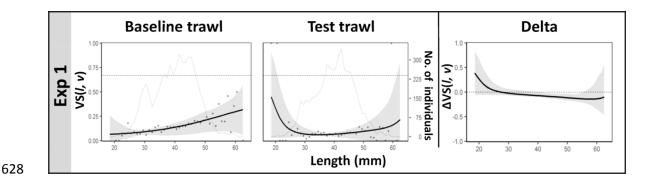


Figure 2. The VS(*l*, *v*) for *Nephrops* in the baseline and test trawls, and ΔVS(*l*, *v*). In the first two columns, the curve (solid line) represents the modelled VS fitted to the experimental points (dots). The grey bands are the 95% CIs and the dotted line is the length distribution of the data. The dashed horizontal line, located at 0.67, describes an equal preference for entering either compartment. In the third column, the solid line represents the difference in VS between the baseline and test trawls, accounting for synchronized hauls. The grey bands are the 95% CIs and the dashed line represents no difference in VS.

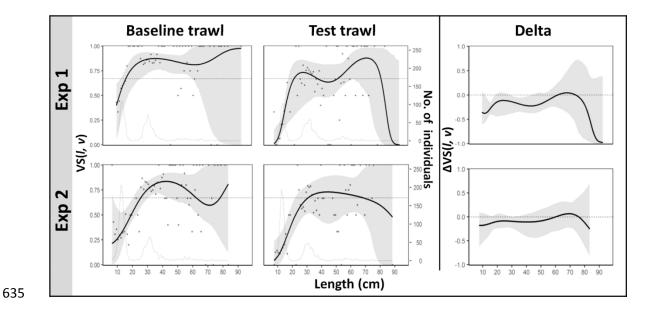


Figure 3. The VS(*l*, *ν*) for cod in the baseline and test trawls, and ΔVS(*l*, *ν*). In the first two columns, the curve
(solid line) represents the modelled VS fitted to the experimental points (dots). The grey bands are the 95%
Cls and the dotted line is the length distribution of the data. The dashed horizontal line, located at 0.67,
describes an equal preference for entering either compartment. In the third column, the solid line
represents the difference in VS between the baseline and test trawls, accounting for synchronized hauls.
The grey bands are the 95% CIs and the dashed line represents no difference in VS.

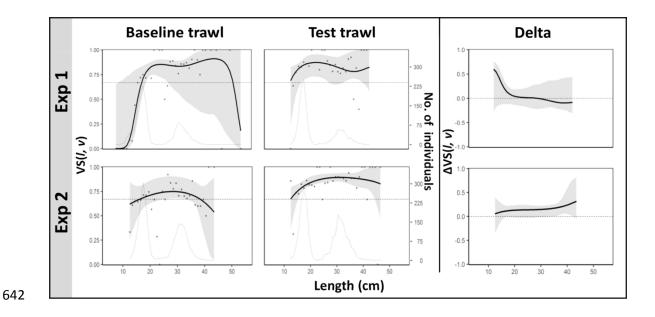


Figure 4. The VS(*l*, \mathbf{v}) for haddock in the baseline and test trawls, and Δ VS(*l*, \mathbf{v}). In the first two columns, the curve (solid line) represents the modelled VS fitted to the experimental points (dots). The grey bands are the 95% CIs and the dotted line is the length distribution of the data. The dashed horizontal line, located at 0.67, describes an equal preference for entering either compartment. In the third column, the solid line represents the difference in VS between the baseline and test trawls, accounting for synchronized hauls. The grey bands are the 95% CIs and the dashed line represents no difference in VS.

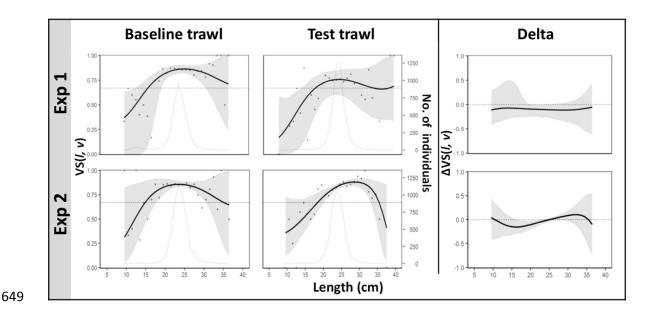


Figure 5. The VS(*l*, \mathbf{v}) for whiting in the baseline and test trawls, and Δ VS(*l*, \mathbf{v}). In the first two columns, the curve (solid line) represents the modelled VS fitted to the experimental points (dots). The grey bands are the 95% CIs and the dotted line is the length distribution of the data. The dashed horizontal line, located at

0.67, describes an equal preference for entering either compartment. In the third column, the solid line
represents the difference in VS between the baseline and test trawls, accounting for synchronized hauls.
The grey bands are the 95% CIs and the dashed line represents no difference in VS.

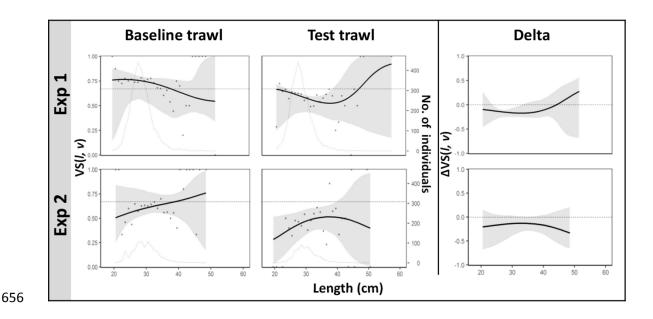
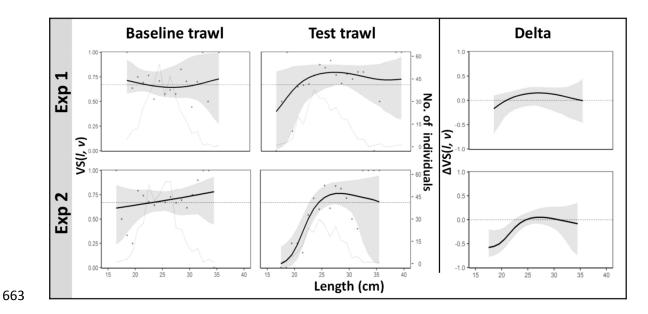


Figure 6. The VS(*l*, \mathbf{v}) of plaice in the baseline and test trawls, and Δ VS(*l*, \mathbf{v}). In the first two columns, the curve (solid line) represents the modelled VS fitted to the experimental points (dots). The grey bands are the 95% CIs and the dotted line is the length distribution of the data. The dashed horizontal line, located at 0.67, describes an equal preference for entering either compartment. In the third column, the solid line represents the difference in VS between the baseline and test trawls, accounting for synchronized hauls. The grey bands are the 95% CIs and the dashed line represents no difference in VS.



- Figure 7. The VS(l, v) of lemon sole in the baseline and test trawls, and Δ VS(l, v). In the first two columns, the curve (solid line) represents the modelled VS fitted to the experimental points (dots). The grey bands are the 95% CIs and the dotted line is the length distribution of the data. The dashed horizontal line, located at 0.67, describes an equal preference for entering either compartment. In the third column, the solid line represents the difference in VS between the baseline and test trawls, accounting for synchronized hauls. The grey bands are the 95% CIs and the dashed line represents no difference in VS.

685 Tables

Table 1. Overview of the experimental hauls, showing the technical and environmental parameters and total catch (kg) for each of the four compartments. BU = baseline upper compartment; BL = baseline lower compartment; TU = test upper compartment; TL = test lower compartment. Hauls were separated in experiments (Exp.) 1 and 2. The position of the treatment was shifted from the Starboard trawl (S) to the

690 Port trawl (P).

Haul	F	Test	Start time	Towing time	Depth	Wind	Speed	BU	BL	TU	TL
No.	Exp.	trawl	(hh:mm)	(hh:mm)	(m)	(m/s)	(kn)	(kg)	(kg)	(kg)	(kg)
1	1	Р	05:35	00:30	86	3	2.8	99	145	181	285
2	1	Р	07:50	00:50	84	3	2.8	735	410	825	474
3	1	Р	01:45	00:30	77	3	2.9	170	126	230	178
4	1	S	05:05	00:30	82	3	2.9	244	113	70	140
5	1	S	08:25	00:45	80	2	2.9	219	175	120	155
6	1	S	11:20	00:45	84	2	2.9	480	200	226	176
7	1	S	14:35	01:30	54	2	2.9	24	106	61	110
8	1	S	08:10	01:30	46	1	2.6	73	155	76	148
9	1	S	12:40	01:00	45	0	2.6	22	33	30	61
10	1	S	14:25	01:00	48	0	2.6	17	52	42	63
11	2	Р	08:20	00:45	77	5	2.9	415	175	180	170
12	2	Р	12:40	00:45	86	6	2.9	385	230	205	230
13	2	Р	16:05	00:45	85	7	2.9	127	140	240	240
14	2	Р	20:40	00:45	85	7	2.9	130	181	275	174
15	2	Р	23:30	00:45	86	6	2.9	60	147	80	52
16	2	Р	17:24	00:30	86	6	2.9	117	130	241	147
17	2	S	21:08	00:45	83	4	2.9	115	163	120	172
18	2	S	00:00	00:45	84	8	2.9	177	117	158	145

Table 2. Number of hauls and number of individuals per species per compartment included in the analyses
of each experiment, 1 and 2. U = upper compartment; L = lower compartment. Species that were
subsampled are indicated with the raised total number and the actual number of individuals measured (in
brackets).

Experiment 1								
		Baselin	Test	trawl				
	Hauls	nU	nL	nU	nL			
Nephrops	4	782	4688 (2545)	371	4675 (2466)			
Cod	8	707	256	508	463			
Haddock	6	1040	453	1017	203			
Whiting	10	3398 (2803)	627	3858	1293			
Plaice	6	2244 760		1758	1186			
Lemon sole	6	238 123		219	70			
	Experiment 2							
	;		a dura cul	Test trawl				
		Baselin	le trawi	lest	trawl			
	Hauls	nU	nL	nU	trawl nL			
Nephrops	Hauls -							
Nephrops Cod	Hauls - 8							
	-	nU -	nL -	nU -	nL -			
Cod	- 8	nU - 724	nL - 718	nU - 425	nL - 759			
Cod Haddock	- 8 8	nU - 724 1402	nL - 718 582	nU - 425 1812	nL - 759 334			

- 716 **Table 3.** Fit statistics for the modelled vertical separation efficiencies. DoF denotes the degree of freedom
- and was calculated by subtracting the number of model parameters from the number of length classes in
- the dataset.

		Expe	eriment	1		
	B	Test trawl				
	p -value	Deviance	DoF	p -value	Deviance	DoF
Nephrops	0.80	29.56	37	0.01	59.03	37
Cod	0.43	57.19	56	0.02	81.63	58
Haddock	0.02	50.27	32	0.18	28.96	23
Whiting	0.02	38.77	23	0.08	34.17	24
Plaice	0.24	30.81	26	0.33	26.51	24
Lemon sole	0.07	19.87	12	0.32	17.99	16
		Expe	eriment	2		
	B	Test trawl				
	p -value	Deviance	DoF	p -value	Deviance	DoF
Nephrops	-	-	-	-	-	-
Cod	0.16	74.03	63	0.26	57.57	51
Haddock	< 0.01	58.23	26	0.03	45.84	30
Whiting	< 0.01	40.69	22	0.02	39.03	23
Plaice	0.08	33.28	23	0.07	33.85	23
Lemon sole	0.17	18.77	14	0.31	16.11	14