
Resolution of biodiversity and assemblage structure in demersal fisheries surveys: the role of tow duration

Moriarty M. ^{1,2,*}, Sell A. F. ³, Trenkel Verena ⁴, Lynam C. P. ⁵, Burns F. ¹, Clarke E. D. ¹,
Greenstreet S. P. R. ¹, McGonigle C. ²

¹ Marine Scotland Sci, 375 Victoria Rd, Aberdeen AB11 9DB, Scotland.

² Ulster Univ, Environm Sci Res Inst, Cromore Rd, Coleraine BT52 1SA, Londonderry, North Ireland.

³ Thunen Inst Sea Fisheries, Palmaille 9, D-22767 Hamburg, Germany.

⁴ IFREMER, Rue Ile d'Yeu, BP 21105, F-44311 Nantes 03, France.

⁵ CEFAS, Pakefield Rd, Lowestoft NR33 0HT, Suffolk, England.

* Corresponding author : M. Moriarty, email address : Moriarty-M3@ulster.ac.uk

Abstract :

An experiment during a fisheries independent survey in the North Sea was conducted to test whether sampling effort could be reduced without a significant loss in data precision. To examine potential effects of reducing tow duration from the standard 30 min to a proposed 15 min estimates of species encounter rates, species richness, and estimates of abundance, biomass, and body size were analysed. Results show species richness estimates are lower in the short tow category. While biomass and abundance at length and body size are significantly affected by the change in tow duration, estimates of Large Fish Indicator, the Typical length and Mean-max length are not significantly affected by the regime change. The results presented here suggest that a reduction of tow duration did not optimize the resolution of biodiversity, and it may affect other survey objectives, such as, providing estimates of abundance or biomass for assessment of commercial species.

Keywords : abundance, biomass, body size, fisheries independent survey, IBTS, International Bottom Trawl Survey, linear mixed model, North Sea, species diversity

24 **Introduction**

25 Maximising survey resources in pressing economic conditions is a major concern in fisheries science.
26 Since 1998 the standard tow duration for the International Bottom Trawl Survey (IBTS) in the North
27 Sea has been 30 minutes (ICES, 2012; 2015a). Recently tow duration has come under scrutiny within
28 the International Council for the Exploration of the Sea (ICES) community (IBTS Working Group;
29 IBTSWG). An experiment to test the effect of moving to a tow duration of 15 minutes was initiated on
30 the basis that this would:

- 31 1. Reduce the risk of gear damage during any single tow, thereby reducing the number of tows
32 classified as invalid due to gear damage;
- 33 2. Potentially allow more tows to be carried out, which could improve the precision of species
34 abundance indices, and
- 35 3. Potentially reduce overall survey time, with consequent savings in resources (ICES, 2015b).

36 Fisheries independent bottom trawl surveys have historically been undertaken to meet fisheries
37 management requirements under the European Common Fisheries Policy (CFP) and Data Collection
38 Framework (DCF). However, in 2014 the member states involved in the IBTS nominated their own
39 surveys to fulfil monitoring obligations under the Marine Strategy Framework Directive (MSFD) (EC,
40 2008; 2010). Therefore, the IBTS must supply the data required to derive the ecological indicators
41 necessary to assess the status of the whole fish community. Changes in survey design must now take
42 account of the needs of stock assessments used for fisheries management purposes and should also
43 consider the data requirements for the indicators used for broader ecological assessments (Jennings,
44 2005).

45 Several different types of indicators have been used to assess variation in the state of fish communities
46 (Trenkel and Rochet, 2003; Shin *et al.*, 2010; Shannon *et al.*, 2010; Greenstreet *et al.*, 2012a). Some
47 focus on community size composition such as the large fish indicator (LFI) (Greenstreet *et al.*, 2011;
48 Shephard *et al.*, 2011; Modica *et al.*, 2014), mean fish weight (Greenstreet and Rogers, 2006) and the

49 size spectra slope coefficient (Gislason and Rice, 1998). Others focus on species composition,
50 capturing aspects of the evenness of species abundance across all species sampled (Bianchi *et al.*,
51 2000; Greenstreet and Hall, 1996; Greenstreet *et al.*, 1999; Heath *et al.*, 2011). Outside of this
52 established framework, additional studies address changes in the abundance of specified suites of
53 species (Greenstreet *et al.*, 2012b). Any change in survey design that alters the apparent relative
54 abundance of scarce components (rare species, large size classes) compared with the more abundant
55 components (common species, small size classes) will have an impact on these indicator values.

56 Scientific surveys provide fisheries independent indices of species abundance. Fisheries managers are
57 concerned about commercial fish, which are generally the more abundant species. However,
58 ecosystem assessments are often concerned with some of the rarer species (Dulvy *et al.*, 2003;
59 Greenstreet *et al.*, 2012b). Metrics of species richness, for example, are confounded by survey
60 techniques that inadequately sample rare species (Greenstreet and Piet, 2008). Previous work has
61 examined the effects of tow duration (eg. Ehrich and Stransky, 2001), where a reduction from 60 to
62 30 minutes led to a slight reduction in the number of observed species. Changes in survey design that
63 may have little impact on indices of abundance of more common species could potentially have
64 considerable and adverse consequences for abundance metrics in rarer species (Magurran, 2014).

65 Two commonly accepted concepts in fisheries science are: 1) a longer tow provides a more reliable
66 measure of species richness occurring in the habitat being sampled as they cover a larger swept area
67 presenting a greater opportunity to resolve rarer species, and 2) large fish that are stronger swimmers
68 are more efficiently captured (Wardle, 1986). Conversely the “catch-by-surprise” hypothesis held by
69 Godø *et al.* (1990), suggests that the catch per unit effort of herding fish species may decrease with
70 increased tow duration. Nevertheless, the number of individuals caught before and after the official
71 duration (end effect) increases in shorter tows, which can primarily affect abundant species with a
72 higher degree of mobility (Battaglia *et al.*, 2006).

73 Fisheries survey data are highly variable, effects on catch rates may be associated with fish reaction
74 to the survey gear. Reactions to gear are partially determined by their distribution in the water
75 column, size/shape, behaviour, or the degree of association to the seabed (Engås and Godø, 1986;
76 Aglen, 1996; Godø, 1990; Fréon *et al.*, 1993; Adlerstein and Ehrich, 2002). The catchability of different
77 species depends on many factors, including fish behaviour in relation to the gear type (otter trawl or
78 beam trawl), herding efficiency, and the probability of escape at the entrance to the net (Wardle,
79 1993; Engås, 1994). For some species, catch rates may vary because their behaviour changes
80 throughout the day (Trenkel *et al.*, 2008; Doray *et al.*, 2010); while for other species catch rates may
81 also vary over the duration of the tow due to spatial heterogeneity (Kingsley *et al.*, 2002) .

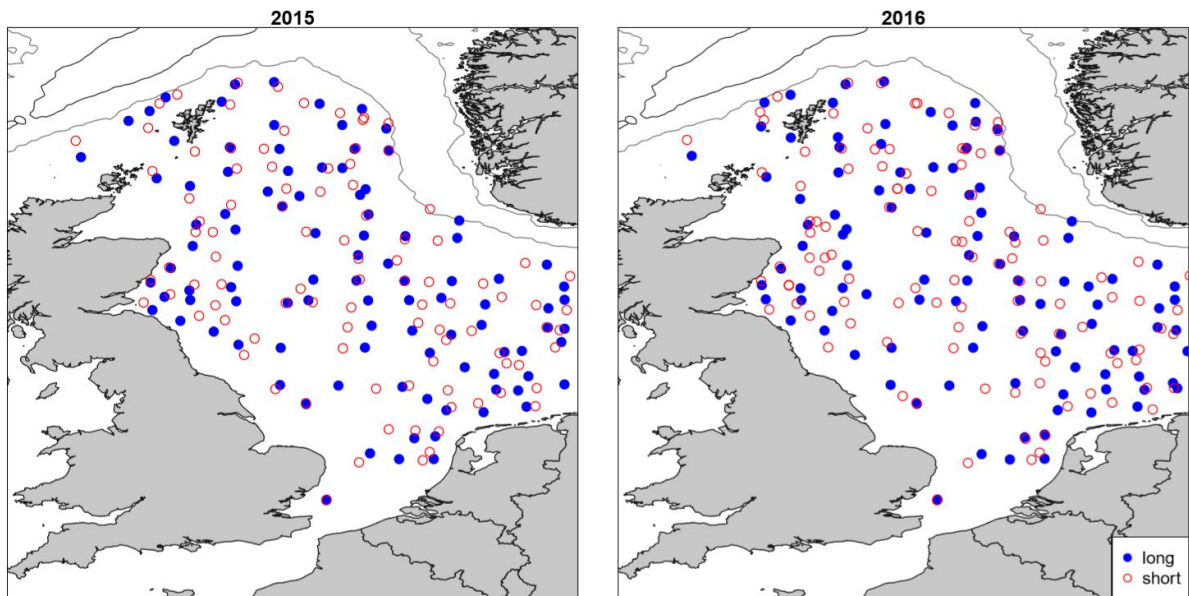
82 No significant difference in the mean length of fish caught or the catch per unit effort between 15 min
83 and 30 min survey tows (Godø *et al.*, 1990; Walsh, 1991) was identified for cod (*Gadus morhua*),
84 haddock (*Melanogrammus aeglefinus*) and long rough dab (*Hippoglossoides platessoides*), yellowtail
85 flounder (*Limanda ferruginea*) and thorny skate (*Amblyraja radiata*). Similarly, no significant effect
86 was found on catch per unit effort, size composition or notably maximum length for Northern shrimp
87 (*Pandalus borealis*) and Greenland halibut (*Reinhardtius hippoglossoides*) off West Greenland
88 (Wieland and Storr-Paulsen, 2006). However, Somerton *et al.*, (2002) noted that the catch per swept-
89 area increased significantly for two commercial species of crab when tow duration was decreased
90 from 30 min to 15 min.

91 The overall aim of this current research is to demonstrate the impact of varying tow duration on catch
92 composition for groundfish surveys in the North Sea, at scales relevant to fisheries management. Here
93 we look at the fish community sampled by the gear using the longer tows (28-32 minute) and ascertain
94 if the shorter tows (14-16 minute) are significantly different in terms of the features that they resolve.
95 We examine the variance in abundance and biomass estimates in both long and short tow categories
96 using linear mixed models. We also examine evenness and richness across the sample area and test
97 the MSFD community and population level indicators.

98 **Data and Analysis**

99 *Survey design*

100 The Greater North Sea International Otter Trawl Survey is a coordinated survey involving England,
101 Scotland, Norway, Germany, Sweden and Denmark in the annual sampling during quarter 3. The
102 survey follows a systematic unaligned sampling design (Cochran, 1977), where each ICES statistical
103 square is sampled at least twice. The general protocol is that each vessel fishes for 30 minutes at a
104 speed of 4 knots using a standardised *Grande Overture Vertical trawl*. *Fish species, numbers at length*
105 *and weight are some of the parameters that are recorded*. In 2015 and 2016, the IBTSWG elected to
106 do experimental tows, where at least one of the tows in each rectangle would be 15 minutes and at
107 least one would be 30 minutes. This resulted in an almost 50: 50 split in 2015, whereas in 2016 there
108 was an increased effort to produce 15 minute tows (Figure 1).



110 *Figure 1: Stations sampled in 2015 and 2016 North Sea Q3 survey which were selected as part of this*
111 *study.*

112 *Data source*

113 The quality assured monitoring and assessment data set for the Greater North Sea International
114 Quarter 3 Otter Trawl Survey (Moriarty and Greenstreet, 2017), derived from the NS-IBTS Q3 ICES
115 DATRAS dataset, was used for this study. This is a publicly available data source with supporting
116 technical documentation describing techniques used to quality assure the DATRAS data downloaded
117 on 30-03-2017 (Moriarty *et al.*, 2017; Greenstreet and Moriarty, 2017a/b). The catch data for all
118 species is expressed as recorded numbers at length, numbers per km² at length or biomass per km² at
119 length. Table S1 highlights taxonomic corrections made to the quality assured monitoring and
120 assessment data set, which were made in consultation with expert advice (e.g. Heessen *et al.*, 2015).
121 The tow data includes geographical position (longitude, latitude), depth (m), tow number, vessel,
122 statistical rectangle, tow duration (minutes), swept area (in km²) and year.

123 *Data selection*

124 A subset of data was selected from the 2015 and 2016 survey data based on two criteria. The first
125 criteria was that an ICES rectangle must have been sampled at least twice one long tow (30 ±2 minute)
126 and one short tow (15 ±1 minute). The second criteria was that the experimental short tow must be
127 within 30% of the depth range of the standard long tow. This was chosen arbitrarily to reduce variation
128 caused by samples with extreme depth ranges. The depth difference in most of the tows are small,
129 but in 16% of the tows there is a substantial difference in the depth (e.g. a tow at 17m and a tow at
130 73m giving a difference of 56m; Figure S1, supplementary material). The largest difference in the
131 depth of paired tows within the same rectangle was 102m (Figure S1 in supplementary material).
132 These two criteria produced a suite of tows covering 97 ICES rectangles (0.5 x 1°), consisting of 99 long
133 and 99 short tows in 2015 and 103 long and 110 short tows in 2016 (Figure 1). To assess the individual
134 tow variability per rectangle between short and long tows the range of depth, time and the differences
135 in speed over ground were examined (Figure S2, supplementary material).

136 *Analyses of biodiversity*

137 The primary aim was to demonstrate the effect of varying tow duration on species diversity, richness
138 and evenness in the North Sea survey in Q3. The mean species richness for the long and short tows
139 for each year was calculated to ascertain if there was a difference between the two categories.

140 Linear mixed effect models were used to determine the relationships between richness and tow
141 duration, ship, speed over ground, time of tow (diel fluctuations), year, month/day, and depth. The
142 interactions between tow duration and ship, and tow duration and year were also tested. ICES
143 statistical rectangle was added as a random effect in the model to account for spatial auto correlation.
144 Models were implemented using the package “lme4” (Bates *et al.*, 2015) in R (R Core Team, 2017).
145 The global linear mixed effect model had the form

146 Equation 1:
$$\gamma = X\beta + Zu + \varepsilon$$

147 Where $N = 411$, and γ is a $N \times 1$ column vector of the outcome variable (e.g. richness of fish in a
148 tow). X is a $N \times p$ matrix of the $p = 9$ fixed effects predictor variables; tow duration (long/short),
149 ship (5 ships), speed over ground (km/hr), time of day (diel fluctuations), year, month/day (Julian
150 days), and depth (m), the interactions between tow duration and ship, and the interactions between
151 tow duration and year. β is $p \times 1$ column vector of fixed effect regression coefficients. Z is a $N \times q$
152 matrix with 1 for the corresponding random effect of ICES statistical square and 0 otherwise, $q = 97$,
153 as we suspect that samples in the same statistical square are correlated. u is a $q \times 1$ vector of the
154 random effects; and ε is a $N \times 1$ column vector of the residuals not explained by $X\beta + Zu$. A gaussian
155 identity link distribution was used. Parameters were estimated by maximum likelihood. The best
156 fitting model was determined based on Akaike’s information criterion (AIC) scores. All pairwise
157 interactions of explanatory variables were tested.

158 Species richness curves with bootstrapped confidence intervals were plotted against number of tows
159 for both long and short tows categories using a randomised method. Pielou’s evenness index, derived
160 from the Shannon diversity index, was calculated for both the long and the short tows. Exploratory

161 analysis demonstrated violations of assumptions for parametric testing, therefore, a Scheirer–Ray-
162 Hare test (Dytham, 1999), was performed to test the hypothesis there is no difference in mean species
163 evenness in long and short tows in each year, and no significant interaction between haul duration
164 and year. In addition to using non-parametric test, we log transformed the data and assessed the
165 interactions using linear models. Both approaches gave the same results, so have elected to report
166 only the Scheirer–Ray-Hare test.

167 *Differences in abundance and biomass*

168 The second aim was to determine if varying tow duration affected the biomass and abundance
169 estimates calculated from the survey data. Again, a linear mixed effects model was employed, the
170 global model followed Equation 1, where γ was the log transformed abundance (n/km^2) and the log
171 transformed biomass (kg/km^2) respectively. The same model parameters and model selection criteria
172 were used.

173 *Differences in body size*

174 To assess differences in average body size, fish were grouped in 10 cm length classes and the log
175 transformed mean biomass/abundance at grouped length classes by tow in each tow category and
176 year. To assess if there were significant differences in actual body size, estimates of mean size and
177 standard deviation per tow category per year were calculated and a Pearson's Chi-squared test with
178 simulated p-value (based on 2000 replicates sampled with replacement from all tows) was
179 undertaken.

180 To test if there was a significant difference between the short and long tows in estimates of MSFD
181 indicators being derived from this survey the Large Fish Indicator (LFI), the Typical length (TyL) and
182 Mean-max length (MML) were calculated for the appropriate suite of species in the samples (OSPAR,
183 2017). The LFI is the ratio of the average biomass (kg/km^2) of large demersal fish ($\geq 50\text{ cm}$) per ICES
184 statistical rectangle over the average biomass (kg/km^2) of all demersal fish sizes per ICES statistical

185 rectangle. The LFI were calculated in both 2015 and 2016 to test for a significant difference in the
 186 estimated LFI for long and for short tows. TyL is the geometric mean length where length is weighted
 187 by biomass; MML is the arithmetic average of the maximum length obtained by species in the survey
 188 weighted by biomass; the species were split into two groups, “pelagic” and “demersal” species for the
 189 two indices. It should be noted, however, that all of these results are based on comparisons of relative
 190 abundance, relative biomass and relative mean length; therefore, accuracy cannot be evaluated as
 191 true values are unknown.

192 **Results**

193 *Biodiversity*

194 The best fitting linear mixed model for estimation of the mean species richness in the tow suggested
 195 that tow duration was a significant factor in describing the variability seen in the data. Other fixed
 196 effect variables that were important in describing the mean species richness were time of day, the
 197 effect of ship, the depth (m) and the year (Table S3, Figure S3). There was no significant interaction
 198 between any fixed effects, and they were therefore not included in the final model (Table 1).

199 *Table 1: Summary of explanatory variables included (✓) or excluded (✗) in the best fitting linear mixed*
 200 *models for estimating the factors that explain the variance in species richness, abundance (n/km²) and*
 201 *biomass (kg/km²) in tows.*

Fixed Effects	Richness (no spp)	Abundance (n/km ²)	Biomass (kg/km ²)
Tow Duration	✓	✓	✓
Ship	✓	✓	✓
Tow Duration : Ship	✗	✗	✗
Year	✓	✗	✓
Tow Duration : Year	✗	✗	✗
Month/Day (Julian days)	✓	✓	✗
Time of Day (diel fluctuation)	✓	✓	✓
Depth (m)	✓	✗	✗
Speed Over Ground (km/hr)	✗	✗	✗
Random Effect			
1 ICES Statistical Square	✓	✓	✓

202 Sixteen species were uniquely present in long tows, but not short tows. These include some pelagic
203 fish like *Belone belone* (Garfish) *Sarda sarda* (Atlantic bonito) and *Scomber colias* (chub mackerel),
204 flatfish like *Phrynorhombus norvegicus* (Norwegian topknot) and *Zeugopterus punctatus* (topknot) and
205 rays such as *Leucoraja fullonica* (Shagreen ray). Conversely, seven species were collected in short tows
206 but not in long tows these included elasmobranchs such as *Etmopterus spinax* (lantern shark),
207 *Mustelus spp.* (smooth-hound) and *Raja brachyura* (blond ray). Sharks and rays such as *L. fullonica*
208 (Shagreen ray) and *R. brachyura* (Blond ray), *E. spinax* (lanternshark), *Mustelus spp* (smooth-hounds)
209 were not consistently sampled (see Table S1 for full list). In the area selected for analysis the mean
210 number of species collected in the five years prior to the start of the experiment (2010-2014) was 78
211 species. While the long tows are consistent with previous years with 77 and 78 species encountered,
212 as expected when looking at a similar total number of hauls, the short tows fell short of this with 71
213 and 73 species encountered respectively (Table 2). The increased effort to sample more diverse
214 habitats meant the total number of species reported in 2015 and 2016 was above average in the area
215 sampled (83 and 87 species, respectively), the increased species were predominantly reported by
216 England, who exclusively fished for 30 min and fished similar stations in both years. In 2016, within
217 our study area, England was the only country to report *Belone belone* (Garfish), *C. maximus* (basking
218 shark), *L. liparis liparis* (common seasnail), *L. vahlii* (Vahl's eelpout), *P. marinus* (sea lamprey) and *S.*
219 *trutta trutta* (sea trout).

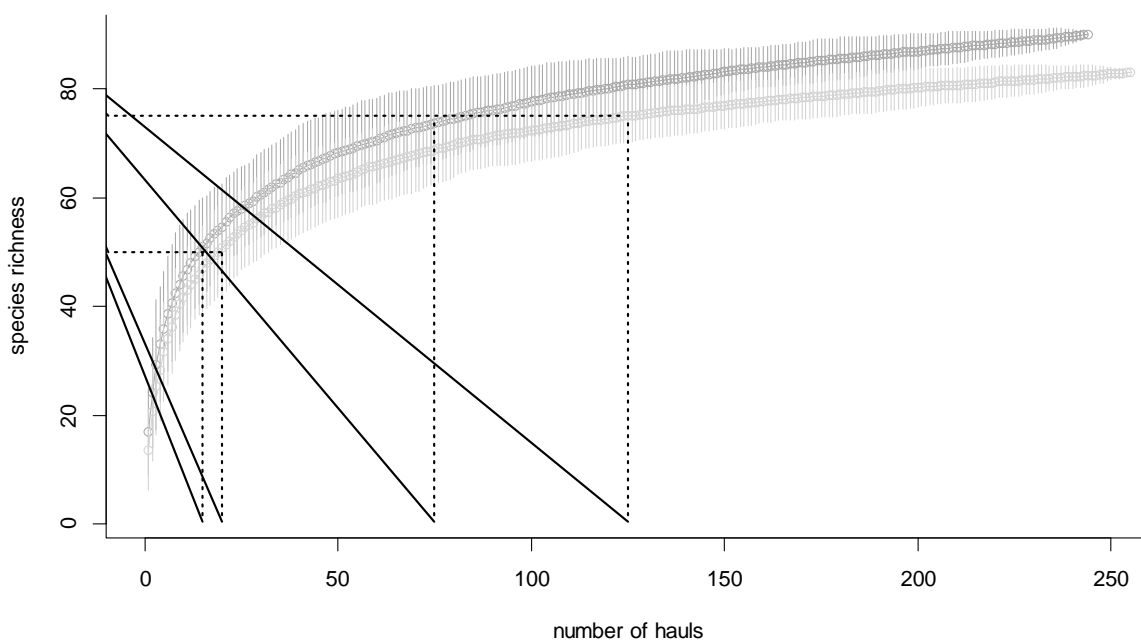
220 All species encountered and the number of times a species occurred is listed in Table S1. In some
221 cases, species only occurred once within the study area, 50 species occurred in less than 5% of
222 samples. To ascertain the effect of these species which were not well sampled testing for differences
223 in abundance and biomass was performed on the full data set and a reduced dataset that excluded
224 the poorly sampled species. The results were not significantly different between the two data sets;
225 therefore, the following analyses included all the species listed in Table S1. There was no significant
226 interaction between year and tow duration, nor were any significant differences found for the year or
227 tow duration in the Pielou's evenness.

228 *Table 2: Summary of the mean number of species encountered per ICES rectangle in each category and*
 229 *year. In 2015 a total of 83 fish species were encountered while in 2016 87 species were identified. The*
 230 *average number of species in sampled in the period from 2010-2014 was 78.*

Year	Category	Mean number of species per rectangle	Standard deviation	Total number of species encountered
2010	long	17.54	3.98	75
2011	long	18.14	4.31	78
2012	long	18.61	3.94	78
2013	long	17.68	4.89	78
2014	long	18.62	4.39	82
2015	long	16.29	3.96	77
2015	short	13.94	3.64	71
2016	long	16.87	4.06	78
2016	short	14.77	4.35	73

231

232 The difference in potential species richness within the two tow categories, showing the difference in
 233 ability to reach a species richness of 50 species is highlighted in figure 2. The long tow category was
 234 33% more effective at sampling species richness, this suggests that a 33% increase in the number of
 235 short tows would provide a similar species richness estimate. When increased to a species richness of
 236 75 species this gap widens and a 67% increase in the number of short tows to long tows would be
 237 needed.



238

239 *Figure 2: Cumulative species richness curves for long tows in dark grey and short tows in light grey. The*
240 *black dotted lines show that to reach a species richness of 50 species, approximately 15 tows in the*
241 *“long” or 20 tows in the “short” tow category are needed (33% increase in effort). Whereas to reach a*
242 *species richness of 75 species, using the “long” tow category approximately 75 tows are needed and*
243 *using the “short” tow category approximately 125 tows are needed (67% increase in effort). Vertical*
244 *lines provide the standard deviation from random permutations of the data.*

245 *Abundance and Biomass*

246 The best fitting linear mixed model for estimation of the mean abundance (n/km^2) in the tow
247 suggested that tow duration is a significant factor in describing the variance seen in the data. Other
248 fixed effect variables that were important in describing the mean abundance (n/km^2) according to the
249 best fit model were time of day, the effect of ship, and the day of the month (Table S4, Figure S4).
250 There was no significant pairwise interaction between any fixed effects (Table 1). Similarly tow
251 duration was a significant factor in describing the variance seen in the mean biomass (kg/km^2), other
252 fixed effect variables that are important in describing the mean biomass (kg/km^2) are time of day, the
253 effect of ship, and the year (Table S5, Figure S5).

254 *Body Size*

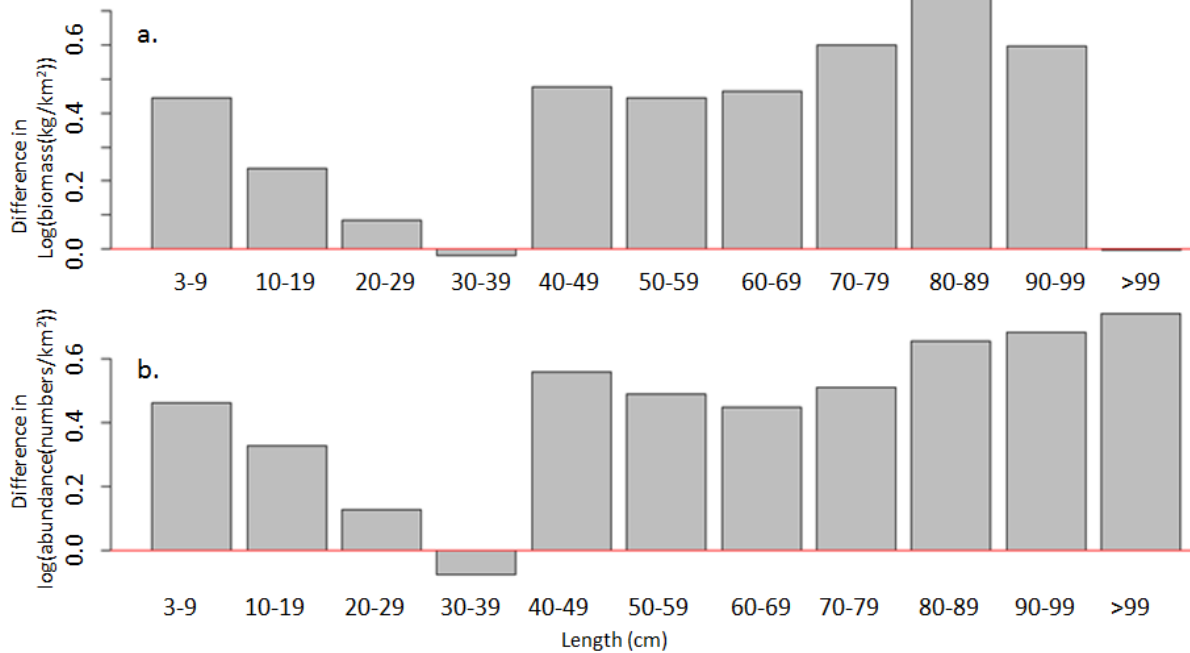
255 When samples were grouped into length classes and the average biomass/abundance at size was
256 compared, evidence for differences between the short and long tows was found for abundance. The
257 results showed that there was no significant interaction between year and tow duration, but there
258 were significant differences ($p < 0.05$) in the tow categories, and year was not found to be a significant
259 factor. The log-transformed mean abundance and mean biomass calculated by summing the the log
260 transformed mean biomass/abundance at grouped length classes are outlined in table 3. Generally
261 short tows had a higher mean biomass and abundance at size, in particular for larger sizes (> 40 cm)
262 than long tows when the data was standardised for swept area (km^2) (Figure 3). The > 99 cm class

263 shows there is a higher mean abundance at size for short tows, while the biomass reflects virtually no
 264 difference, this is due to several larger fish in the long tows that balanced out the more numerous
 265 smaller fish in the short tows.

266 The 30-39 cm class is dominated by three pelagic species Atlantic horse mackerel (*Trachurus*
 267 *trachurus*), herring (*Clupea harengus*), and mackerel (*Scomber scombrus*) which accounted for about
 268 65% of the abundance in this length class in long tows and 40% of the catch in short tows. The other
 269 dominant species in this class are haddock (*M. aeglefinus*) and whiting (*M. merlangus*) which
 270 accounted for about 25% of the abundance in this length class in long tows and 37% of the catch in
 271 short tows.

272 *Table 3: Summary of the mean across length classes of the log-transformed abundance and biomass*
 273 *at length in each tow duration category and year.*

Year	Category	Mean log-abundance (numbers/km ²)	Standard deviation (Log-abundance)	Mean log-biomass (kg/km ²)	Standard deviation (Log-biomass)
2015	long	4.24	1.99	4.16	1.22
2015	short	4.77	1.94	4.50	1.11
2016	long	4.10	1.89	4.02	1.22
2016	short	4.58	1.69	4.47	1.12



275

276 *Figure 3 (a.) Bar charts showing the difference (short tow – long tow) between log-transformed mean*
 277 *biomass (kg/km²) in short and long tow categories for groups of length of all fish over the two years.*
 278 *(b.) Showing the difference between log-transformed mean abundance (numbers/km²) in short and*
 279 *long tow categories for groups of length of all fish over the two years.*

280 Given the apparent differences in abundance at size between short and long tow categories a
 281 Pearson’s chi-squared (χ^2) test was carried out to examine differences in size composition of fish in
 282 each category. A χ^2 value of 2963600 ($p < 0.001$) for 2000 bootstrapped resamples was calculated. This
 283 suggests a significant relationship between the tow duration categories for the length of fish caught.
 284 Table 4 highlights the mean size of fish caught in each category and year. The long tow category had
 285 a higher mean size than the short tow category.

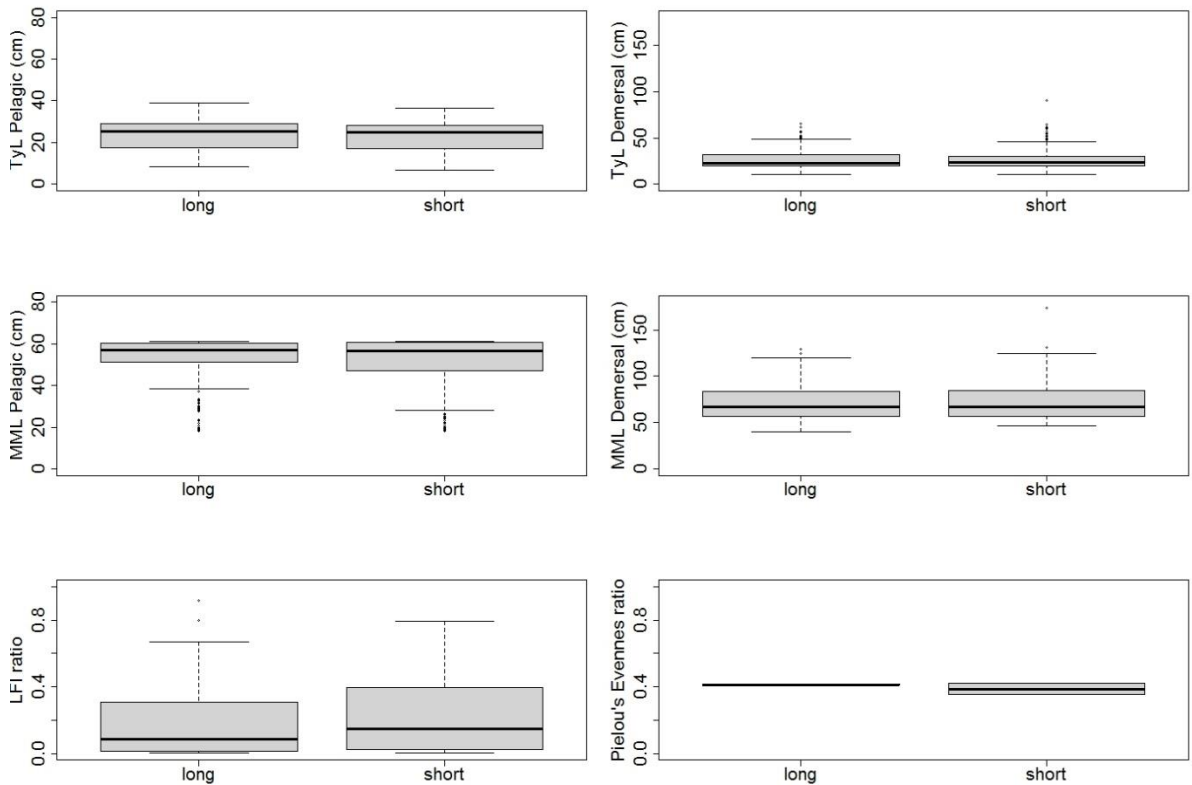
286 *Table 4: Summary of the mean size and standard deviation of fish caught in each category and year,*
 287 *based on number/km² of individuals caught in the haul.*

Year	Category	Mean size of fish (cm)	Standard deviation
2015	Long	13.28	6.13

2015	Short	12.2	5.58
2016	Long	13.19	7.11
2016	Short	11.89	6.80

288

289 The LFI with a 50 cm threshold was dominated by common skate (*Dipturus batis*), followed by cod
 290 (*Gadus morhua*), monkfish (*Lophius piscatorius*), pollack (*Pollachius virens*), and hake (*Merluccius*
 291 *merluccius*). Other species which made up the community of larger fish included rays and sharks
 292 (*Squalus acanthias*, *Raja clavata*, *R. montagui*, *Mustelus spp.*), and commercially important species
 293 such as haddock (*M. aeglefinus*). There was no significant difference ($p = 0.05$) in the MSFD indicator
 294 (LFI, MML and TyL) results in the long and short tows (Figure 4).



295

296 *Figure 4. Box plots show the mean and the variance for TyL, MML LFI and Pielou's evenness metrics in*
 297 *both long and short tow categories. There was no significant difference between long and short tow*
 298 *categories in any of these metrics.*

299

300 **Discussion**

301 This study demonstrates that tow duration , depth (m), diel fluctuation, ship, and year, are significant
302 variables in predicting number of species in a haul (Table 1; Table S3; Figure S3). The long tow category
303 reached a higher species diversity than the shorter tows (Table 2). The individual species recorded did
304 differ in each category in each year, with rarer species not consistently present across years. The
305 cumulative frequency curves in figure 2 highlight the disparity between the long and short tows.
306 Subsampling the 30 min tows has been found to limit the species richness in a similar manner to the
307 shortened tow duration (Ehrich and Stransky, 2001), so understanding to what degree are stations
308 subsampled in the current 30 min tow regime is important. If one country consistently subsamples
309 stations it may lead to a bias in species richness over time in that area. On the balance of evidence
310 presented, in terms of the species richness estimates staying with the longer 30 minute tows is
311 capturing additional information, and will give better estimates of species richness (this is a function
312 of the larger net swept area in the longer tows). However, this experiment only addresses the
313 consequences of a reduction in fishing effort, as the data available generally has one short tow for
314 each long tow in each rectangle sampled. Therefore, in order to see how this applies more broadly we
315 would need to examine paired tows that account other factors that we cannot adequately test here,
316 such as vessel and crew effect.

317 With a longer tow and a greater net swept area the probability of encountering a rare species
318 increases, the argument stands that using a shorter tow duration and at the same time an increased
319 number of stations might allow additional habitats to be sampled and could thereby increase the
320 probability of encountering rare species (Pennington and Vølstad, 1991). However, this only holds if
321 the time gained permits to carrying out additional tows (including steaming time) in a given day, and
322 the survey design moves from rectangle to habitat stratification. The increase in species richness
323 through sampling a variety of habitats in the North Sea is demonstrated in Wieland (2017a). Species
324 richness varied at different depths, being significantly higher at deeper stations, due to an increase in

325 numbers of sharks and rays (Wieland, 2017a). This is reflected in our linear mixed model investigating
326 species richness, depth was a significant variable in predicting number of species in a haul (Table S3).
327 A key aspect of reducing tow duration is to adapt the current sampling regime and sample more
328 habitats within the North Sea. In 2016 a greater variety of habitats were sampled, Wieland, (2017a)
329 found that there was an increase in biomass at depth. Depth of the tow will affect the community
330 composition and the performance of the gear, so rectangles with paired tows that have a large
331 difference in depth may not be directly comparable; this has been addressed by limiting the depth
332 band of tows within rectangles for the standard survey area. Thus, by reducing the tow time to 15 min
333 and freeing up time to sample more habitats at different depths the survey may in fact become
334 impaired in its primary goal of detecting trends in abundance and biomass in the fish community.

335 The general picture in the abundance in the short tow category is higher than in the long tow, with
336 the exception of fish in the 30-39 cm class and the >100cm class (Figure 3). The same picture is seen
337 in the biomass estimates. The short tow category had a significantly higher logged mean abundance
338 at length than the long tow category. The investigation of arithmetic mean body size class by
339 abundance/biomass suggested a significant difference in the mean body size caught in long and short
340 tows, with long tows catching slightly larger fish on average than the short tows. However, the
341 geometric mean length weighted by biomass (T_{YL}) was robust to this influence. Similarly, the species
342 composition metric (MML) was also robust to the change in tow duration.

343 The effective sample sizes for estimating population characteristics (e.g. age) are typically low for the
344 IBTS surveys, around one fish at length, on average, per tow, this implies that there may be little to
345 gain by increasing tow duration beyond 15 min for estimating population characteristics. Devine and
346 Pennington (2017) suggest that for the IBTS survey, 15 min tows are more efficient for estimating
347 catch per unit effort series than 30 min tows. In addition, other studies on the North Sea Q3
348 experimental tow data have examined the effect on catch rates by ages for individual species such as
349 cod (*G. morhua*), and whiting (*Merlangius merlangus*) (Wieland, 2017b), haddock (*M. aeglefinus*) and

350 Norway pout (*Trisopterus esmarkii*) (Jaworski *et al.*, 2017). There was no clear indication that the
351 experimental 15 min tows were any less representative than the standard 30 min for catch rates at
352 age of these four species (Jaworski *et al.*, 2017; Wieland, 2017b).

353 Attributing the variation in species richness, abundance, biomass and body size in a tow to just one
354 factor, duration of a tow, is not always possible, as the survey data is highly variable the community
355 structure varies in space and time, and the North Sea environment is heterogeneous. Efforts have
356 been made to standardize protocols in the North Sea surveys, by fixing tow duration, vessel speed and
357 standardizing the gear. However, in practice, tow duration varies, for example if a very large pelagic
358 shoal is detected on the sonar then a chief scientist may decide to tow early to protect the nets.

359 Vessel speed, also known as speed over ground, is difficult to regulate as this is only one measure of
360 speed, without a clear measure of speed in water it is difficult to ascertain how the variation of vessel
361 speed will affect the catch composition. Figure S2 shows how each vessel performed at 30 min tows
362 and 15 min tows respectively. In some cases, the vessels deviated from the expected 4 knots (speed
363 over ground). The protocol set out for this survey, to maintain a constant speed of 4 knots through
364 water and over ground is impracticable. A departure from target speed has been found to affect catch
365 rates of target species in previous studies (Adlerstein and Ehrich, 2002; Koeller, 1991; Main and
366 Sangster, 1981; Neproshin, 1979; Ona and Chruickshank, 1986; Olsen *et al.*, 1982; Olsen, 1990; Ona
367 and Godø, 1990). In our linear mixed models speed was not a significant factor in describing variance
368 in richness, abundance or biomass estimates (Table 1), which is not surprising, since vessels operate
369 around a given target speed (Figure S2). It is noted that the “standard” gear as described in the survey
370 manual is not used by any participating nation (ICES, 2015b).

371 Time of day plays a part in variation of catch rates for some species, this is reflected in our linear mixed
372 models, where time of day is a significant factor in all three models. In this study the time of day varies
373 for paired tows in a given rectangle, in some cases the tows occur as close as 2 mins apart, in other
374 cases the range is much higher, for example 2.45 am for one tow and 6.55 pm for the second. Catches

375 of several species are known to fluctuate with time of day, (Adlerstein and Trumble, 1993; Adlerstein
376 and Ehrich, 2002; Ehrich and Gröger, 1989; Pitt *et al.*, 1981; Wieland *et al.*, 1998), so paired tows
377 should be performed as close together as possible to limit bias. Depth of the tow will affect the
378 community composition and the performance of the gear, so rectangles with paired tows that have a
379 large difference in depth may not be directly comparable. Estimates of wing swept area are also
380 imprecise. These mechanical parameters alongside fish behaviours lead to uncertainty in estimates of
381 fish abundance (numbers per km²) and biomass (kg/km²).

382 These considerations may compromise the ability to assess the differences in one factor, as best
383 practice would be to control all other variables. Given the time and financial constraints on
384 participating nations in the current economic climate, it would not be practical to perform such an
385 experiment on this scale. As these experimental tows are not truly paired tows, i.e. two vessels towing
386 side by side, at the same speed and at the same depth, there is a high amount of additional variation.
387 However, when paired experiments have been carried out, the results still showed a large variability
388 between tows carried out in close proximity at the same time (Doray *et al.*, 2010). This makes it very
389 difficult to draw any significant results from any tests performed. As a result of this variation we have
390 elected to look at the average changes over the whole study area, to ascertain if a signal is present
391 that suggests a consistent bias based on tow duration.

392 Optimisation of survey resources while managing the needs and expectations of the end users is an
393 issue that affects many nations. In this case the discussion that has been initiated on optimising the
394 survey design will require big picture thinking. This experiment, addressing one factor, tow duration,
395 must be set in the context of the wider discussion which considers all the potential future changes,
396 such as a new fishing gear, that will be required to maintain this survey, and other similar surveys into
397 the future. Fisheries survey data are highly variable and disentangling within survey variation and
398 understanding how this affects individual samples is a difficult task. By changing a key factor in the
399 survey design there is a risk of undermining the primary goal of the survey. Such a change must be

400 decided on balance of the potential gains for example, reducing tow duration may increase precision
401 of a survey by allowing time to collect more samples. The average number of stations sampled by the
402 full survey from 2011-2014 was 323 (Table S2 in supplementary material), assuming reducing tow
403 duration to 15 mins would allow one additional tow per day for each vessel, this increases the total
404 number of stations sampled to 424 stations, representing a 31% increase in the number of stations
405 sampled. If each nation could carry out 1.5 extra tows per day then there would be a 47% increase in
406 stations sampled, however this is unlikely given the distance between stations. Based on projections
407 using a semi-Gleason fit on the species accumulation curves, a 31% increase in short hauls may provide
408 a similar amount of species richness information as the current survey design.

409 A major concern when looking at historic surveys with longer time series is disrupting the time series
410 and therefore losing long term information. In this particular case, there is another survey conducted in
411 Q1 which largely samples the same community (with the exception of a few migratory species) and
412 over a much longer time period therefore the historical information for this community may still be
413 maintained despite change to the Q3 survey. There are many practical benefits to implementation of
414 a reduction of tow duration within the North Sea Q3 survey such as less wear and tear on gear;
415 increased coverage of habitats; a reduction in subsampling of large tows; and a potential reduction in
416 animal mortality. Reducing the impact of marine surveying is important and a reduction in tow
417 duration may be part of the solution. However, if there is a substantive increase in number of tows
418 carried out, the displacement in effort may impact on more habitats. The results presented illustrate
419 the potential losses involved as it supports the assertion that a reduction in tow duration, given the
420 current survey design, would have a negative impact on the capacity to resolve species richness, and
421 may also affect the main survey objectives to supply data to the assessment working groups to fine-
422 tune North Sea regional calculations of estimates of species abundance and biomass in support of the
423 first quarter assessments. Before any longterm changes are made to a survey's design it is imperative
424 that a broader strategy on survey modernisation and impact reduction is discussed and agreed upon.

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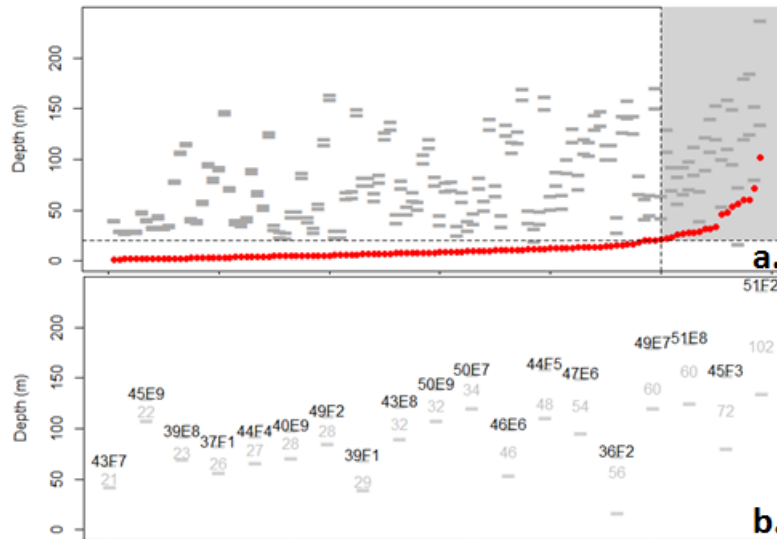
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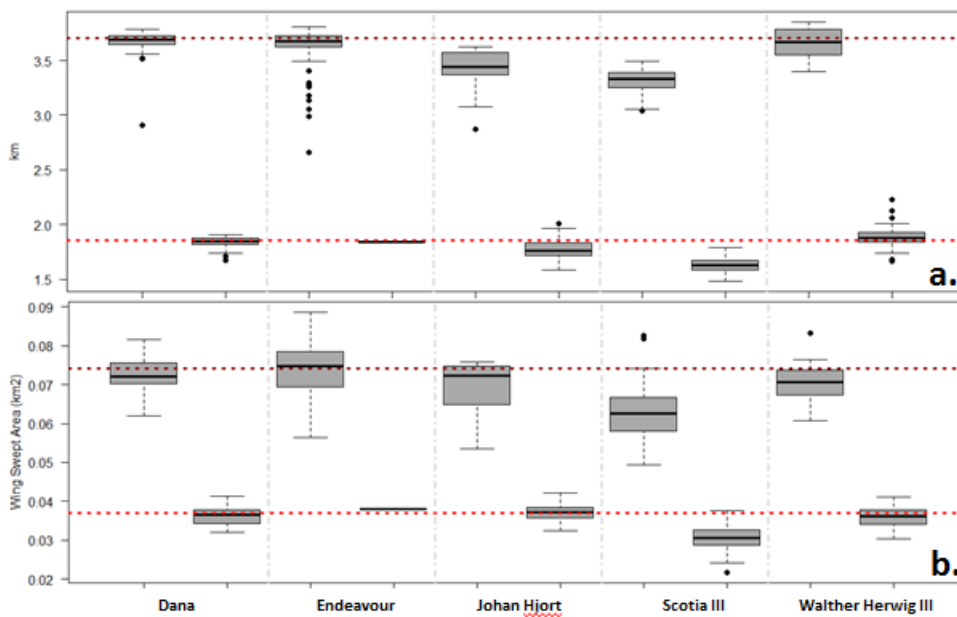
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614

615 **Supplementary Material; Impact of trawl tow duration on species diversity, and**
 616 **community composition in bottom trawls**



617
 618 *Figure S1. (a.) Differences in depth of paired long and short tows. The majority of rectangles (84%)*
 619 *have paired tows with depth difference of 20m or less. The red dots show the spread of the depths and*
 620 *the grey lines show the actual depths recorded. (b.) This graph highlights the rectangles of paired tows*
 621 *of more than 20m depth differences (grey box in top graph).*



622

623 Figure S2 (a.) The top boxplot shows the distance towed for long and short tows the dark red line shows
 624 the expected distance towed for 30min at 4 knots (3.7km) the light red line shows the expected distance
 625 towed in 15mins at 4 knots (1.85km) for the 2015 and 2016 sample area. (b.) The bottom boxplot
 626 shows the wing swept area estimates (km²) for long and short tow durations at a mean wingspread of
 627 20m. Analysis of variance shows that ship is a significant factor for explaining differences in distance
 628 and speed. The mean speed in the long group is 3.86 knots while in the short group it is 3.76 knots.

629

630 Table S1: Species occurrence in each tow category and in each year in the study area. Over the two-
 631 year period 89 species were collected in long tows, 80 species were recorded in short tows. 95
 632 different species were recorded in total. Resolution of taxonomic discrepancies carried out by
 633 Moriarty et al., (2017) are noted below the table.

	Common Name	long, 2015	long, 2016	short, 2015	short, 2016	% of occurrence in survey for both years
Actinopterygii						
Beloniformes						
<i>Belone belone</i>	Garfish	0	1	0	0	0.24
Clupeiformes¹						
<i>Alosa alosa</i>	Allis shad	1	0	1	0	0.49
<i>Alosa fallax</i>	Twaite shad	3	1	1	0	1.22
<i>Clupea harengus</i>	Herring	88	93	74	78	81.02
<i>Engraulis encrasicolus</i>	Anchovy	12	6	8	3	7.06
<i>Sardina pilchardus</i>	Pilchard	5	4	2	2	3.16
<i>Sprattus sprattus</i>	Sprat	53	49	44	37	44.53
Gadiformes						
<i>Ciliata mustela</i>	Five-bearded rockling	0	0	0	1	0.24
<i>Enchelyopus cimbrius</i>	Four-bearded rockling	17	19	7	11	13.14
<i>Gadiculus argenteus</i>	Silvery pout	3	9	5	12	7.06
<i>Gadiculus thori</i>	Pout	2	2	2	1	1.70
<i>Gadus morhua</i>	Cod	52	59	54	65	55.96
<i>Melanogrammus aeglefinus</i>	Haddock	67	74	59	81	68.37
<i>Merlangius merlangus</i>	Whiting	92	102	92	108	95.86

<i>Merluccius merluccius</i>	Hake	39	46	37	42	39.90
<i>Micromesistius poutassou</i>	Blue whiting	15	8	13	13	11.92
<i>Molva molva</i>	Ling	14	14	15	20	15.33
<i>Phycis blennoides</i>	Greater forkbeard	2	0	1	0	0.73
<i>Pollachius pollachius</i>	Pollack	0	1	1	1	0.73
<i>Pollachius virens</i>	Saithe	35	42	32	33	34.55
<i>Trisopterus esmarkii</i>	Norway pout	46	53	45	57	48.91
<i>Trisopterus luscus</i>	Bib	1	3	3	1	1.95
<i>Trisopterus minutus</i>	Poor cod	19	24	18	27	21.41
Lophiiformes						
<i>Lophius budegassa</i>	Black bellied angler	3	4	0	1	1.95
<i>Lophius piscatorius</i>	Angler	34	45	27	27	32.36
Osmeriformes^{2/3}						
<i>Argentina silus</i>	Greater argentine	12	8	12	11	10.46
<i>Argentina sphyraena</i>	Lesser argentine	33	39	31	45	36.01
Perciformes						
Ammodytidae ⁴	Sandeels	23	16	20	20	19.22
<i>Anarhichas lupus</i>	Catfish	3	8	2	4	4.14
<i>Callionymus lyra</i>	Dragonet	39	40	30	39	36.01
<i>Callionymus maculatus</i>	Spotted dragonet	24	32	17	24	23.60
<i>Callionymus reticulatus</i>	Reticulated dragonet	0	4	1	0	1.22
<i>Capros aper</i>	Boarfish	3	4	3	5	3.65
<i>Echiichthys vipera⁵</i>	Lesser weever	13	12	13	11	11.92
Gobiidae ⁶	Gobies	2	8	3	13	6.33
<i>Leptoclinus maculatus</i>	Spotted snake blenny	1	0	0	0	0.24
<i>Lumpenus lamprætaeformis</i>	Snake blenny	2	0	5	2	2.19
<i>Lycodes gracilis</i>	Eelpout	1	0	2	1	0.97
<i>Lycodes vahlii</i>	Eelpout	0	1	0	0	0.24
<i>Mullus surmuletus</i>	Striped red mullet	17	14	13	7	12.41
<i>Pholis gunnellus</i>	Butterfish	1	2	0	4	1.70
<i>Sarda sarda</i>	Atlantic bonito	1	0	0	0	0.24
<i>Scomber colias</i>	Atlantic chub mackerel	1	0	0	0	0.24
<i>Scomber scombrus</i>	Mackerel	76	73	63	52	64.23
<i>Trachinus draco</i>	Greater weever	0	0	1	1	0.49
<i>Trachurus trachurus</i>	Horse mackerel	60	71	32	43	50.12
Pleuronectiformes						
<i>Arnoglossus laterna</i>	Scaldfish	18	16	9	11	13.14
<i>Buglossidium luteum</i>	Solenette	24	25	19	23	22.14
<i>Glyptocephalus cynoglossus</i>	Witch	23	18	15	15	17.27
<i>Hippoglossoides platessoides</i>	Long rough dab	75	74	69	81	72.75

<i>Hippoglossus hippoglossus</i>	Halibut	2	3	3	2	2.43
<i>Lepidorhombus whiffiagonis</i>	Megrim	18	16	12	19	15.82
<i>Limanda limanda</i>	Common dab	87	93	82	96	87.10
<i>Microchirus variegatus</i>	Thickback sole	2	2	0	2	1.46
<i>Microstomus kitt</i>	Lemon sole	85	84	72	87	79.81
<i>Phrynorhombus norvegicus</i>	Norwegian topknot	1	0	0	0	0.24
<i>Platichthys flesus</i>	Flounder	3	4	6	1	3.41
<i>Pleuronectes platessa</i>	Plaice	85	86	77	86	81.27
<i>Scophthalmus maximus</i>	Turbot	7	12	7	8	8.27
<i>Scophthalmus rhombus</i>	Brill	4	4	3	6	4.14
<i>Solea solea</i>	Dover sole	6	9	6	3	5.84
<i>Zeugopterus punctatus</i> ⁷	Topknot	0	1	0	0	0.24
Salmoniformes						
<i>Salmo trutta trutta</i>	Sea trout	0	1	0	0	0.24
Scorpaeniformes						
<i>Agonus cataphractus</i>	Hooknose	14	18	10	11	12.90
<i>Chelidonichthys cuculus</i> ⁸	Red gurnard	5	5	6	10	6.33
<i>Chelidonichthys lucerna</i> ⁸	Tub gurnard	7	9	10	9	8.52
<i>Cyclopterus lumpus</i>	Lumpsucker	1	1	1	0	0.73
<i>Eutrigla gurnardus</i> ⁹	Grey gurnard	98	102	95	105	97.32
<i>Helicolenus dactylopterus</i>	Bluemouth	1	2	0	0	0.73
<i>Liparis liparis liparis</i>	Striped seasnail	0	1	0	0	0.24
<i>Myoxocephalus scorpius</i>	Bullrout	11	4	7	1	5.60
<i>Sebastes viviparus</i> ¹⁰	Norway haddock	8	11	10	4	8.03
<i>Trigla lyra</i> ¹¹	Piper gurnard	7	7	0	0	3.41
<i>Triglops murrayi</i>	Moustache sculpin	1	2	0	0	0.73
Stomiiformes						
<i>Maurolicus muelleri</i>	Pearlside	0	4	2	1	1.70
Syngnathiformes						
<i>Entelurus aequoreus</i>	Snake pipefish	0	0	0	1	0.24
<i>Syngnathus acus</i> ¹²	Great pipefish	0	0	0	1	0.24
Zeiformes						
<i>Zeus faber</i>	John dory	3	2	1	1	1.70
Chondrichthyes						
Lamniformes						
<i>Cetorhinus maximus</i>	Basking shark	0	1	0	0	0.24
Elasmobranchii						
Carcharhiniformes						
<i>Galeorhinus galeus</i>	Tope	0	3	0	1	0.97
<i>Mustelus asterias</i>	Starry smooth hound	3	2	3	3	2.68
<i>Mustelus mustelus</i>	Smooth hound	0	0	2	3	1.22
<i>Scyliorhinus canicula</i>	Lesser spotted dogfish	23	40	22	28	27.49

Rajiformes						
<i>Amblyraja radiata</i>	Starry ray	34	37	22	28	29.44
<i>Dipturus batis</i> ¹³	Blue skate	2	0	1	2	1.22
<i>Leucoraja fullonica</i>	Shagreen ray	1	1	0	0	0.49
<i>Leucoraja naevus</i>	Cuckoo ray	9	13	6	12	9.73
<i>Raja brachyura</i>	Blond ray	0	0	0	3	0.73
<i>Raja clavata</i>	Thornback ray	4	3	2	2	2.68
<i>Raja montagui</i>	Spotted ray	3	4	1	5	3.16
Squaliformes						
<i>Etmopterus spinax</i>	Velvet belly	0	0	1	0	0.24
<i>Squalus acanthias</i>	Spurdog	12	9	2	5	6.81
Myxini						
Myxiniformes						
<i>Myxine glutinosa</i>	Hagfish	6	8	6	8	6.81
Petromyzonti						
Petromyzontiformes						
<i>Lampetra fluviatilis</i>	European river lamprey	1	0	0	0	0.24
<i>Petromyzon marinus</i>	Sea lamprey	0	1	0	0	0.24

634 ¹ Clupeidae reported on 5 occasions by England resolved to species level using k-NN (Moriarty et al., 2017), This
635 resulted in 4 Clupeidae estimated as *C. harengus* and 3 Clupeidae estimated as *S. sprattus*

636 ² Argentinidae reported on 36 occasions by England resolved to species level using k-NN. This resulted in 416
637 species level estimations.

638 ³ *Argentina* reported on 1 occasion by Norway resolved to species level using k-NN.

639 ⁴ Ammodytidae (Sandeels) are grouped to family level.

640 ⁵ England uses the genus *Echiichthys* to report *E. vipera*, all occurrences changed to reflect species level.

641 ⁶ All Gobiidae are grouped to family level.

642 ⁷ England uses the genus *Zeugopterus* to report *Z. punctatus*, all occurrences (n=2) changed to reflect species
643 level.

644 ⁸ *Chelidonichthys* reported by England resolved to species level using k-NN. This resulted in 19 species level
645 estimations.

646 ⁹ England uses the genus *Eutrigla* to report *E. gurnardus*, all occurrences changed to reflect species level.

647 ¹⁰ England uses the genus *Sebastes* to report *S. viviparus*, all occurrences (n=3) changed to reflect species level.

648 ¹¹ England uses the genus *Trigla* to report *T. lura*, all occurrences changed to reflect species level.

649 ¹² One occurrence of *Syngnathus*, by Germany has been changed to *S. acus*.

650 ¹³ One occurrence of *Dipturus*, by England has been changed to *D. batis*.

651

652 *Table S2. The number of stations (s) carried out by each nation and the number of days(d) at sea during*

653 *the Greater North Sea Q3 survey from 2011 to 2016.*

	2011		2012		2013		2014		2015		2016	
	s	d	s	d	s	d	s	d	s	d	s	d
Denmark (Dana)	49	15	49	15	50	17	50	17	59	17	59	17
Sweden (Dana)	45	13	45	11	45	11	45	11	45	11	45	11
England (CEFAS Endeavour)	75	25	75	24	76	25	73	26	76	24	78	26
Norway (Johan Hjort)	45	17	37	15	46	19	46	19	48	23	67	20
Scotland (Scotia III)	84	19	84	20	84	18	84	21	91	20	99	19

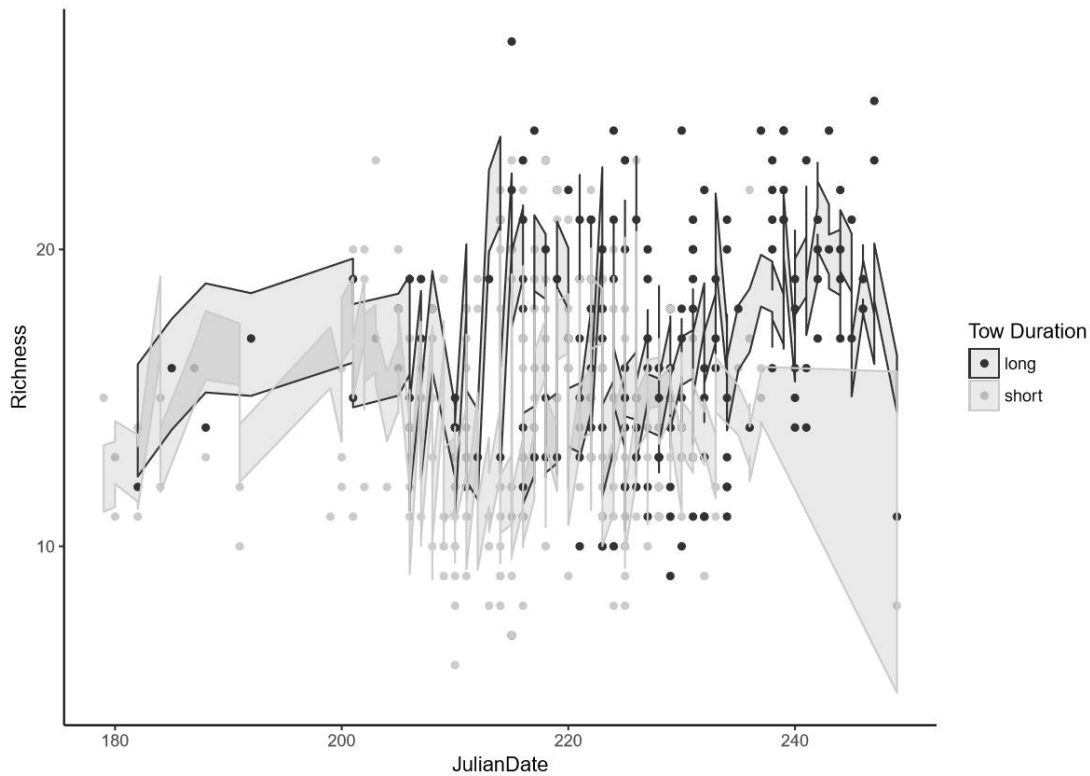
Germany (Walther Herwig III)	29	13	29	13	17	9	29	13	33	13	33	12
Total number of stations	327		319		318		327		352		381	

654

655 *Table S3. Summary of best fitting model for explaining variance in species richness in a haul. During*
656 *model selection 208 model combinations of fixed effects were tested. Importance was ranked from 0-*
657 *1. For Example: Ship scored an importance (I) of 1 and was present in 128 models. Ship (I=0.1, N=128),*
658 *Tow Duration (I=1, N=144), Year(I=0.86, N=123), Time of Day(I=0.53,N=104), Julian Day(I=0.50,*
659 *N=104), Speed(I=0.35, N=104), Depth(I=1, N=104), Tow Duration : Year (I=0.23, N=48), Tow Duration :*
660 *Ship (I=0.24,N=48).*

Best Fit Model			
Richness ~ Year + Julian Days + Ship + Depth + Tow Duration + Time of day + (1 ICESStSq)			
AIC (best fit) 2015.8		AIC (global fit) 2021.4	
Random effects:	Variance	Std.Dev.	
ICESStSq	3.141	1.772	
Residual	5.595	2.365	
Number of obs: 411, groups: ICESStSq, 97			
Fixed effects:	Estimate	Std. Error	t value
(Intercept)	15.9720	0.4459	35.82
Year (2016)	0.6654	0.2643	2.52
Julian Day	-0.3825	0.2522	-1.52
Depth (m)	2.1952	0.2361	9.30
Ship (CEFAS Endeavour)	0.7962	0.5600	1.42
Ship (Johan Hjort)	-2.2949	0.7118	-3.22
Ship (Scotia III)	0.6044	0.4683	1.29
Ship (Walther Herwig III)	-1.4575	0.4985	-2.92
Tow Duration (short)	-1.6257	0.3061	-5.31
Time of Day	-0.1957	0.1316	-1.49

661



662

663 *Figure S3. Model Prediction of best fit model for explaining variance in species richness in each haul.*

664 *The long tows have a higher species richness on average than the short tows.*

665 *Table S4. Summary of best fitting model for explaining variance in abundance by haul. During model*

666 *selection 208 model combinations of fixed effects were tested. Importance was ranked from 0-1. For*

667 *Example: Ship scored an importance (I) of 1 and was present in 128 models. Ship (I=1, N=128), Tow*

668 *Duration (I=0.89, N=144), Year(I=0.72, N=128), Time of Day(I=0.63, N=104), Julian Day(I=0.57, N=104),*

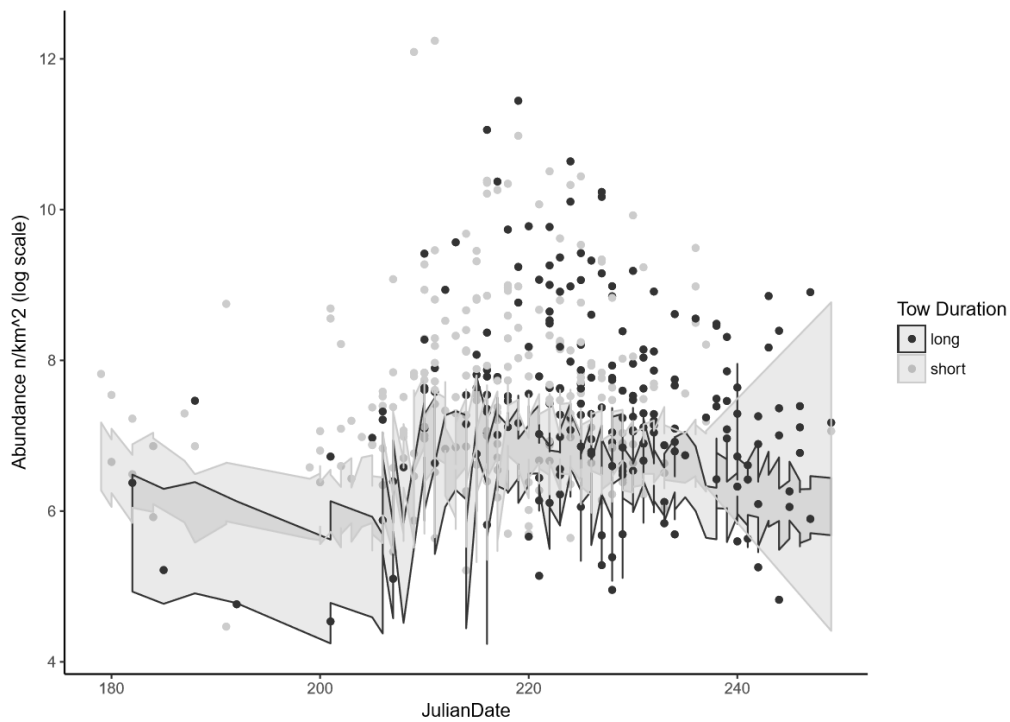
669 *Speed(I=0.50, N=104), Depth(I=0.41, N=104), Tow Duration : Year (I=0.21, N=48), Tow Duration : Ship*

670 *(I=0.19, N=48).*

Best Fit Model			
log(Abundance) ~ Julian Days + Ship + Tow Duration + Time of day + (1 ICESStSq)			
AIC (best fit) 1263.8		AIC (global fit) 1268.2	
Random effects:	Variance	Std.Dev.	
ICESStSq	0.3339	0.5779	
Residual	0.9781	0.9890	
Number of obs: 411, groups: ICESStSq, 97			

Fixed effects:	Estimate	Std. Error	t value
(Intercept)	6.77396	0.16356	41.42
Julian Day	-0.19024	0.08999	-2.11
Ship (CEFAS Endeavour)	-0.19752	0.21967	-0.90
Ship (Johan Hjort)	-1.27258	0.24803	-5.13
Ship (Scotia III)	-0.11734	0.17963	-0.65
Ship(Walther Herwig III)	-0.44640	0.20229	-2.21
Tow Duration (short)	0.28700	0.12616	2.27
Time of Day	0.09384	0.05399	1.74

671



672

673 *Figure S4. Model Prediction of best fitting model for explaining variance in haul abundance (n/km^2).*

674 *The short tows have a higher abundance (n/km^2) on average than the long tows.*

675

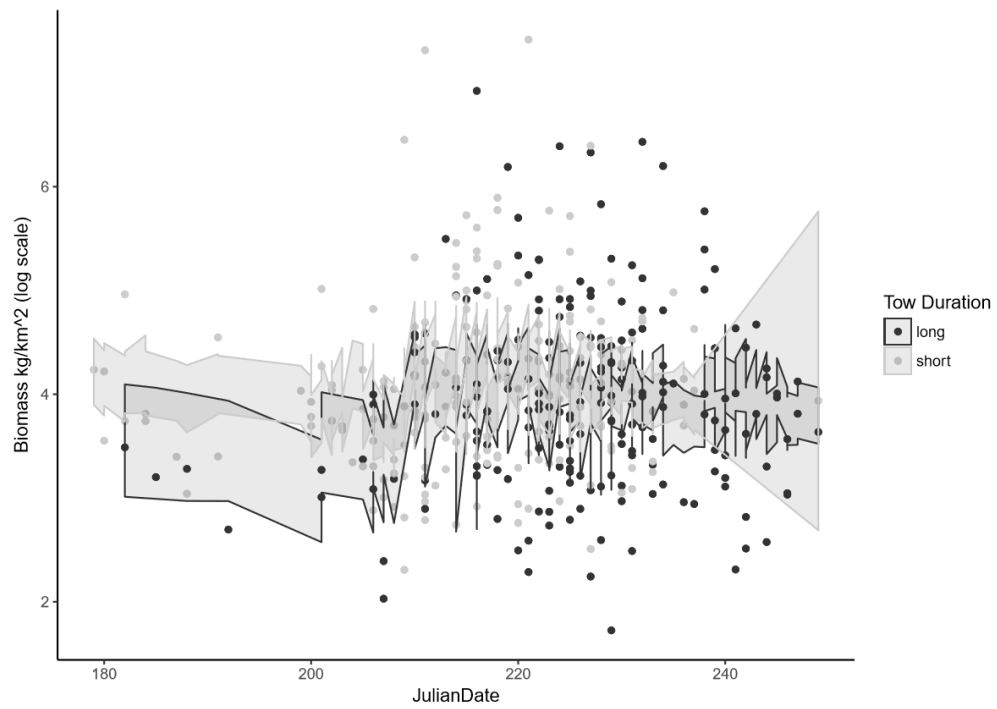
676 *Table S5. Summary of best fitting model for predicting biomass. During model selection 208 model*

677 *combinations of fixed effects were tested. Importance was ranked from 0-1. For Example: Ship scored*

678 an importance (*I*) of 0.87 and was present in 128 models. Ship (*I*=0.87, *N*=128), Tow Duration (*I*=0.94,
679 *N*=144), Year(*I*=1, *N*=123), Time of Day(*I*=0.53,*N*=104), Julian Day(*I*=0.32, *N*=104), Speed(*I*=0.28,
680 *N*=104), Depth(*I*=0.31, *N*=104), Tow Duration : Year (*I*=0.25, *N*=48), Tow Duration : Ship
681 (*I*=0.07,*N*=48).

Best Fit Model			
log(Biomass) ~ Year + Ship + Tow Duration + Time of day + (1 ICESStSq)			
AIC (best fit) 973.5		AIC (global fit) 985.6	
Random effects:	Variance	Std.Dev.	
ICESStSq	0.1919	0.4381	
Residual	0.4704	0.6858	
Number of obs: 411, groups: ICESStSq, 97			
Fixed effects:	Estimate	Std. Error	t value
(Intercept)	4.150e+00	1.434e-01	28.947
Year (2016)	-2.918e-01	6.821e-02	-4.278
Ship (CEFAS Endeavour)	-1.374e-01	1.402e-01	-0.980
Ship (Johan Hjort)	-4.726e-01	1.469e-01	-3.218
Ship (Scotia III)	-2.363e-01	1.252e-01	-1.887
Ship (Walther Herwig III)	-4.047e-01	1.400e-01	-2.891
Tow Duration (short)	2.332e-01	8.786e-02	2.655
Time of Day	1.259e-04	8.487e-05	1.483

682



683

684 *Figure S5. Model prediction of best fit model for explaining variance in haul biomass (kg/km²). The*

685 *short tows have a higher biomass (kg/km²) on average than the long tows.*

686