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1 **Inferring the location and scale of mixing between habitat areas of**  
2 **lesser sandeel through information from the fishery**

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4 **Abstract**

5 Sandeels are small pelagic fish which play an important role in the diet of a range of  
6 natural predators. Due to their low occurrence in traditional survey gear, little is known  
7 about their large scale distribution or the degree of mixing between habitat areas. We  
8 used detailed information collected directly from the fishery to map fishing grounds and  
9 assumed these to reflect the foraging habitat of sandeel. Length distributions from  
10 individual hauls were used to assess differences in length distributions as a function of  
11 the distance between samples. Sandeel foraging habitat covered approximately 5% of  
12 the total area of the North Sea. Mixing between neighbouring fishing grounds was too  
13 low to eliminate differences in length distributions at distances between grounds down  
14 to 5 km. Within fishing grounds, mixing was sufficient to eliminate differences in  
15 length distributions at scales less than 28 km but insufficient at greater distances. The  
16 lack of mixing between grounds may result in large differences in sandeel abundance  
17 among adjacent fishing grounds. Further, high abundance at one end of a large fishing  
18 ground is not necessarily indicative of high abundance at the other end.

19 **Key words**

20 Fishery cooperation, habitat mapping, sandeel, scale of mixing

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## 27 **Introduction**

28 Sandeels (*Ammodytes* spp.) are small semi pelagic fish with a worldwide distribution  
29 (Smith and Heemstra, 1986). They usually constitute a high proportion of the fish  
30 biomass in the regions where they occur (see e.g. Reay, 1970), and are an important  
31 prey species for numerous fish, seabirds and mammals (Daan, 1989; Furness, 1990;  
32 Wanless *et al.*, 1998). In addition, they are the target of a large scale industrial fishery in  
33 the North Sea (ICES, 2008a). This has led to concerns as to whether fisheries pose a  
34 threat to top predators through their reduction of the food supply (Macer, 1966;  
35 Monaghan, 1992; Wright, 1996; Wanless *et al.*, 1998; Engelhard *et al.*, 2008). Most  
36 sandeel species inhabit shallow, turbulent sandy areas, located on depths between 20  
37 and 70 m where the content of the finest particles silt and clay is low (Macer, 1966;  
38 Reay, 1970; Wright *et al.*, 2000). Because of the limited availability of such substrate  
39 (Wright *et al.*, 1998), the distribution of post-settled sandeels is highly patchy (Macer,  
40 1966; Wright *et al.*, 2000; Freeman *et al.*, 2004; Holland *et al.*, 2005). Post-settled  
41 sandeels are rarely found further than 15 km away from known habitat (Wright, 1996;  
42 Engelhard *et al.*, 2008) and the maximum distance travelled by tagged individuals  
43 displaced from grounds was 64 km (Gauld, 1990). This lack of large scale dispersal

44 combined with a limited larval exchange between areas (Proctor *et al.*, 1999;  
45 Christensen *et al.*, 2009) means that local aggregations may be vulnerable to depletion  
46 by the fishery and increases the risk of adverse effects on local predators even if the  
47 North Sea stock is inside biologically safe limits. Unfortunately, the lack of knowledge  
48 on the location of the majority of these aggregations in the North Sea and the population  
49 dynamics within them has hindered studies of local depletion except in a few local areas  
50 (Wright, 1996; Rindorf *et al.*, 2000; Daunt *et al.*, 2008; Engelhard *et al.*, 2008).

51 There are several reasons for the limited knowledge of sandeel distribution and  
52 population dynamics. Firstly, sandeel bury into the sediment when not feeding in the  
53 water column or when approached by predators foraging near the seabed (Winslade,  
54 1974a,b,c; Girsu and Danilov, 1976; Pearson *et al.*, 1984; Pinto *et al.*, 1984). This  
55 burying behaviour makes their accessibility to sampling in the water column highly  
56 variable. Due to this variability and the patchy distribution of habitat, none of the  
57 regular North Sea acoustic or trawl surveys provide reliable means of mapping sandeel  
58 distribution, although both approaches have been used to investigate density in a few  
59 areas of the North Sea (Greenstreet *et al.* 2006, ICES 2008b, Johnsen *et al.* 2009).  
60 Secondly, although the requirement for specific habitats is likely to limit sandeel  
61 movement, little direct information exists on the extent of horizontal movements of  
62 post-settled sandeels within or between habitat areas. The few mark-recapture  
63 experiments that have been conducted were restricted to small regions because of the  
64 difficulty of marking a representative number of this abundant species. Furthermore, the  
65 recapture location could not be determined since the species is not sorted onboard  
66 fishing boats (Gauld, 1990). Consequently, the distribution of habitat areas must be

67 derived from non-conventional methods and movements of this species throughout a  
68 large region such as the North Sea must be assessed from indirect methods.

69 Movements between habitat areas may be detected by differences between length  
70 distributions. Local differences in recruitment, growth or mortality will result in  
71 differences between areas unless fish mix between different areas. If differences arise  
72 from variation in recruitment between areas, subsequent mixing would lead to a  
73 decrease in the difference between length distributions over the season. Alternatively,  
74 increasing differences in length distributions over the season could result from variation  
75 in growth or mortality and lack of mixing between adjacent areas during the season.  
76 This increase should be greater the longer the distance between the habitat areas if  
77 growth and mortality differences increase with distance. Alternatively, if mixing occurs  
78 at small scales while growth and mortality varies independently of distance, differences  
79 between length distributions should increase at small distances but vary independently  
80 of distance at large scales. Based on the extent of identified sandeel aggregations  
81 (Freeman *et al.*, 2004; Holland *et al.*, 2005) and the apparent limited movements of  
82 settled sandeels it is possible that mixing could be limited both within as well as among  
83 habitat areas.

84 The determination of length distributions in local aggregations repeatedly over a  
85 longer period of time is a costly exercise if scientific vessels are required to sample the  
86 fish. However, the sandeel fishery could potentially provide crucial information at  
87 comparatively low costs. The fishery targets foraging sandeel near areas where the  
88 sandeels bury and the fishing grounds should therefore provide information on the  
89 distribution of sandeel habitat areas (Jensen 2001). Recognizing that information on  
90 sandeel habitat areas was crucial to the validity of the scientific advice given, a

91 collaboration between the Danish Fishermen's Association and the Danish Institute for  
92 Fisheries Research, now Danish Technical University, was started in 1999 in order to  
93 provide the information needed to improve the understanding of North Sea sandeel  
94 population dynamics. Under this collaboration, data were collected by Danish sandeel  
95 skippers directly from the fishing vessels.

96 The objective of this study was to use the detailed data collected in the fishery to  
97 produce a map of the foraging habitat of sandeel and then examine the extent of mixing  
98 between and within foraging habitats. Foraging habitats are defined here as areas with  
99 potential large densities of non-buried sandeel as sandeel bury when not feeding  
100 (Winslade, 1974a). Four predictions were made of the relationship between the  
101 difference in length distributions and distance between samples in time and space and  
102 the extent of mixing:

- 103 1) If the difference between length distributions increases with distance *within* a  
104 fishing ground, the degree of mixing between subareas of the fishing ground  
105 must be limited.
- 106 2) If the difference between length distributions increases with distance *between*  
107 fishing grounds, the degree of mixing between fishing grounds must be limited.
- 108 3) If the difference between length distributions *decreases* over the season, initial  
109 differences caused by differences in e.g. recruitment slowly disappear through  
110 mixing of fish.
- 111 4) If the difference between length distributions *increases* over the season, initial  
112 differences are enhanced through changes in growth, mortality or emergence  
113 behaviour and lack of mixing.

114 In both 1) and 2), the distance at which length distributions become significantly  
115 different indicates the distance at which the rate of mixing becomes too low to  
116 compensate for differences in recruitment, growth and mortality.

## 117 **Methods**

### 118 **Sandeel foraging habitat**

119 Three types of information were combined to derive the spatial distribution of  
120 foraging habitat: global positioning system (GPS) loggings from individual ships, vessel  
121 monitoring system (VMS) data and evaluation of maps by fishermen. GPS based  
122 computer systems are used by the fishermen together with information from sea charts  
123 and past experience to map and log fishing grounds and fishing activities. The maps  
124 contain data on longitude and latitude, and, in some cases, names of the fishing grounds.  
125 This detailed information was used to map about 10% of the grounds. To supplement  
126 this data, information about catches of sandeel in individual trawl hauls for which the  
127 latitude and longitude of hauling were known were used to locate another 50% of the  
128 grounds. The remaining 40% of the fishing grounds were obtained from VMS data from  
129 Danish vessels fishing sandeel. These data are logged continually while the vessel is at  
130 sea. This means that the time not spend fishing for sandeel is included and must  
131 subsequently be excluded through filtering. These filtering routines were based on  
132 distance between succeeding sample points/positions and additional information  
133 collected from Danish fishermen on the physical characteristics (i.e. depth and seabed  
134 type etc.) of each fishing ground and the time of the year the ground is usually fished.

135 From the data collected, the final map of the sandeel fishing grounds was produced  
136 using ArcMap and the Spatial Analyst extension (ESRI ArcGIS)(see supplementary

137 material S1). Each fishing ground is defined as a polygon, adjusted manually  
138 considering raw data, information about individual grounds, the location of fishing  
139 tracks and information about topography. During this process the highest weight was  
140 given to the information in the raw data. Fishermen from different harbours evaluated  
141 the map of fishing grounds, after which it was modified according to the guidelines  
142 given by the fishermen. The evaluation by the fishermen resulted in the inclusion of  
143 additional grounds (from additional navigation data) and deletion of non sandeel  
144 grounds. The map was subject to several such evaluations before being finalized.

#### 145 **Length distributions of sandeels**

146 From 1999 to 2008, Skippers from 55 sandeel fishing vessels have collected detailed  
147 haul information on 2774 individual trawl hauls. Each fishing vessel records  
148 information about the exact location and time of shooting and hauling of the trawl, the  
149 name of the fishing ground, and an estimate of the total weight of the catch in each  
150 individual trawl haul. Further, a sample of between 0.5 and 1 kg fish is collected from  
151 each haul and frozen on board. In the laboratory, the sampled fish are thawed, the  
152 sandeel are sorted by species, and total length of all fish is measured to nearest half cm  
153 below. Samples where less than 50 fish were measured were excluded due to the low  
154 accuracy of length distributions based on small samples. Further, as the objective was to  
155 compare length distributions between sites, hauls with more than 50 km between start  
156 and end positions and hauls with a distance greater than 25% of the length of the fishing  
157 ground were excluded.

158 To derive an estimate of the variation in length distributions within and between  
159 fishing grounds while accounting for the unbalanced sampling of weeks and vessels,  
160 length distributions were analyzed using generalized linear models of continuation-ratio

161 logits (Rindorf and Lewy, 2001; Marques *et al.*, 2005). This method allows statistical  
162 testing of the effect of both continuous and discrete variables. Further, by utilizing the  
163 smoothness of length distributions as a function of length this method provides more  
164 accurate estimates of length distributions than traditional methods (Rindorf and Lewy,  
165 2001). The observations analyzed were distributions of observed lengths in half cm for  
166 each of the hauls sampled. They were modelled by fitting fifth degree polynomials to  
167 the continuation-ratio-logits (Rindorf and Lewy, 2001).

168 All models were fitted using the SAS<sup>®</sup> GENMOD procedure (SAS<sup>®</sup> version 9.1 for  
169 Windows; SAS<sup>®</sup> Institute Inc. 2004). The dispersion parameter was estimated by  
170 Pearson's  $\chi^2$  statistic divided by the degrees of freedom. Only length groups with at  
171 least one sandeel on average in a sample were included in tests.

#### 172 **Within fishing ground variation**

173 To examine whether length distributions differed within fishing grounds, fishing  
174 grounds where more than 20 samples were taken in a 2-week period in a given year  
175 were selected. This resulted in seven combinations of fishing ground and time. These  
176 fishing grounds were then divided into four parts. North-south oriented fishing grounds  
177 were divided according to latitude whereas east-west oriented grounds were divided  
178 according to longitude. Individual trawl hauls were then attributed to each of these  
179 subareas based on the midpoints between the shooting and hauling positions. Of the  
180 fishing grounds selected, Scooter Plads had hauls all originating in the same quarter of  
181 the fishing ground and for this fishing ground, this quarter of the fishing ground was  
182 divided into two.

183 The statistical difference between subareas of a fishing ground was estimated using  
184 F-tests to compare the deviance of a common length distribution to that of separate  
185 length distributions in different subareas (Rindorf and Lewy, 2001), still using fifth  
186 degree polynomials to model length distributions. Fishing grounds were analyzed  
187 separately to assure that the values obtained were independent. From the F-test, a value  
188 of F and a probability of this value at the given number of degrees of freedom are  
189 obtained. If the number of degrees of freedom is unaltered, a larger value of F signifies  
190 greater difference between samples.

#### 191 **Between fishing ground variation**

192 To examine whether length distributions differed between fishing grounds, grounds  
193 where more than five samples were taken in a 2-week period were selected. The  
194 distances between all hauls were computed and for each pair of fishing grounds in a 2-  
195 week period, the hauls were grouped in bins of 10 km-distance between hauls. Haul  
196 pairs from the same fishing ground or hauls more than 75 km apart were excluded. Two  
197 models were then fitted for each combination of fishing grounds and distance using the  
198 method described in the previous section: one modelled a common length distribution  
199 and the other modelled two length distributions, one for each fishing ground. From the  
200 residual deviances, the F-value of assuming a common length distribution was estimated  
201 along with the probability of this value. This resulted in a list (cleaned for doublets) of  
202 name of fishing ground 1, name of fishing ground 2, distance-group (10 km groups), F-  
203 values and the probability of all samples being derived from a common length  
204 distribution.

205 **Trends over time**

206 To examine whether the difference between length distributions generally decreased  
207 or increased over time, the correlations between F of the between fishing ground  
208 comparison and week of the year were estimated for each distance-group. Only groups  
209 where three or more 2-week-periods were sampled in the main fishing season (week 14  
210 to 22) were included.

211 **Results**

212 **Sandeel foraging habitat**

213 A total 217 individual habitat areas were identified with a total area of 33 566 km<sup>2</sup>  
214 equivalent to approximately 5% of the area of the North Sea and Skagerrak (Figure 1).  
215 The habitat areas vary greatly in size as the area ranges from 1 km<sup>2</sup> to 4023 km<sup>2</sup> (Figure  
216 2). Given the average estimated biomass of sandeel in the North Sea (ICES 2008a), this  
217 leads to a density within habitat areas of on average 58 ton per km<sup>2</sup>. With an average  
218 weight of sandeel of 7 g (ICES 2008a), this corresponds to eight sandeels per m<sup>2</sup>  
219 habitat.

220 **Within fishing ground variation**

221 Length distributions of sandeels from 187 hauls taken at five fishing grounds were  
222 used (Figure 1). Of these fishing grounds, the number of samples taken exceeded 20 in  
223 two consecutive 2-week periods on two of them. It is clear from visual inspections of  
224 the length distributions that the variation between fishing grounds is much larger than  
225 the within fishing ground variation (Figure 3). The length distributions differed  
226 significantly between subareas of the fishing ground on two fishing grounds (a total of  
227 three cases, Table 1, Figure 4) and the difference increased significantly with length of

228 the fishing ground (correlation between F and distance between outer subarea  
229 midpoints=0.86, P=0.0135). The regression line exceeded an F-value of two (roughly  
230 equal to a difference significant at the 5% level when the number of degrees of freedom  
231 is large) at a minimum distance between subareas of 28 km (Figure 5). At smaller  
232 distances, the length distributions were not significantly different and hence mixing  
233 most likely occurred at these scales. As the distance refers to the distance between  
234 fishing ground subarea centres and subareas are defined as quarters of fishing grounds,  
235 this corresponds to a total mixing of fish at fishing grounds of lengths less than 112 km.

### 236 **Between fishing ground variation**

237 The length distributions differed significantly between fishing grounds in a total of  
238 55 cases (90%). Length distributions of sandeels from 1038 hauls taken at 11 fishing  
239 grounds were used, resulting in a total of 61 combinations of fishing ground pair and 10  
240 km distance group (see Supplementary material S2). The F-value of the difference  
241 between length distributions increased significantly with distance between fishing  
242 grounds (correlation between F and distance group=0.30, P=0.0184)(Figure 6a) and the  
243 regression line exceeded an F-value of two at a minimum distance between fishing  
244 grounds of 5 km. The difference between length distributions was substantially higher  
245 between fishing grounds than within fishing grounds even at the same geographical  
246 distance (Figure 6b). Whereas within-fishing ground comparisons did not reveal  
247 significant differences at distances below 40 km (Figure 5), all of the between-fishing  
248 ground comparisons made at distances less than 20 km (total of three) and all but one  
249 made at distances of less than 30 km (total of 10) were significantly different (Figure 7).

250 **Trends over time**

251 None of the correlations between F and week were significant at the 5% level when  
252 performed separately for each distance group and hence differences did not increase or  
253 decrease significantly over time at a given distance. However, the correlation between F  
254 and week within a distance group increased significantly with distance (Pearson  
255 correlation coefficient=0.93, P=0.0211)(Figure 8). This indicates that there was no  
256 tendency for nearby grounds to become more similar over time (correlation between F  
257 and time was zero) while distant grounds became more different over time (F between  
258 distant grounds increased over time).

259 **Discussion**

260 This study utilized the first North Sea wide map of lesser sandeel distribution to  
261 evaluate dynamics over a complex mosaic of grounds differing widely in size and  
262 proximity to each other. The mixing of sandeel between these grounds was insufficient  
263 to eliminate significant differences in length distributions at spatial scales down to 5 km.  
264 Within grounds, the mixing is greater and at fishing grounds with a length smaller than  
265 112 km, no difference in length distributions was found. However, beyond this distance,  
266 the mixing was again insufficient to eliminate differences in length distributions. This  
267 lead to increased differences between fishing grounds late in the season as differences in  
268 growth and mortality enhanced early season differences. The lack of mixing between  
269 fishing grounds potentially increases the risk of adverse effects of the fishery on local  
270 predators even if the population at a larger scale is inside biologically safe limits.

271 The validity of the map as an indicator of sandeel foraging habitat depends on  
272 whether all habitat areas are known and fished by the fishery and whether fishing is  
273 restricted to foraging areas. Comparison with smaller scale topographical and benthic

274 mapping suggests that the fishery tends to concentrate in areas where sandeel forage,  
275 which often coincide with the edge of fishing grounds (Jensen, 2001; Holland *et al.*,  
276 2005; Mackinson and van der Kooij, 2006; Engelhard *et al.*, 2008). Given the close  
277 proximity between foraging habitat and preferred substrate, fishing distribution should  
278 provide a good proxy for areas of sandeel habitat (Wright *et al.*, 2000; Van der Kooij *et*  
279 *al.*, 2008). However, vessels only fish in areas with clear tows and a high catch rate and  
280 avoid shallow waters as well as areas within the territorial limits of countries other than  
281 Denmark. Hence, rugged and coastal habitat may be underrepresented in the map. The  
282 majority of the catch from coastal habitats is, however, likely to consist of the more  
283 coastal sandeel species *Ammodytes tobianus* (Jensen *et al.* 2004).

284 We are not aware of any similar investigations where mixing has been deduced from  
285 comparisons of length distributions. There may be several reasons for this. Firstly,  
286 comparisons of length distributions is not straight forward when the number of fish  
287 measured is limited (Rindorf and Lewy, 2001). Secondly, a difference in length  
288 distributions is not equivocal as this may be caused either by lack of mixing and highly  
289 variable growth and mortality rates or by size-dependent migration where fish migrate  
290 to specific areas when they reach a certain size. Similarly, identical length distributions  
291 may be a result of identical recruitment, growth and mortality patterns combined with a  
292 lack of mixing. The lack of difference in length distribution seen within small fishing  
293 grounds is therefore not necessarily a result of mixing but could be a result of  
294 homogeneous recruitment pattern combined with low differences in growth and  
295 mortality rates. However, as one subarea of the fishing ground did not consistently hold  
296 larger fish in the fishing ground sampled in two consecutive 2-week periods (Figure 4),  
297 it seems unlikely that size dependent migration is the cause of the difference in length

298 distributions between fishing ground subareas. Furthermore, it seems unlikely that such  
299 size dependent migration should be larger between fishing grounds than within fishing  
300 grounds which would be required to explain the larger differences between grounds.  
301 While size-dependent migration may thus occur, it is insufficient to explain the large  
302 differences between fishing grounds. This is consistent with the very high recapture  
303 rates of tagged sandeels recorded on fished grounds (Kunzlik *et al.*, 1986). The recorded  
304 differences between length distributions reveal not only lack of extensive movement but  
305 also large differences in local recruitment, growth or mortality and possibly also in  
306 burying behaviour. Burying behaviour affects the length distribution if the proportion of  
307 time spent buried varies between different lengths of sandeel. If this behaviour  
308 furthermore varies between fishing grounds, the effect can be increased differences over  
309 the season. Significant regional differences in length distribution, growth and maturity  
310 have also been found in other studies (Wright, 1996; Bergstad *et al.*, 2001; Boulcott *et*  
311 *al.*, 2007; Johnsen *et al.*, 2009). The present study provides further explanation for this  
312 regional variability in dynamics.

313 In the extreme, local depletion may occur in one end of a large ground while there  
314 are high sandeel densities in the other end or at one of two neighbouring fishing  
315 grounds. This could be caused by fishing if the fishery remains on the low abundance  
316 end of the ground even when density is higher in the other end, a behaviour which  
317 would however not appear to maximise profit. The limited exchange between nearby  
318 areas potentially increases the effectiveness of closing local areas to fishing as the  
319 sandeel inside the area will not simply 'spill-over' into adjacent fishing grounds and be  
320 caught there. However, the relationship between exchange and differences in local  
321 densities were not investigated and hence a 'spill-over' effect could potentially occur if

322 there were large density differences between two adjacent areas. In this case, lower  
323 competition for food in the low-density area may give sandeel energetic reasons to  
324 switch area. Furthermore, the present analysis deals only with mixing in the feeding  
325 season. Mature sandeel emerge from the sandbanks in December and January to spawn  
326 (Gauld and Hutcheon, 1990; Boulcott *et al.*, 2007), and whether mixing takes place  
327 during this event is unknown. However, as egg and early larval distributions closely  
328 match known overwintering habitat, this appears unlikely (Wright and Bailey, 1996;  
329 Munk *et al.*, 2002). After hatching, larvae may drift considerable distances (Proctor *et*  
330 *al.*, 1998; Christensen *et al.*, 2009) and the horizontal movements of pre-settled sandeel  
331 (Wright, 1996) most likely leads to exchange of recruits between fishing grounds.  
332 Hence, closing a particular fishing ground will protect sandeel during the fishing season  
333 and may contribute to recruitment on other fishing grounds but is unlikely to assure the  
334 presence of sandeel in the closed fishing ground in coming years.

335 In conclusion, the distribution of sandeel in the North Sea is highly patchy and there  
336 is limited exchange between even close fishing grounds during the fishing season. Some  
337 mixing occurs within fishing grounds but the mixing between grounds appears to be  
338 very low. Management through closed fishing grounds or fishing ground subareas  
339 therefore has the potential to protect local aggregations of sandeel during the fishing  
340 season and may result in increased recruitment to nearby fishing grounds, but such a  
341 protection is unlikely to assure continuous recruitment to the particular fishing ground.

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## 350 **Supplementary material**

351 The following supplementary material is available at *ICESJMS* online: Material S1  
352 shows the sandeel map and procedures for its derivation whereas Table S2 lists results  
353 of the comparison of length distributions between fishing grounds.

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471 Table 1. Comparison of length distributions between subareas within fishing grounds.  
 472 Length indicates maximum distance between midpoints of subareas sampled. Total  
 473 deviance and df indicates the deviance from a common length distribution and the  
 474 degrees of freedom of this common length distribution. Subarea deviance indicates the  
 475 reduction in deviance obtained by modelling the length distribution in each subarea  
 476 separately and the associated loss of degrees of freedom.

Fishing ground	Length		Total		Subarea		
	(km)	deviance	df	deviance	df	F	P(F)
Scooter Plads	6	830.8	329	22.7	6	1.498	0.1780
Berwick Bank	13	1 191.7	281	46.8	7	1.576	0.1422
Berwick Bank	13	805.3	257	10.9	6	0.580	0.7464
Inner Shoal	25	1 166.3	468	27.2	6	1.819	0.0936
Sorel	41	806.4	307	98.7	10	3.758	0.0001
Elbow Spit	121	1 205.7	337	260.5	15	4.854	<0.0001
Elbow Spit	121	1 635.8	341	336	19	3.686	<0.0001

477

478

479 **Captions**

480 Fig. 1. Sandeel habitat areas (areas with potential high density of non-buried sandeel)  
481 and named fishing grounds referred to in the text.

482 Fig. 2. Frequency distribution of area (in km<sup>2</sup>) of individual sandeel habitat areas.  
483 Lower axis indicates lower limit of 100 km<sup>2</sup>-intervals..

484 Fig. 3. Length distributions at fishing grounds where more than 20 hauls were taken in a  
485 2-week period. a: Scooter Plads (maximum distance between subarea midpoints 6 km),  
486 b and c: Berwick bank (maximum distance between subarea midpoints 13 km) week 22  
487 and 24, respectively, d: Inner Shoal (maximum distance between subarea midpoints 25  
488 km), e: Sorel (maximum distance between subarea midpoints 41 km), f and g: Elbow  
489 Spit (maximum distance between subarea midpoints 121 km) week 16 and 18,  
490 respectively. Colours indicated subarea of fishing ground.

491 Fig. 4. Length distributions in different subareas. a: Sorel, b: Elbow Spit, week 16, c:  
492 Elbow spit week 18. Solid black lines: subarea immediately west of centre, hatched  
493 black lines: subarea close to the western end of the fishing ground, solid grey lines:  
494 subarea immediately east of centre, hatched grey lines: subarea close to the eastern end  
495 of the fishing ground.

496 Fig. 5. F-value of comparison of common and subarea-specific length distributions as a  
497 function of the distance between sampled fishing ground subareas. Line is a regression  
498 line.

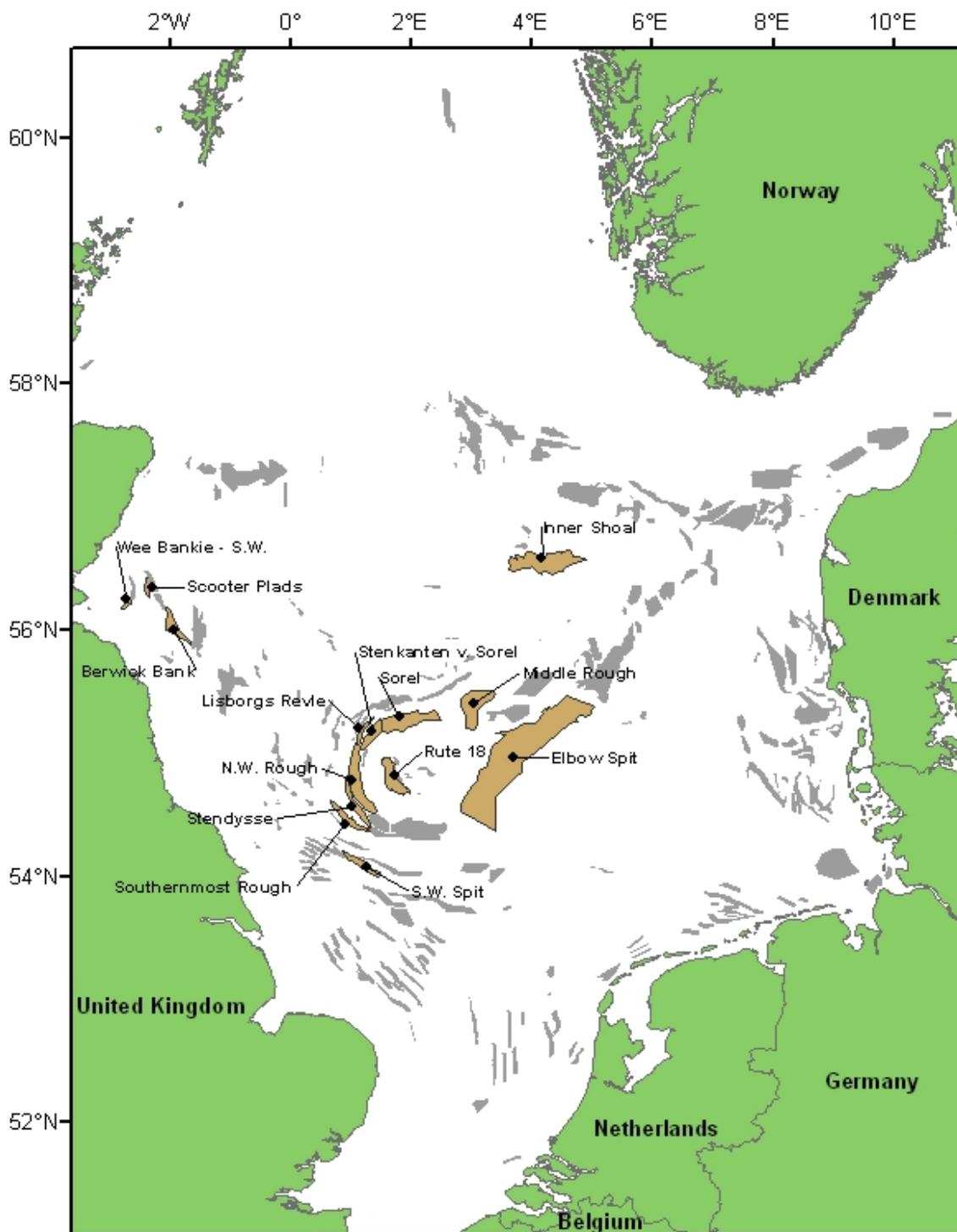
499 Fig. 6. F-value of comparison of common and fishing-ground-specific length  
500 distributions as a function of the distance between sampled fishing grounds (a) and a

501 comparison of within and between fishing ground results (b). Line is a regression line.  
502 Filled symbols, solid line: between fishing ground comparisons. open symbols, hatched  
503 line: within fishing ground comparisons. Note that the values on the y-axis differs  
504 between figures as b shows only the lower half of a.

505 Fig.7. Proportion of analyses showing significant differences as a function of distance.  
506 Filled symbols, solid line: between fishing grounds, open symbols, hatched line: within  
507 fishing grounds.

508 Fig. 8. Correlation between week and F for given distance. Positive values indicate a  
509 general rise in F over the season, negative a decrease. Line indicates regression line.

510 Fig. 1.

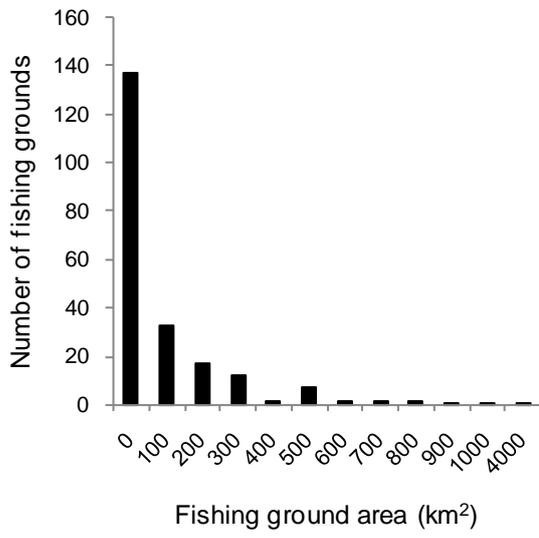


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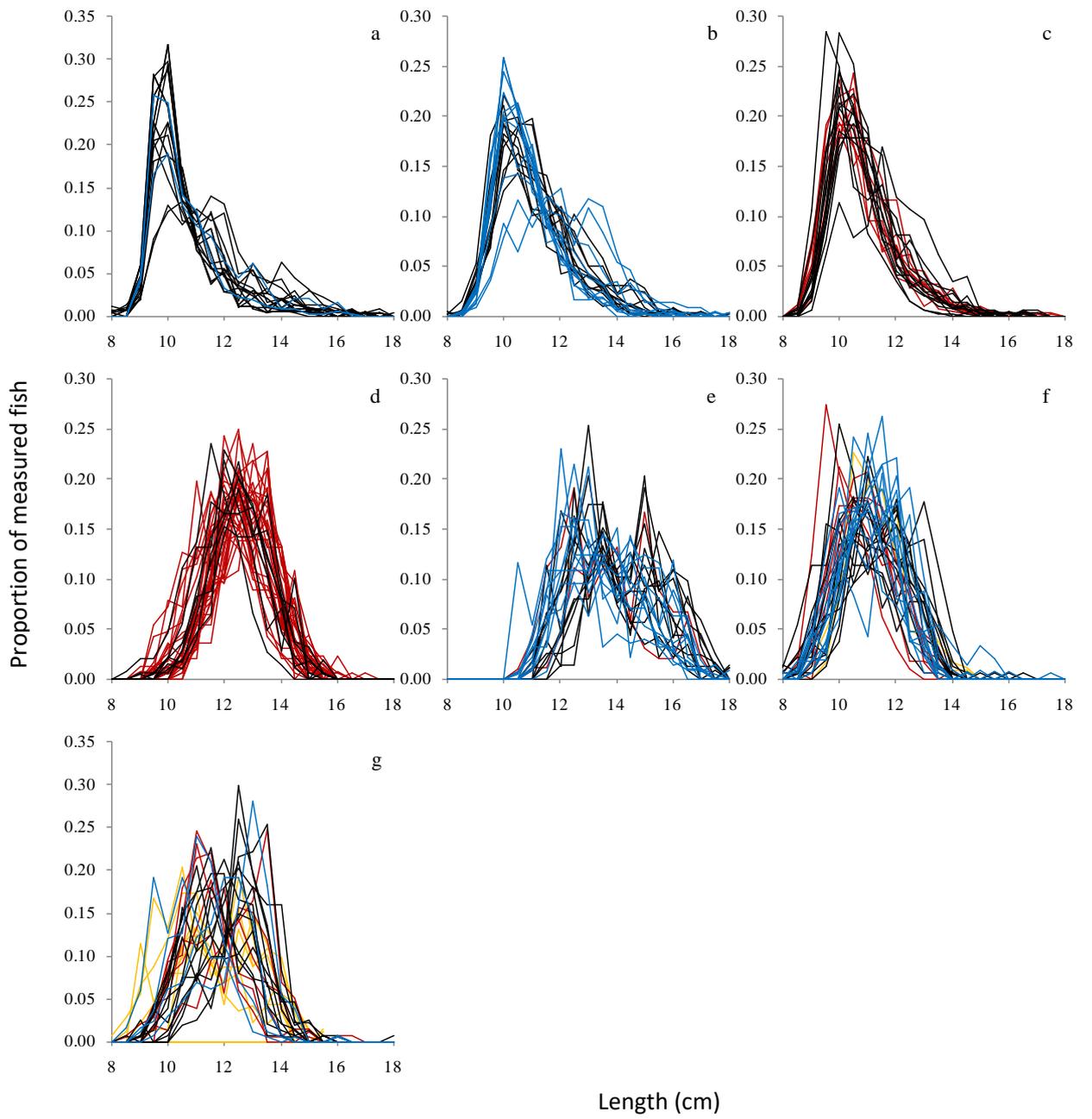
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514 Fig. 2.



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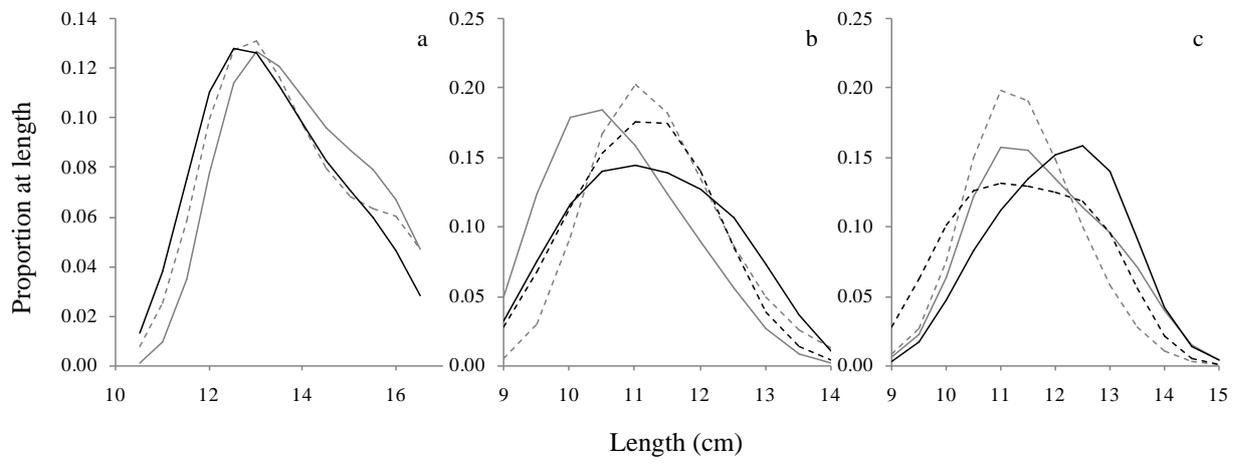
516 Fig. 3.



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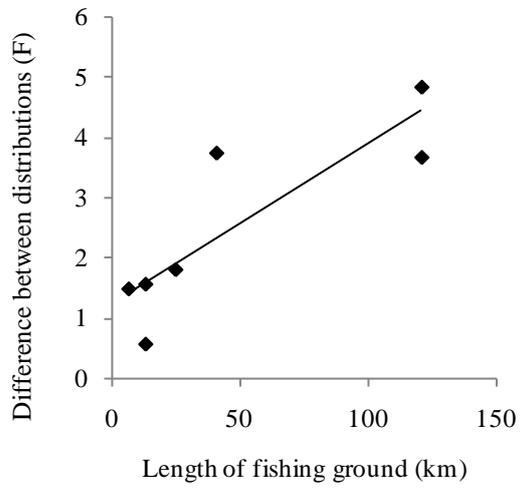
519 Fig. 4.



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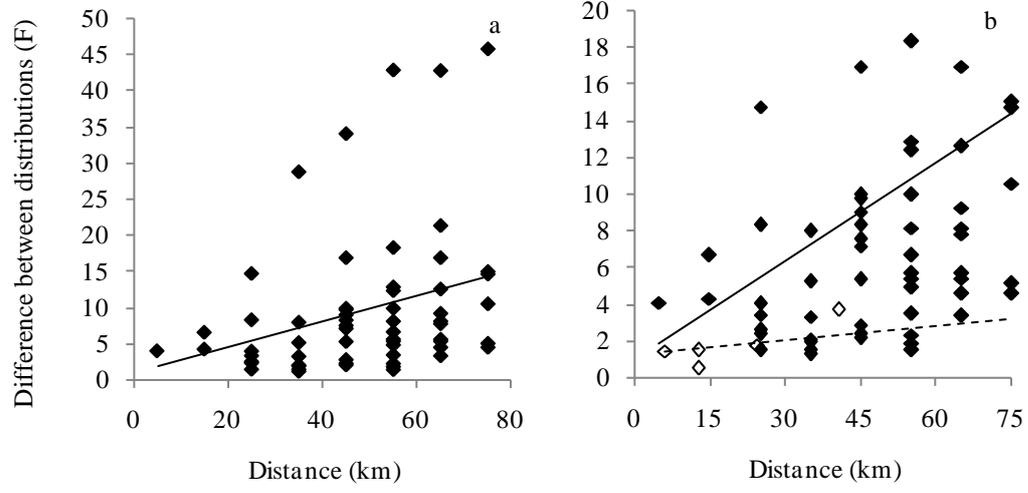
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522 Fig. 5.



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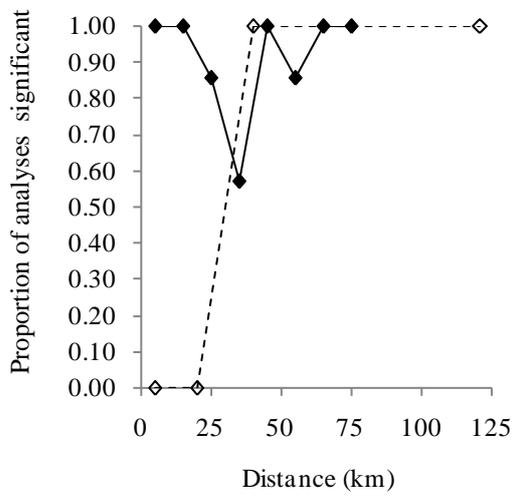
524 Fig. 6.



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527 Fig. 7.

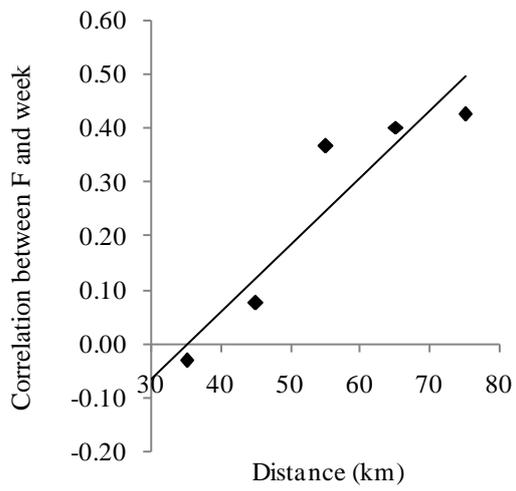


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530 Fig. 8. Correlation between week and F for given distance. Positive values indicate a  
531 general rise in F over the season, negative a decrease. Line indicates regression line.

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## Deriving the map of sandeel habitats (S1)

From the data collected (Figure S1), the final map of the sandeel fishing grounds was produced using the following 5-step procedure:

- 1) A point shapefile with the data was created from a textfile using ArcMap (ESRI ArcGIS).
- 2) A kernel density analysis (Silverman, 1986) was applied on the shapefile using a quadratic kernel function to fit a smoothly tapered surface to each point (search radius: 0.015 decimal degrees, output cell size: 0.006 decimal degrees) and produce a grid using the Spatial Analyst extension with ArcGIS .
- 3) From this grid, a new grid including only cells with a density of points greater than 50 000 was produced. This grid was afterwards converted to a shapefile so that each fishing ground is defined as a polygon.
- 4) The polygons were adjusted manually considering raw data, information about individual grounds, the location of fishing tracks and information about topography. During this process the highest weight was given to the information in the raw data.

Lastly, fishermen from different harbours evaluated the map of fishing grounds, after which it was modified according to the guidelines given by the fishermen. The evaluation by the fishermen resulted in the inclusion of additional grounds (from additional navigation data) and deletion of non sandeel grounds. The map was subject to several such evaluations before the final map was accepted (Figure S2).

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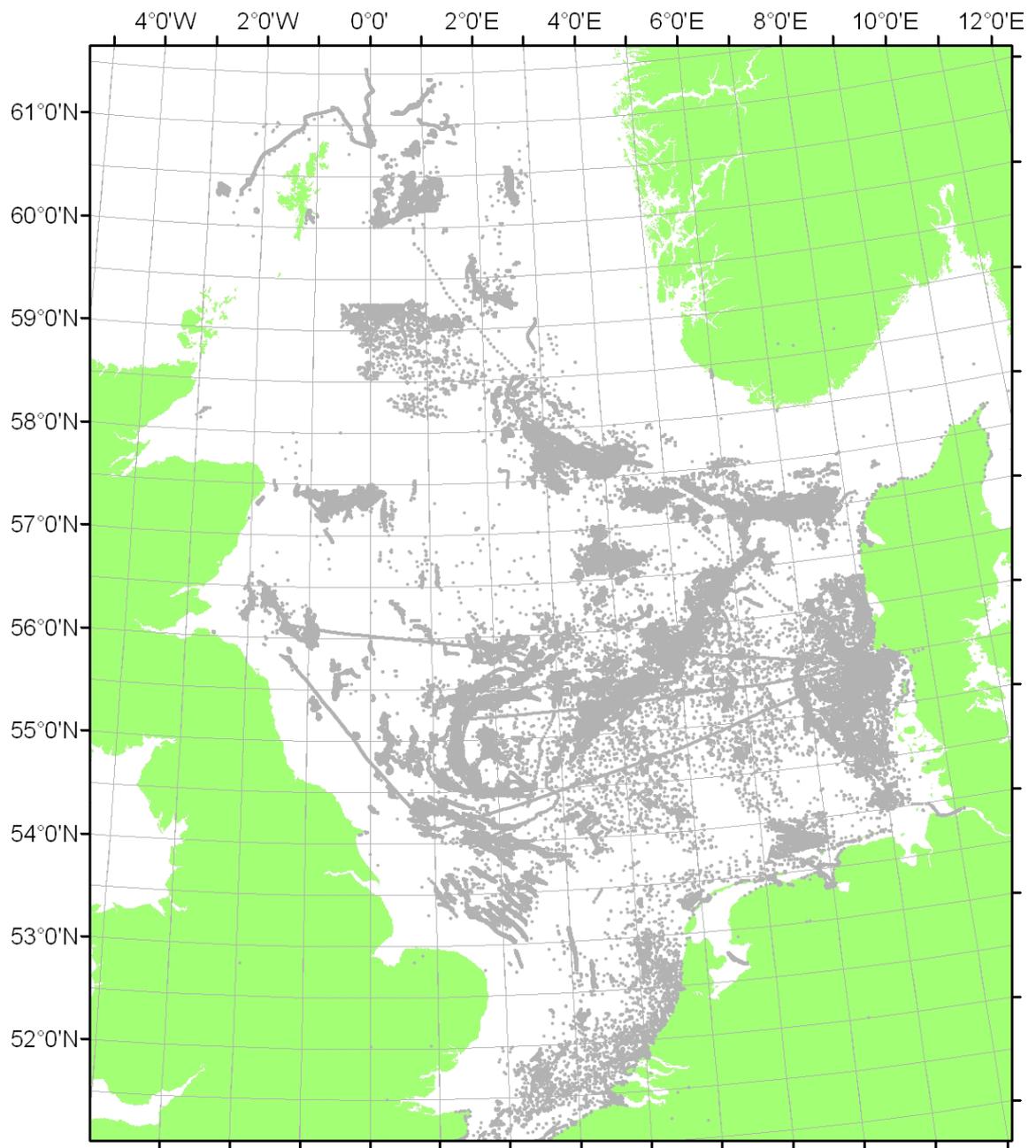


Fig. S1. Map of raw data from various GPS based navigation systems.

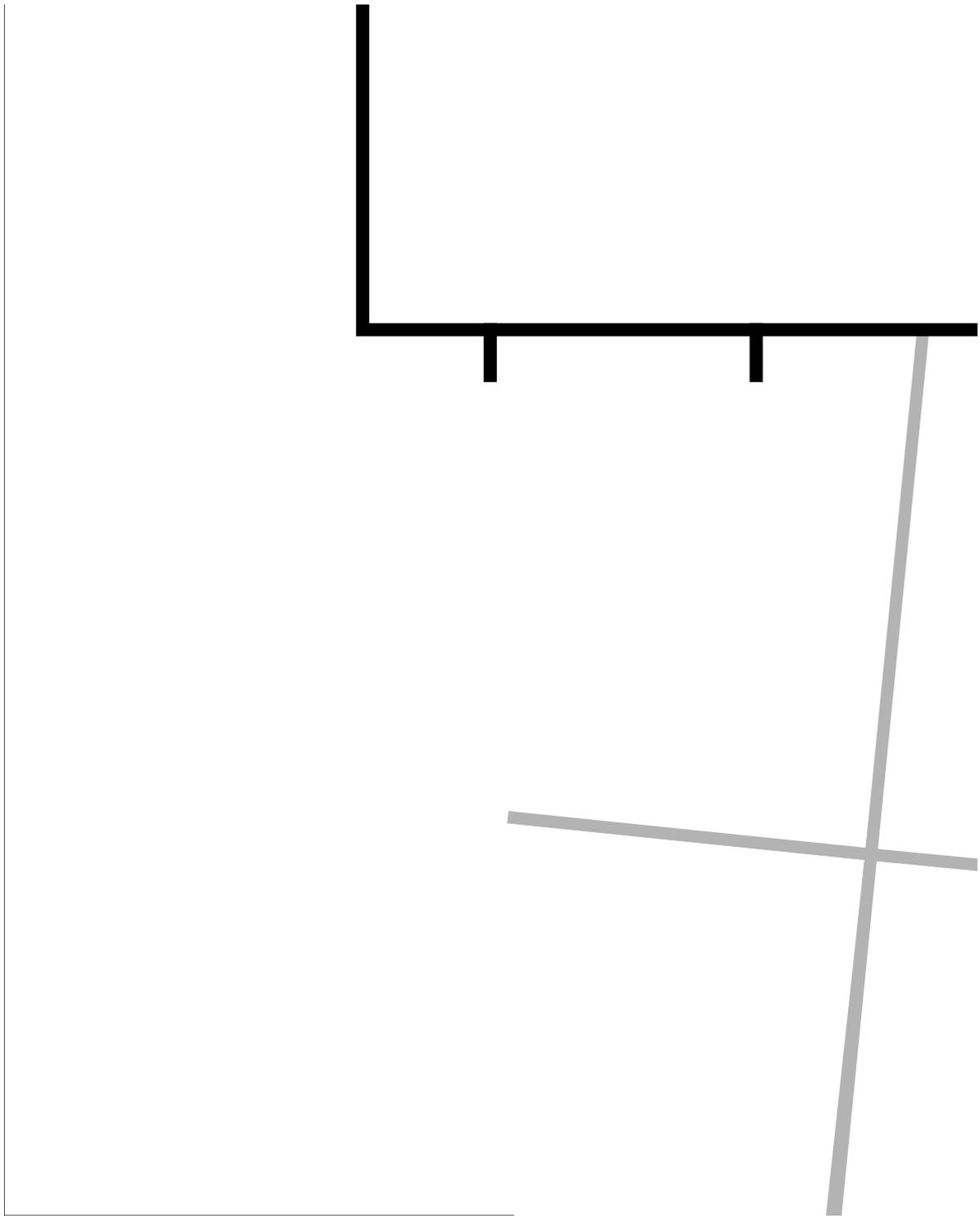


Fig. S2. Sandeel habitat areas.

Table S2. Results of the comparison of length distributions between fishing grounds. Total deviance and df indicates the deviance from a common length distribution and the degrees of freedom of this common length distribution. Ground specific deviance indicates the reduction in deviance obtained by modelling the length-distribution in each area separately and the associated loss of degrees of freedom. Distance groups are 10 km groups denoted by the lowest distance in the group (e.g. 0 equals the group 0-10 km).

Ground 1	Ground 2	Distance group	Total		Ground specific		F	P(F)
			deviance	df	deviance	df		
N.W. Rough	Stendysse/Lissis Revle	0	416	159	52	5	4.11	0.0012
N.W. Rough	Stendysse/Lissis Revle	10	433	174	53	5	4.35	0.0007
N.W. Rough	Stendysse/Lissis Revle	10	1 150	179	249	6	6.67	<0.0001
N.W. Rough	Southernmost Rough	20	430	153	43	6	2.64	0.0159
N.W. Rough	Southernmost Rough	20	995	239	84	6	3.45	0.0022
N.W. Rough	Southernmost Rough	20	1 112	196	81	6	2.45	0.0234
N.W. Rough	Stendysse/Lissis Revle	20	474	160	120	5	8.39	<0.0001
N.W. Rough	Stendysse/Lissis Revle	20	892	228	36	6	1.57	0.1524
Rute 18	N.W. Rough	20	278	129	42	5	4.08	0.0014
Scooter Plads	Wee Bankie - S.W.	20	1 243	382	284	6	14.79	<0.0001
N.W. Rough	Southernmost Rough	30	482	168	56	6	3.36	0.0030
N.W. Rough	Southernmost Rough	30	1 291	259	63	6	2.15	0.0455
N.W. Rough	Southernmost Rough	30	640	186	36	7	1.56	0.1430
N.W. Rough	Stendysse/Lissis Revle	30	736	178	48	6	2.01	0.0614
Rute 18	N.W. Rough	30	522	179	74	5	5.25	0.0001
Sorel	N.W. Rough	30	1 723	255	1 141	6	28.81	<0.0001
Sorel	N.W. Rough	30	791	164	30	5	1.29	0.2664
Sorel	Stenkanten v. Sorel	30	513	204	118	6	8.06	<0.0001

Middle Rough	Sorel	40	679	177	101	5	5.40	0.0001
N.W. Rough	Southernmost Rough	40	557	157	148	6	7.20	<0.0001
N.W. Rough	Southernmost Rough	40	425	153	47	6	2.91	0.0086
N.W. Rough	Southernmost Rough	40	1 447	270	534	6	16.96	<0.0001
N.W. Rough	Southernmost Rough	40	1 937	388	64	6	2.17	0.0432
N.W. Rough	Southernmost Rough	40	1 313	324	272	7	9.81	<0.0001
Rute 18	Stendysse/Lissis Revle	40	617	159	157	5	8.36	<0.0001
Sorel	Lisborgs Revle	40	663	209	185	6	9.99	<0.0001
Sorel	N.W. Rough	40	2 098	313	1 344	6	34.07	<0.0001
Sorel	N.W. Rough	40	849	197	191	6	7.62	<0.0001
Sorel	N.W. Rough	40	985	248	47	5	2.40	0.0356
Sorel	Stenkanten v. Sorel	40	554	218	135	6	9.08	<0.0001
Middle Rough	Sorel	50	1 148	300	234	5	12.42	<0.0001
N.W. Rough	S.W. Spit	50	434	140	63	6	3.56	0.0019
N.W. Rough	Southernmost Rough	50	580	158	143	6	6.74	<0.0001
N.W. Rough	Southernmost Rough	50	425	138	34	6	1.94	0.0736
N.W. Rough	Southernmost Rough	50	1 591	285	424	6	12.93	<0.0001
N.W. Rough	Southernmost Rough	50	1 762	341	72	6	2.36	0.0284
N.W. Rough	Southernmost Rough	50	2 090	394	575	6	18.35	<0.0001
N.W. Rough	Southernmost Rough	50	1 374	236	280	6	8.21	<0.0001
Rute 18	Southernmost Rough	50	618	168	97	5	5.45	0.0001
Sorel	Lisborgs Revle	50	663	209	185	6	9.99	<0.0001
Sorel	N.W. Rough	50	2 873	441	1 652	6	42.85	<0.0001
Sorel	N.W. Rough	50	813	197	138	6	5.73	<0.0001
Sorel	N.W. Rough	50	820	192	32	5	1.53	0.1788
Sorel	Stenkanten v. Sorel	50	382	154	71	6	4.94	0.0001
Middle Rough	Sorel	60	1 110	299	231	5	12.64	<0.0001
N.W. Rough	Southernmost Rough	60	468	130	118	6	5.71	<0.0001
N.W. Rough	Southernmost Rough	60	1 447	270	534	6	16.96	<0.0001
N.W. Rough	Southernmost Rough	60	1 584	291	110	6	3.44	0.0022

N.W. Rough	Southernmost Rough	60	1 996	380	664	6	21.39	<0.0001
N.W. Rough	Southernmost Rough	60	1 374	236	280	6	8.21	<0.0001
Rute 18	Southernmost Rough	60	618	168	97	5	5.45	0.0001
Sorel	Lisborgs Revle	60	527	153	131	5	7.85	<0.0001
Sorel	N.W. Rough	60	2 819	441	1 619	6	42.78	<0.0001
Sorel	N.W. Rough	60	948	232	222	6	9.29	<0.0001
Sorel	N.W. Rough	60	1 181	293	91	5	4.61	0.0004
Middle Rough	Sorel	70	872	230	273	5	14.71	<0.0001
N.W. Rough	Southernmost Rough	70	943	139	493	5	15.05	<0.0001
N.W. Rough	Southernmost Rough	70	986	188	157	6	5.15	<0.0001
Sorel	N.W. Rough	70	2 975	469	1 720	6	45.76	<0.0001
Sorel	N.W. Rough	70	990	244	252	6	10.60	<0.0001
Sorel	N.W. Rough	70	1 181	293	91	5	4.61	0.0004