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1 **Fecundity and growth of Atlantic cod (*Gadus morhua* L.) along a**  
2 **latitudinal gradient**

3

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22 Running headline: Reproductive tactics of Atlantic cod

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28 KEYWORDS

29 Cod, fecundity, atresia, maturation, temperature

30

31 ABSTRACT

32 Some fish species have wide distribution areas that span very different habitats. In this  
33 investigation we have studied Atlantic cod (*Gadus morhua*), which is an example of  
34 such a species, to demonstrate how this may have caused adaptations to key features  
35 such as fecundity, growth and age and size at first spawning. We have studied cod  
36 from the Barents Sea, Icelandic waters, North Sea and Irish Sea. The ovary sampling  
37 was undertaken over several years, however, not always sequentially, in order to  
38 assess whether the relationships between fecundity and other key features were  
39 constant or variable. Also, we compared historical maturity ogives and growth from  
40 the different regions. There was a clear pattern with fish maturing at a greater age and  
41 size in the north compared to the south. For three of the four cod stocks we  
42 demonstrated a significant reduction in relative potential fecundity as maturity  
43 progressed towards spawning, i.e., as the mean diameter of vitellogenic follicles  
44 increased. To be able to compare potential fecundity in a standardised way both in  
45 time and space, we constructed models that included mean diameter as one of the  
46 independent variables. Our potential fecundity comparisons clearly indicated a north-  
47 south gradient with increasing size-specific fecundity towards the south. The higher  
48 fecundity of the fish in the south could only partly be explained by the higher  
49 condition and temperature that was observed in these waters.

50

51 **1. Introduction**

52 Successful reproduction depends on the adaptation of reproductive physiology and  
53 behaviour of the animal to its environment. Different species of fish have often  
54 evolved intriguing reproductive strategies that reflect local adaptation to surrounding  
55 environmental conditions and ecological niches (Murua and Saborido-Rey, 2003). As  
56 a result, extensive variation characterizes all reproductive traits, such as the timing,  
57 frequency, duration and amplitude of spawning as well as offspring size and numbers  
58 (Wootton, 1998; Wright and Trippel, 2009). The size and number of eggs and larvae  
59 produced by individual fish are therefore determined by the predictability of survival  
60 and trade-offs in energy allocation to reproduction, growth, behaviour and  
61 maintenance (Smith 1974; Stearns, 1992; Roff, 2000). The reproductive strategies  
62 range from spawning once to a number of times either in a single spawning season or  
63 over many (semelparous versus iteroparous), through a range in synchrony and when  
64 fecundity is determined (determinate versus indeterminate fecundity) to variations in

65 the spawning pattern (total versus batch spawners). In addition, there is a wide range  
66 in egg size between species with smaller, but perceptible differences within a species,  
67 which can be regarded as a trade-off between size and number (Wootton, 1998).  
68 Within a widely distributed species, such as the Atlantic cod (*Gadus morhua*) (Fig. 1),  
69 these traits are likely to be plastic and vary extensively among populations that  
70 inhabit different environments (Stearns, 1992, 2000; Rowell, 1993; Yoneda and  
71 Wright, 2004).

72

73 In this paper we focus on four cod stocks, i.e., the ones in the Barents Sea, SW  
74 Icelandic waters, the North Sea and the Irish Sea. These are distributed over a wide  
75 range of environment with annual mean temperatures, at 100 m depth, ranging from 4  
76 °C in the Barents Sea to around 10 °C in the Irish Sea (ICES, 2005; Sundby, 2000;  
77 Sundby and Nakken, 2008). In addition to temperature, these stocks are likely to  
78 differ in many ways due to adaptation to different feeding conditions, predation,  
79 fishing mortality, probability of offspring survival as well as energy invested in  
80 reproductively associated behaviour such as spawning migrations. The Barents Sea  
81 cod typically have a very long spawning migration along the Norwegian coast to spawn  
82 at the coast of Finnmark, Lofoten, or even further south (Bergstad et al., 1987;  
83 Jørgensen et al., 2008). The distance of migration practised by the Icelandic cod stock  
84 can vary from being quite far for those that migrate from Greenland waters (Schopka,  
85 1993) to shorter distances for those that migrate from the feeding areas of the NW or  
86 SE coast (Jonsdottir et al., 2007). The North Sea and Irish Sea stocks have shorter or  
87 even no spawning migration (Jonsdottir et al., 2007; Righton et al., 2007; Robichaud  
88 and Rose, 2004). The length of the spawning migration, and associated energy  
89 demands of each stock, depends on the spatial separation of the centre of egg and  
90 larval production compared to the adult feeding area (Harden-Jones, 1968).

91

92 A key feature amongst fish reproductive traits is the number of eggs that are shed,  
93 also called the realised fecundity. The reproductive investment can be considered as  
94 the ovarian weight or the product of realised fecundity and egg dry weight. The use of  
95 ovary weight can produce bias since weight changes for a variety of reasons through  
96 the developmental process e.g. further sequestration of yolk (vitellogenin) or oocyte  
97 hydration,; the timing of measurements is critical. Hence, the use of egg dry weights  
98 and realised fecundity will clearly provide a better estimate of the actual reproductive

99 investment. Unfortunately, data for egg dry weight and realised fecundity are not  
100 available for any of the stocks in this study. Therefore, potential fecundity, defined as  
101 the number of vitellogenic oocytes present in the pre-spawning fish is often taken as a  
102 proxy for reproductive investment. Indeed a central tenant of the stock and recruit  
103 relationship (Beverton and Holt, 1957) assumes that stock biomass is a suitable proxy  
104 for fecundity subject to a scaling factor. In some cases the realised fecundity is  
105 estimated from the potential fecundity by subtracting the number of atretic  
106 (regressing) oocytes found in the prespawning ovary (Armstrong et al., 2001; Greer  
107 Walker et al., 1994; Ma et al., 1998; Óskarsson et al., 2002; Witthames et al., 2003).  
108 In the case of cod significant progresses have been made in the understanding and  
109 quantification of the atresia regression turnover rate (Witthames et al., this issue) as  
110 well as in the reporting of atretic intensity (Kjesbu et al., this issue) However, these  
111 studies are either experimental or limited to specific waters.

112

113 A recent study on cod (Thorsen et al., 2006) has shown a considerable decrease of  
114 potential fecundity during the vitellogenic phase of ovary development. The work  
115 indicated that the time of sampling in the developmental process had an important  
116 influence on fecundity estimate. The authors therefore recommended that stage of  
117 maturation should be compensated for when comparing fecundities between stocks or  
118 years. Specifically they suggested that mean oocyte diameter could be used as an  
119 indication of proximity to spawning time and hence how far in the development cycle  
120 the fish has progressed and thus included as an independent factor in multiple  
121 regression analysis. Typically vitellogenesis starts at around 250  $\mu\text{m}$  diameter and  
122 ends when the oocyte is 800-900  $\mu\text{m}$  (Kjesbu et al., 1990; Kjesbu and Kryvi, 1993;  
123 Thorsen and Kjesbu, 2001). Finally, egg size seems to a large degree to be determined  
124 during the last 2-3 days of final maturation (development) when the uptake rate of  
125 vitellogenin is particularly large (Kjesbu et al., 1996; Wallace and Selman, 1985).  
126 Furthermore, oocytes take up large quantities of water that may increase their volume  
127 by a factor of 3-5 compared to the prehydration state (Fulton, 1898; Milroy 1898;  
128 Thorsen and Fyhn 1996,). Typical egg size for Atlantic cod seems to be in the range  
129 1.15-1.6 mm while in an extreme case like the Baltic Sea the egg size may be up to  
130 1.8 mm (Marteinsdóttir and Begg 2002; Thorsen et al., 1996).

131

132 In this paper we have used the proposed methods for unbiased fecundity comparison  
133 outlined in Thorsen et al. (2006) to compare cod fecundity for several stocks of  
134 Atlantic cod both in time and space. The material included data on fecundity and  
135 maturation from Barents Sea cod, Icelandic cod, North Sea cod, and Irish Sea cod  
136 together with data on length, weight, and age.

137

## 138 **2. Methods**

139

### 140 *2.1. Age, otolith type, length, weight and maturity*

141 For all stocks we had individual data on length, weight, and age. All cod caught were  
142 measured to the nearest 1 cm below, weighed to the nearest 1 g, the sex identified  
143 from the gonads, and the maturity stage judged macroscopically.

144

145 Maturity ogives for Barents Sea female cod were estimated from a combination of  
146 VPA and survey data. The methods are given in Nash et al. (this issue). Growth in  
147 length for Barents Sea cod was estimated from the central IMR cruise database for  
148 January - April in the years 1986-2006. Most of the cod had been caught by bottom  
149 trawl or Danish seine. Only cod containing otoliths characterized as part of the  
150 Barents Sea population (Rollefsen, 1934) were included.

151

152 Growth in length for Icelandic cod was estimated from data obtained from the public  
153 web data library ([http:// www.hafro.is](http://www.hafro.is)) of the Icelandic Marine Research Institute.  
154 These data originated from the spring research surveys and included cod caught by  
155 Danish seine and bottom trawl for all divisions in the years 1992 to 2005.

156

157 Maturity ogives and a growth curve for North Sea cod were obtained from the first  
158 quarter ICES IBTS (International Bottom Trawl Survey) in the years from 1981-2002.  
159 A standard weighting factor for each observation was calculated as the product of the  
160 number of fish that the observation represented and the inverse of the tow duration.  
161 The survey generally covered most of the North Sea but in the early 1990s included  
162 stations in the Kattegatt and Skagerrak (ICES Division IIIa). Data from IIIa were  
163 removed by excluding all samples collected east of 8°E. A standard GOV trawl was  
164 used with most hauls lasting approximately 30 min. The database consisted of  
165 position and haul duration, lengths (to the nearest cm), sex, coding for mature or

166 immature, and number of fish for each entry. The methods for estimating the female  
167 maturity ogives are given in Nash et al. (this issue).

168

169 Maturity ogives for Irish Sea cod in the years between 1992 – 2006 were obtained  
170 from the annual Irish Sea spring groundfish survey, conducted by the Agri-Food and  
171 Biosciences Institute in Northern Ireland. Growth in length for Irish Sea cod was  
172 estimated from data for 2003-2005. The survey is conducted in March each year using  
173 a rock-hopper otter trawl. A weighting factor for each observation was taken as the  
174 inverse of the distance towed. The maturity ogive results are reported in Nash et al.  
175 (this issue).

176

### 177 *2.2. North Sea and Irish Sea cod fecundity samples*

178 Cod were sampled between December and the beginning of March in the North Sea  
179 and Irish Sea for the 2003 and 2004 spawning seasons (Fig. 1) when the cod  
180 population was in the process of late maturation (vitellogenesis) and spawning.  
181 Potential fecundity and size frequency distributions of vitellogenic follicles were  
182 determined using the auto-diametric fecundity method (Thorsen and Kjesbu, 2001).  
183 During the analyses spawning fish were identified by the presence of spawning  
184 markers (hydrating follicles, hyaline eggs or postovulatory follicles) in the ovary  
185 samples (whole mounts) and these were excluded from the fecundity analyses  
186 (Witthames et al., 2009).

187

### 188 *2.3. Barents Sea cod fecundity samples*

189 Pre-spawning cod were sampled between 1987 and 2006 at Andenes (Fig. 1) as the  
190 Barents Sea cod are migrating southward to the Lofoten and Vesterålen spawning  
191 areas. The samples were taken from commercial landings of locally caught fish in the  
192 first half of March (Kjesbu et al., 1998). Potential fecundity was determined using the  
193 gravimetric method or the auto-diametric method (Thorsen and Kjesbu, 2001;  
194 Thorsen et al. 2006). As above, only fish without any indication of having started  
195 spawning were included in the fecundity analyses. Sagittal otoliths were removed  
196 from each individual for stock separation (Rollefsen, 1934) since coastal cod (a  
197 separate stock) also occur in the same area. Only Barents Sea cod were used in this  
198 investigation. The selection programme was not completely random because the less

199 abundant large females were taken preferentially to ensure all length classes present in  
200 the population were represented.

201

#### 202 *2.4. Icelandic cod fecundity samples*

203 Samples from Icelandic cod were collected each year from 1995 to 2000 in January  
204 to February, i.e., prior to the spawning season, at the main spawning grounds off the  
205 south-west coast of Iceland (Fig. 1, Marteinsdóttir and Begg, 2002). Potential  
206 fecundity estimates were determined gravimetrically from counts of oocytes in  
207 weighed portions (0.3 g) of ovary tissue as detailed in Marteinsdóttir and Begg  
208 (2002). Since oocyte diameters were not recorded for Icelandic cod, oocyte packing  
209 densities (number per gram ovary) from the gravimetric counting were converted to  
210 mean oocyte diameter using the reversed auto-diametric oocyte density versus  
211 diameter relationship (Thorsen and Kjesbu, 2001).

212

#### 213 *2.5. Calculations and statistics*

214 Condition of fish was calculated as:  $100 \times \text{whole fish weight} / \text{total fish length}^3$ .  
215 Fecundity and fish data for all the stocks were combined into a single database and  
216 analyzed using STATA™ 10 (<http://www.stata.com>). Only pre-spawning fish with  
217 mean vitellogenic oocyte diameter larger than 300  $\mu\text{m}$  were included in the data set.  
218 Unless otherwise noted all regression analysis were based on ln transformed data.  
219 Both simple and multiple linear regressions were used.

220

221 Potential fecundity was defined as the standing stock of vitellogenic oocytes, while  
222 relative fecundity was defined as the potential fecundity divided on total fish weight.  
223 In cases where relative fecundity was calculated from model output, fish weight was  
224 calculated from stock-specific length-weight relationships.

225

226 The standing stock of vitellogenic oocytes of cod is known to decrease as the  
227 vitellogenic oocytes grow towards start of spawning due to atresia (Thorsen et al.,  
228 2006). The fecundity samples for this study were collected over many years and at  
229 different locations. We therefore expected that differences in sampling times between  
230 years and locations might lead to skewed fecundity estimates. To standardize across  
231 stocks and years, output from the regression models utilised a constant mean oocyte  
232 diameter for each of the stocks. We chose to use 600  $\mu\text{m}$  as standard value as



233 compromise between being close to start of spawning and to avoid extrapolation of  
234 the regression models. For calculation of cumulative fecundity the same procedure  
235 was used.

236

237 For stocks or years where oocyte diameter measurements were not available, oocyte  
238 packing densities (number per gram ovary) from gravimetric counting were  
239 converted to mean oocyte diameter using the reversed auto-diametric oocyte density  
240 versus diameter relationship (Thorsen and Kjesbu, 2001).

241

### 242 **3. Results**

243

#### 244 *3.1 Characteristics of the sampled fish*

245 The mature female cod sampled in this investigation covered a large length range, 34  
246 to 133 cm (Table 1). On average the Icelandic cod were the largest with a mean length  
247 of 94 cm, followed by the Barents Sea cod (82 cm). The North Sea cod were smaller  
248 (mean length, 69 cm), but still considerably larger than the Irish Sea cod (55 cm).

249 Within each stock the difference in mean length between years was in general small  
250 with two exceptions; the Barents Sea cod sampled in 1987 were about 22 % smaller  
251 than the average for the studied period while the Irish Sea cod differed by 28 %  
252 between the two years sampled.

253

254 The average condition of the sampled cod followed a clear North-South gradient  
255 ranging from 0.89 for the Barents Sea cod to 1.27 for the Irish Sea cod. Within each  
256 stock there was considerable variation between years, but in general there was little  
257 overlap of the averages between stocks.

258

259 Mean oocyte diameter of the sampled fish was on average larger for the Barents and  
260 Irish Sea cod (644 and 672  $\mu\text{m}$ ) than for the Icelandic and North Sea cod (570 and  
261 573  $\mu\text{m}$ ). In regard to an individual fish, spawning usually starts when the mean  
262 diameter is between 600-800  $\mu\text{m}$  (Kjesbu et al., 1990; Kjesbu and Kryvi, 1993;  
263 Thorsen and Kjesbu, 2001, Thorsen et al., 2006) which in this case indicates that at  
264 sampling the Barents Sea and the Irish Sea cod were generally close to the start of  
265 spawning, while the North Sea cod and Icelandic cod were in earlier stages of  
266 development prior to spawning. There was little difference between years in mean

267 oocyte diameter for the Barents Sea and Irish Sea cod while for the Icelandic and  
268 North Sea cod there were large differences.

269

270 Analyses of recent time series (see Section 2.1 and 2.5 for details) on length at age  
271 showed that Barents Sea and Icelandic cod had similar growth rates (Fig. 2). North  
272 Sea and especially Irish Sea cod had considerable higher growth rates. At age three  
273 the Barents Sea cod were on average 34 cm while Icelandic cod were 39 cm. North  
274 Sea and Irish Sea cod aged 3 years, however, were on average 47 and 65 cm,  
275 respectively.

276

277 As a consequence, age at first maturity was much higher for Barents Sea and Icelandic  
278 cod than for the two other stocks (Table 2). Both the Barents Sea and Icelandic cod  
279 females matured, on average, for the first time at about 7 years old, while in North Sea  
280 and Irish Sea cod they were 4 and 2 years old, respectively. Length at first maturity  
281 (Table 2) seemed to follow a North – South gradient with first maturity at much  
282 smaller lengths in the south compared to the north.

283

### 284 3.2. *Potential fecundity*

#### 285 3.2.1. Relative potential fecundity and down-regulation

286 The relative potential fecundity (Fig. 3) for all stocks, except the Irish Sea, decreased  
287 significantly as the mean vitellogenic oocyte diameter increased towards the start of  
288 spawning. This was also mostly the case when data were allocated to year. An  
289 explanation of the lack of decrease in relative fecundity for Irish Sea cod might be that  
290 there was a considerably narrower mean oocyte size range for the sampled fish in this  
291 area than for the other areas. Most of the Irish Sea cod appeared to have been sampled  
292 close to the start of spawning.

293

294 The data were also divided in to three different condition levels (less than 0.9,  
295 between 0.9 and 1.1, and above 1.1). For fish with condition between 0.9 and 1.1,  
296 Irish Sea cod had a reduction in relative fecundity ( $P = 0.056$ ,  $r^2 = 0.55$ ), although the  
297 small number of observations ( $n = 6$ ) in this condition interval did not allow firm  
298 conclusions to be made. The reduction in relative fecundity for the other cod stocks  
299 did not seem to be influenced by condition.

300

301 Because the potential fecundity generally decreased as the mean oocyte diameter  
302 increased, i.e., as spawning time became closer, we included mean oocyte diameter as  
303 one of the independent variables in our fecundity regression models.

304

### 305 3.2.2. Potential fecundity regressions

306 Potential fecundity regressions were made for all stocks and sampling years (Table 3).  
307 All regressions were highly significant ( $P < 0.001$ ). Length was used as an  
308 independent variable either alone or in combination with mean oocyte diameter and/or  
309 condition. When length alone was used as an independent variable  $r^2$  varied between  
310 years from 0.75 to 0.92 and there appeared to be only small differences between the  
311 stocks. When mean oocyte diameter was included as an additional independent  
312 variable,  $r^2$  in all cases increased, typically between 0.01 and 0.03. However, for Irish  
313 Sea cod this was less and insignificant ( $P > 0.05$ ). When condition was also added as  
314 one of the independent variables there was a greater increase in  $r^2$ , typically 0.03 to  
315 0.04, resulting in  $r^2$  for several cases being above 0.94.

316

### 317 3.2.3. Potential fecundity from year independent regression models

318 When calculating potential fecundity (Fig. 4) from the year independent models there  
319 were only minor differences in output when using only length (Fig. 4 A) or including  
320 mean oocyte diameter (Fig. 4 B) as an additional independent variable. For  
321 calculating the output from models including mean oocyte diameter, a diameter of 600  
322  $\mu\text{m}$  was used as the normalised setting for all cases. This number was not very far  
323 from the actual overall averages for each of the stocks (Table 1), which explains the  
324 small differences between the two model types. In general the models showed that  
325 there was a north-south difference with considerably higher fecundity in the south.  
326 This difference was slightly larger for large fish than for small fish; using the model  
327 with length and oocyte diameter as independent variables (Fig. 4 B) a 60-cm cod from  
328 the Irish Sea was about 2.5 times more fecund than a 60-cm cod from the Barents Sea,  
329 but this factor increased to about 2.8 for 90-cm fish. Using the models including  
330 length and oocyte diameter (Fig. 4 B) a 60-cm fish from Icelandic waters was slightly  
331 less fecund than a similar sized fish from the Barents Sea (0.76 versus 0.64 million  
332 oocytes) while this was the opposite for a 90-cm fish (3.30 versus 4.05 million). The  
333 model output indicated that North Sea cod was considerably more fecund than the two

334 northerly stocks while the Irish Sea cod was even higher. A 60-cm Irish Sea cod was  
335 27 % more fecund than a similar North Sea cod while a 90-cm fish was predicted to  
336 be 49 % more fecund.

337

338 Comparing relative fecundity (Table 4, see section 2.5 for how relative fecundity was  
339 calculated) for the different stocks revealed that the Barents Sea and Icelandic stocks  
340 were similar for small fish, but Icelandic cod seemed to become disproportionately  
341 more fecund as their body mass increased. North Sea cod was considerable more  
342 fecund than the two northerly stocks while Irish Sea cod was even higher.

343

344 We also calculated fecundity for 60 and 90 cm fish from the models that included  
345 both length, mean oocyte diameter and condition as independent variables (Fig. 4 C),  
346 again mean oocyte diameter was set to 600  $\mu\text{m}$ , while 1.1 was chosen as a standard  
347 condition factor value. This value was chosen since the stocks at this point had  
348 overlap in condition even though their mean condition levels were different (Table 1).  
349 Comparing output from this model revealed smaller differences between the stocks  
350 (Fig. 4 C). Barents Sea cod and Icelandic cod had a similar level of fecundity, while  
351 the North Sea and Irish Sea cod fecundities were still about 30-50 % higher than the  
352 more northerly stocks. When comparing North Sea and Irish Sea cod, a 60-cm fish  
353 from the two stocks was almost equally fecund, while for a 90-cm fish the Irish Sea  
354 cod was still about 17 % more fecund.

355

#### 356 3.2.4. Year effects on potential fecundity

357 For Barents Sea and Icelandic cod stocks, yearly variations in fecundity over the 10  
358 and 6 years time series were examined (Figs. 5 and 6). In both cases we chose to  
359 compare a 80-cm fish since this size was represented in all years in both stocks (Table  
360 1) and also could be considered as a typical size of spawning fish. For Barents Sea  
361 cod (Fig. 5) there was little difference between the output from the models with  
362 length or length and mean oocyte diameter as independent variables. This was  
363 probably because for this stock there was little difference between the overall mean  
364 oocyte diameters for the sampled material (Table 1) and the standard setting of 600  
365  $\mu\text{m}$  that we used for input in the models that included mean oocyte diameter.

366 For the Icelandic cod however, there were larger differences in the sampled mean  
367 oocyte diameter (Table 1). Therefore, in this case including diameter in the model

368 changed the output considerably (Fig. 6). Except for 1998 the years were very similar  
369 with a maximum of 10 % difference. However, between 1998 and the other years the  
370 difference increased since the sampled fish were much less developed, i.e., farther  
371 away from initiating spawning, than in the other years. In 1998 the mean oocyte  
372 diameter was only 493  $\mu\text{m}$ . In the length based model there was a maximum of 42 %  
373 difference in fecundity between the highest (1999) and the lowest (1998) year while  
374 this increased to 51 % (compared to 1996) when mean oocyte diameter was included.  
375 A closer examination of the 1998 data showed that the reduction in relative fecundity  
376 by increasing diameter was highly significant ( $P \leq 0.000$ ,  $r^2 = 0.22$ ,  $n = 92$ ) and that  
377 the whole range of diameters from 400-600  $\mu\text{m}$  was well represented in the data. Thus  
378 the large reduction in predicted fecundity that we calculated for Icelandic cod in 1998  
379 seemed justified.

380

381 Comparing the output from the model (Fig. 5) with length and mean oocyte diameter  
382 the Barents Sea cod had less difference between the high and low fecundity years than  
383 did the Icelandic cod (Fig. 6). For the Barents Sea cod the most fecund year was 2003  
384 and the less fecund year was 1987, which was 37 % lower (from model including  
385 length and mean oocyte diameter).

386

387 In an attempt to reveal how condition affected potential fecundity condition was  
388 added as an independent variable in the regression models that already included  
389 length and mean oocyte diameter (Figs. 5 and 6). Here we used the average condition  
390 of fish in the stock for all years as an input. If condition was the major driving force  
391 for the observed yearly differences in fecundity using an overall average as input  
392 should remove most of these differences. For Barents Sea cod using the grand average  
393 condition factor of 0.89 made the different years in general more similar (Fig. 5). For  
394 the Icelandic cod the average condition of fish in the stock was 1.06. Using this as an  
395 input for the Icelandic cod altered the output, but less than for Barents Sea cod, and  
396 the differences between years were similar to previous models including length and  
397 diameter (Fig. 6). The larger effect of condition we saw on the Barents Sea cod  
398 fecundity can probably be explained by the larger variation in condition between  
399 years that exist for this stock. For the Barents Sea cod the yearly averages varied  
400 between 0.73 and 0.95, a 30 % difference, while the Icelandic cod only varied  
401 between 1.00 and 1.13, a difference of 13 %.

402

403 The stocks on average spawn for the first time at different age and size (Table 2) and  
404 have different growth rates (Fig. 2) and condition (Table 1). To see how the egg  
405 production compared over time we calculated cumulative fecundity by age and  
406 number of spawning periods (Fig. 7). Doing this we could clearly see that the Irish  
407 Sea cod produced far fewer eggs during the first spawning period than did the other  
408 stocks. While the Irish Sea cod only produced about 0.3 million eggs during the first  
409 spawning period the other stocks produced from 1.7 - 2.2 million eggs. However,  
410 since the Irish Sea cod started at much younger age they produced many more eggs  
411 than did the other stocks at the following ages. At an age of 5 when the Irish Sea cod  
412 had finished 4 spawning periods and produced 14 million eggs the Barents Sea cod  
413 and Icelandic cod had not even started to spawn. After 4 spawning periods the  
414 number of spawned eggs were rather similar for all the stocks except for the North  
415 Sea cod that seemed to produce about 40 % more than the others.

416

#### 417 **4. Discussion**

418 This study demonstrated large differences in egg production among Atlantic cod  
419 distributed over a wide latitudinal and temporal range. Cod from southerly located  
420 stocks were shown to be substantially more fecund than those residing at northerly  
421 located latitudes.

422

423 Growth rate is generally considered to be a key factor that influences age at first  
424 maturity (Karlsen et al., 2006; Kuparinen et al., 2008; Olsen et al., 2009; Svåsand et  
425 al., 1996; Taranger et al., 2009;) and is strongly dependent on temperature in  
426 combination with food intake. The difference in temperature regime from the Barents  
427 Sea in the north to the Irish Sea in the south can be considered to represent the full  
428 thermal range for cod (Sundby, 2000). These differences in temperature is probably a  
429 major driving force for the differences that we see in growth rate, age at first maturity  
430 and maybe also fecundity (Kjesbu et al., 2010) for the four cod stocks. However, we  
431 also see a gradient from north to south in prespawning condition, with much higher  
432 conditions in the south. To attain the very high condition factors found in the south,  
433 food availability may be higher and for longer during the year. In addition the more  
434 southern stocks do not undertake such long migrations thus there are less alternate  
435 energetic demands on calorie intakes. The cod stocks in the south have been severely

436 reduced during the last decades by high fishing pressure (Brunel and Boucher, 2007;  
437 Kell et al., 2006), - although changes in environment and recruitment failure may also  
438 have contributed to the situation. The low abundance of cod in the south possibly  
439 reduces competition for food with increased growth rates and condition as results.  
440 However, high fishing mortality may also favour fish that genetically has a tendency  
441 for early maturation (Jørgensen et al., 2008). Thus, high fishing pressure may cause  
442 both phenotypic responses causing rapid growth and early maturation as well as  
443 genetic drift over time pushing in the same direction. Even for Barents Sea cod, which  
444 is regarded to be in a fairly good state, the age and size at first maturity seems to have  
445 been reduced during the last decades compared to the post-war situation (Nash et al.,  
446 this issue). For North Sea cod the situation is less clear. Females during the period  
447 from 1981-2001 on average matured at a length of 62 cm (Table 2), but with very  
448 large variation from 40-77 cm (Nash et al., this issue). Older reports by Graham  
449 (1924) and Holt (1883) both suggested an average maturation length of 74 cm. Stock  
450 depletion may, however, not be the only reason for today's situations, since in the last  
451 two decades there has been a rise in temperature both in the North Sea (Dulvy et al.,  
452 2008; Skogen et al., 2009) and the Barents Sea (Ingvaldsen, 2009).

453

454 Barents Sea cod and Icelandic cod apparently experience similar temperature regimes  
455 (Sundby, 2000) and although our data suggests Icelandic cod are slightly more fecund  
456 than the Barents Sea cod they are basically relatively similar. The slightly lower  
457 fecundity of the Barents Sea cod might be explained by the very long spawning  
458 migration of this cod. The North Sea cod and the Irish Sea cod on the other hand  
459 experience higher temperatures, especially the Irish Sea cod. These cod stocks also  
460 seem to have considerably higher fecundities, especially the Irish Sea cod which has a  
461 relative fecundity far above the other cod stocks. The elevated fecundities at higher  
462 temperatures are in agreement with laboratory studies of Kjesbu et al. (2010).

463

464 A 90-cm Irish Sea cod in our investigation had a predicted relative potential fecundity  
465 about 80 % higher than a Barents Sea cod (Table 4). Also this type of fecundity  
466 estimate was considerable higher than for the other cod stocks. However, when  
467 comparing fecundity at the first and second spawning the Irish Sea cod had  
468 considerable lower fecundity than the other stocks. Due to a high mortality we can  
469 probably consider that spawning more than twice is rare for some of the cod stocks in

470 question (Ottersen, 2008). At any age expected fecundity of Irish Sea cod is far higher  
471 than the other stocks, but since they start production at such low age and size our  
472 estimations indicate a low production during their expected reproductive life (Fig. 7).  
473 This may indicate that high mortality of cod in the Irish Sea is a dominant factor that  
474 favours individuals with an extremely early start of egg production, both in terms of  
475 age and size. However, experiments with Barents Sea cod in tanks (Svåsand et al.,  
476 1996) also suggest that at a large part of the reason for this is a direct physiological  
477 response to high temperature and growth. Barents Sea cod females in aquaculture  
478 have been reported to mature at an age of 2 years and at an average length of 45 cm  
479 (Svåsand et al., 1996).

480

481 Both for Barents Sea cod and Icelandic cod we found considerable variation in  
482 fecundity between years. Adding condition factor to the multiple regression models  
483 helped reveal whether these differences were caused by yearly differences in  
484 prespawning condition. Our results indicated that prespawning condition could only  
485 partly explain the yearly differences in fecundity. Skjæraasen et al. (2006) found in  
486 tank experiments that female cod energy reserves at the onset of vitellogenesis 3-4  
487 months before spawning had the highest explanatory power for potential fecundity.  
488 Possible the recruitment of oocytes into vitellogenesis is strongly influenced by the  
489 condition at onset of vitellogenesis, while condition closer to spawning or during  
490 spawning determines the level of atresia that reduced the standing stock of maturing  
491 oocytes to the numbers that were actually going to be spawned. In our investigation it  
492 was the prespawning condition that was used. If the condition at start of vitellogenesis  
493 had been used instead, or in addition, the explanatory power of condition might have  
494 been higher, although it has been recently shown that temperature influences the  
495 timing of this peak production of oocytes (Kjesbu et al., 2010).

496         Determinate spawners are often classified as capital breeders and reproductive  
497 investment is heavily dependent on the feeding season prior to the major yolk  
498 production that take place during vitellogenesis (Boulcott and Wright, 2008). A  
499 typical example of such is the Norwegian spring-spawning herring that incorporate  
500 the majority of yolk into the oocytes after the feeding season has ended in early  
501 autumn (Kurita et al., 2003), and then spawn in the following spring without  
502 significant feeding in between (Dommasnes et al., 2004). Cod do not, in general, seem  
503 to have such an extreme strategy, feeding is common also during late vitellogenesis



504 and may also take place during parts of the spawning cycle (Dolgov, 2002; Michalsen  
505 et al., 2008). Therefore fecundity of cod is probably influenced both by condition at  
506 the onset of vitellogenesis (Skjæraasen et al., 2009) and condition during subsequent  
507 oocyte maturation and spawning. Most likely, the condition at the onset of  
508 vitellogenesis is determinate for the number of oocytes that will start vitellogenesis  
509 while feeding and condition later during maturation influence final fecundity by  
510 atresia.

511

512 The timing of sampling over these time series varied with respect to the proximity to  
513 the spawning season of the stock in question. Since atresia can significantly reduce  
514 the standing stock of maturing oocytes as spawning approaches such differences can  
515 bias fecundity estimations considerably (Kennedy et al., 2007; Kurita et al., 2003;  
516 Thorsen et al., 2006; Witthames et al., 2009). Following the recommendations given  
517 by Thorsen et al. (2006), we have included mean oocyte diameter, using as a proxy  
518 for maturity, as one of the independent variables in the fecundity regressions to  
519 account for the loss of fecundity prior to spawning. The objective was to minimise  
520 any effects of the maturity schedule (annual timing of development) on the fecundity  
521 estimations and standardize the estimations of fecundity to prespawning levels. In our  
522 investigation this mostly made a difference in the comparisons between years and  
523 very little when comparing stocks. The explanation for this can be found when  
524 comparing mean oocyte diameters (Table 1); grand averages for the four stocks  
525 showed only minor differences while within stock comparisons in some cases  
526 revealed differences that had considerable influence on the yearly estimates. This was  
527 especially the case for Icelandic cod.

528

529 The use of mean oocyte diameter as a proxy for maturation has the advantage for time  
530 series such as those dealt with here because it can be calculated from the number of  
531 oocytes per gram ovary (Thorsen et al., 2006). Both individual ovary weight and  
532 fecundity are usually available in the fecundity data sets since it is the basis for the  
533 calculation of potential fecundity. However, for determinate batch spawners, such as  
534 cod, the leading cohort diameter (mean of the largest 10% of advanced oocytes in the  
535 ovary) may be a better proxy for maturation because of its close link and sensitivity to  
536 the start of spawning (Kjesbu, 1994; Kjesbu et al., 2010). In pilot tests we have found  
537 that leading cohort can be used instead of mean oocyte diameter in our present

538 models. We have not used this information here because it is only available for some  
539 of the stocks and only in the most recent observations where fecundity was  
540 determined by image analysis (Thorsen and Kjesbu, 2001).

541

542 Using mean oocyte diameter to standardize to pre-spawning fecundity can be  
543 considered as a way of accounting for pre-spawning atresia without the laborious  
544 estimation of atresia levels. The alternative is to measure the standing stock of atresia  
545 throughout maturation, by histology, and then estimate the reduction of the standing  
546 stock of maturing oocytes (Andersen, 2003; Hunter and Macewicz, 1985; Hunter et  
547 al., 1992; Kurita et al., 2003; Murua et al., 2003). However, to make this adjustment it  
548 is also necessary to know the duration of the counted atretic stage (usually the alpha-  
549 stage) and the time until start of spawning (Murua et al., 2003). The duration of the  
550 atretic stage is seldom accurately known (Witthames et al., this issue) and is generally  
551 difficult to estimate. To estimate realised fecundity it is also necessary to estimate the  
552 atretic loss during the spawning period which is even further complicated since,  
553 during this period, oocytes are lost both by spawning events and atresia. Whilst we are  
554 aware of this and research is being undertaken, further research is still necessary  
555 before quantitative relationships can be included.

556

557 In our between year fecundity comparisons, Icelandic cod in 1998 stood out as  
558 exceptionally low fecundity compared to the other stocks and years. However, this  
559 was only apparent when mean oocyte diameter was introduced into the regression and  
560 oocyte diameter was standardised to a prespawning level (600  $\mu\text{m}$ ). Without this  
561 standardisation the fecundity of 1998 was still low, but only slightly lower than for  
562 1995 and 1997. We consider that the explanation of fecundity loss observed during  
563 the maturation process is consequential to the production of atretic follicles from  
564 normal developing oocytes. This view is further supported by Kjesbu et al. (this issue)  
565 and from earlier work (Kurita et al., 2003; Thorsen et al., 2006; Witthames et al.,  
566 2009) including other determinate species such as sole (*Sole solea*) (Witthames and  
567 Greer Walker, 1995). An alternative explanation to this however, is that this is a trade-  
568 off between size and number of spawned eggs. There are two reasons why we do not  
569 think this is an important factor. First, the sharpest reduction in relative fecundity  
570 seems to occur during early vitellogenesis (300-500  $\mu\text{m}$ ) which is well before the  
571 oocytes are ready to start final maturation. Typically the oocytes have a mean

572 diameter of 600-800  $\mu\text{m}$  just prior to final maturation (Table 1). A second argument  
573 against the size versus number trade-off is that much of the spawned egg size  
574 adjustment actually seems to happen during final maturation that take place the last 2-  
575 3 days before release of each batch (Kjesbu et al., 1996). During this phase the uptake  
576 rate of vitellogenin may be extraordinary large (Wallace and Selman, 1985).

577

578 In summary, we conclude that both size and age of sexual maturity, growth and  
579 fecundity of cod in the North Eastern part of the Atlantic is extremely variable with  
580 clear gradients from North to South. Cod in cold waters have low growth rate and  
581 fecundity and also mature later in life. Cod in warmer water have much higher growth  
582 rates and fecundity but mature at a very early age. The major driving force for these  
583 differences are probably temperature, but fishing pressure and food availability most  
584 probably also contribute.

585

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587

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592

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#### 784 FIGURE LEGENDS

785 Fig. 1. Sampling, spawning, and distribution areas for the four studied cod stocks.  
786 Isolines show yearly mean temperature at 100 m depth. Redrawn from Sundby  
787 (2000).

788

789 Fig. 2. Growth in length for female cod in the Barents Sea, Icelandic waters, North  
790 Sea and Irish Sea based on recent time series.

791

792 Fig. 3. Relative potential fecundity (number of oocytes/total fish weight) versus mean  
793 oocyte diameter for Barents Sea cod, Icelandic cod, North Sea cod, and Irish Sea cod.

794

795 Fig. 4. Estimated potential fecundity for 60- and 90-cm cod from regression models  
796 using length (A), length and mean oocyte diameter (B), or length, mean oocyte  
797 diameter, and condition as independents (C). For calculating output from the models a  
798 mean oocyte diameter of 600  $\mu\text{m}$  and a condition of 1.1 was used. Models included  
799 data for all observed years.

800

801 Fig. 5. Annual variations in fecundity of Barents Sea cod using different models.

802 Inputs: Length = 80 cm, mean oocyte diameter = 600  $\mu\text{m}$ , condition = 0.89 (grand  
803 average for Barents Sea cod).

804

805 Fig. 6. Annual variations in fecundity of Icelandic cod using different models and split  
806 on years. Inputs: Length = 80 cm, mean oocyte diameter = 600  $\mu\text{m}$ , condition = 1.06  
807 (overall average for Icelandic cod).

808

809 Fig. 7. Model output on cumulative potential fecundity by age. Each marker illustrates  
810 a spawning period. The potential fecundity was calculated from models including  
811 length, mean oocyte diameter and condition. Inputs: mean oocyte diameter = 600  $\mu\text{m}$ ;  
812 condition = grand average for stock (Table 1); length =  $L_{50}$  (Table 2) for first  
813 spawning period, mean length at age (Fig. 2) for later spawning periods.

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Figure 1

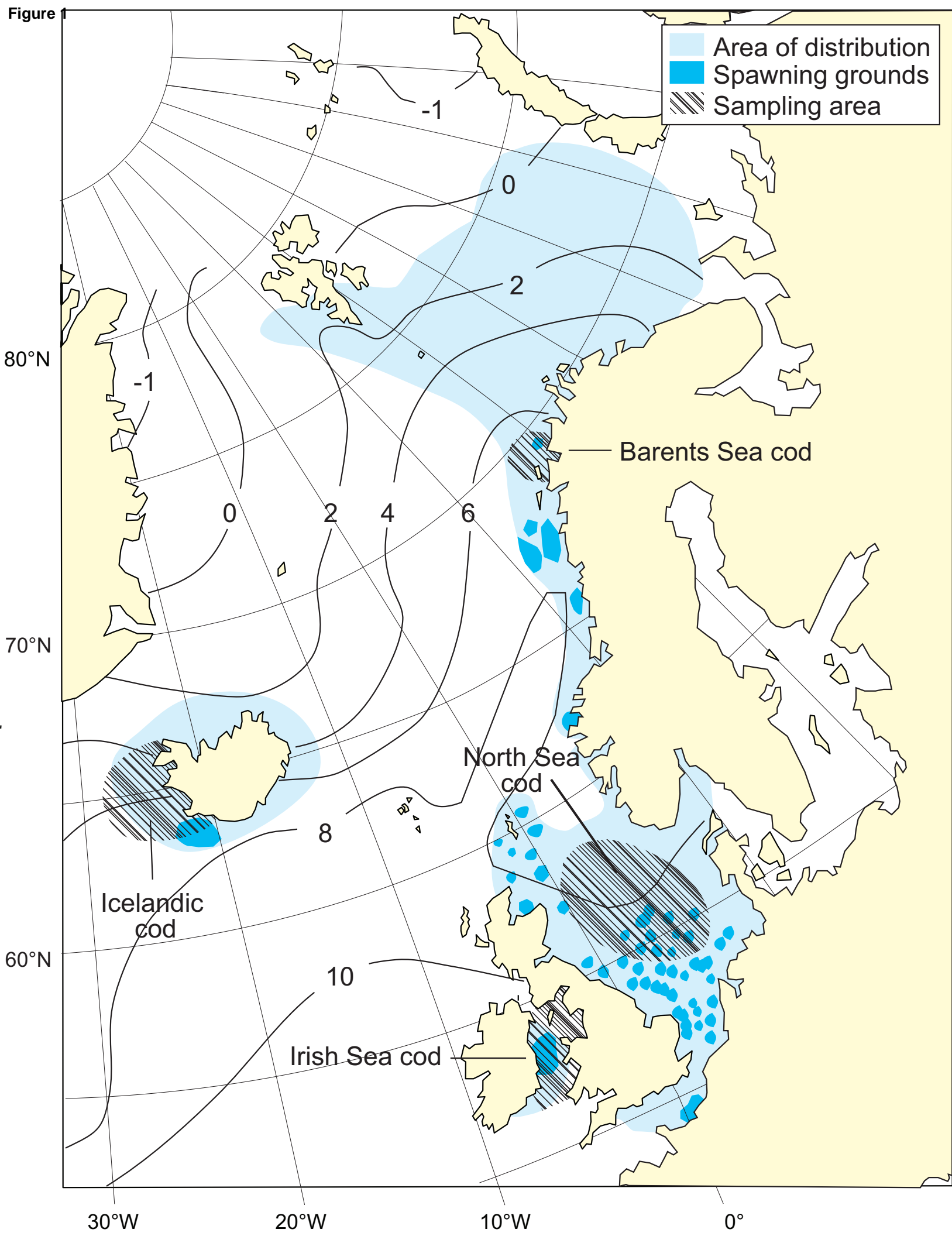


Figure 2

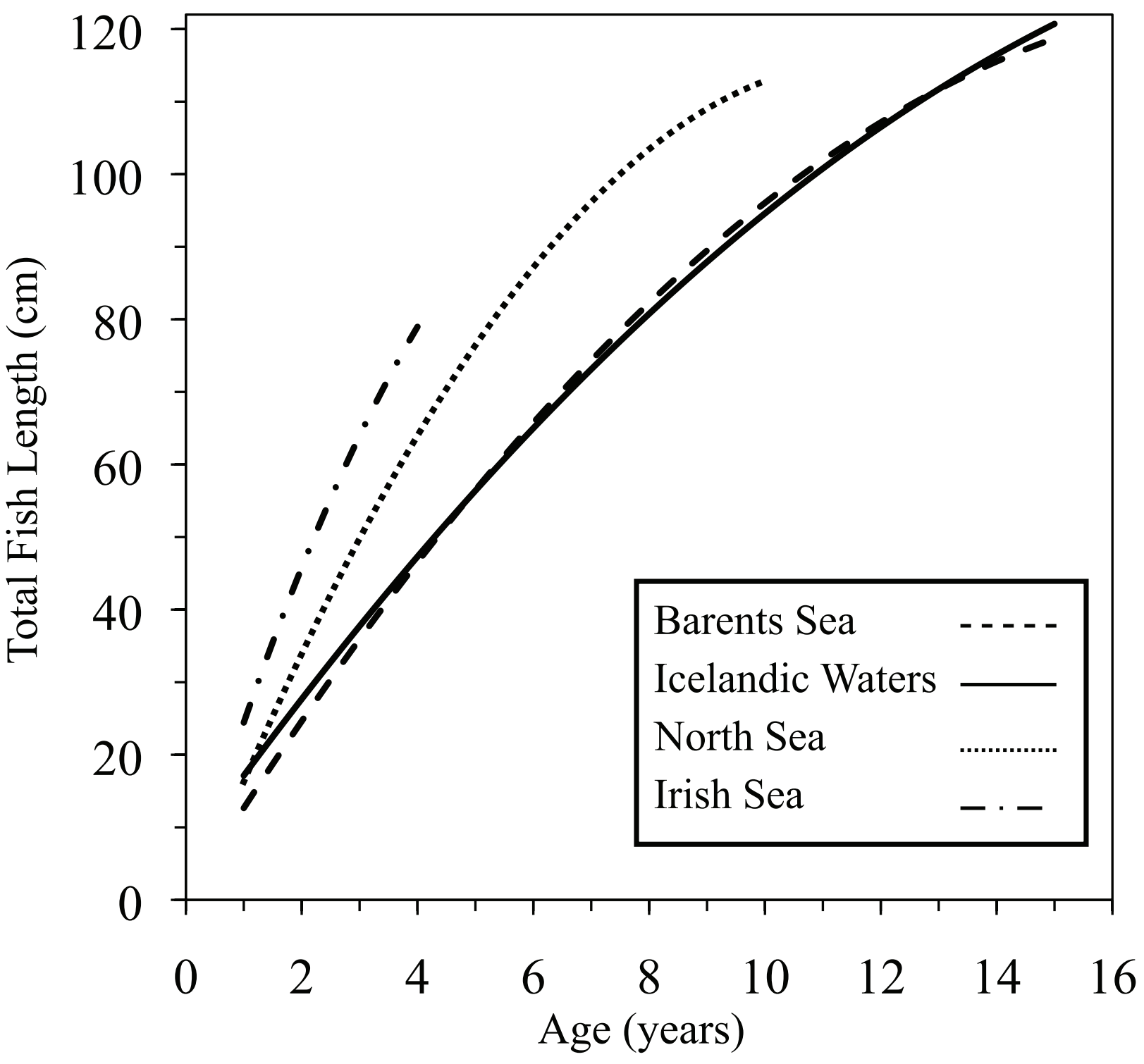


Figure 3

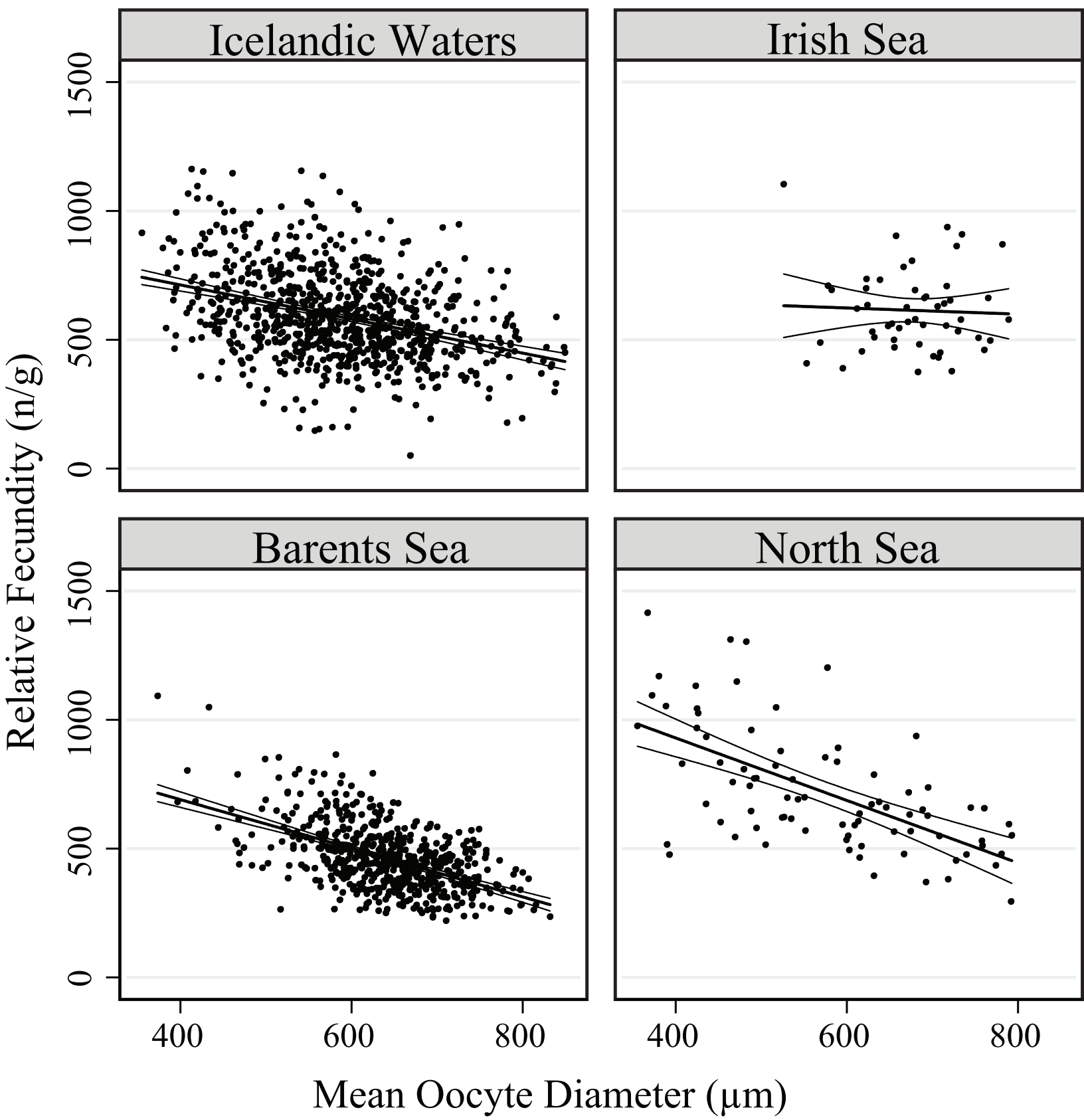
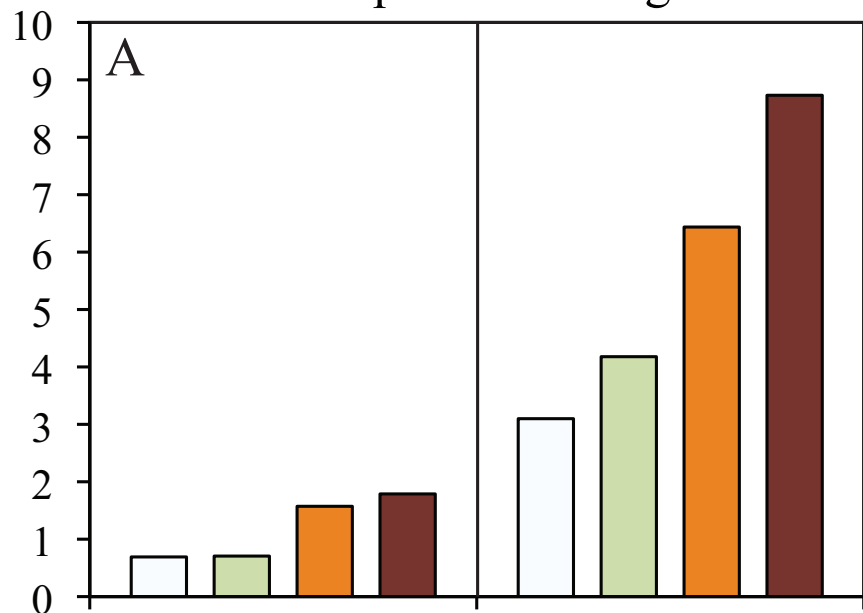
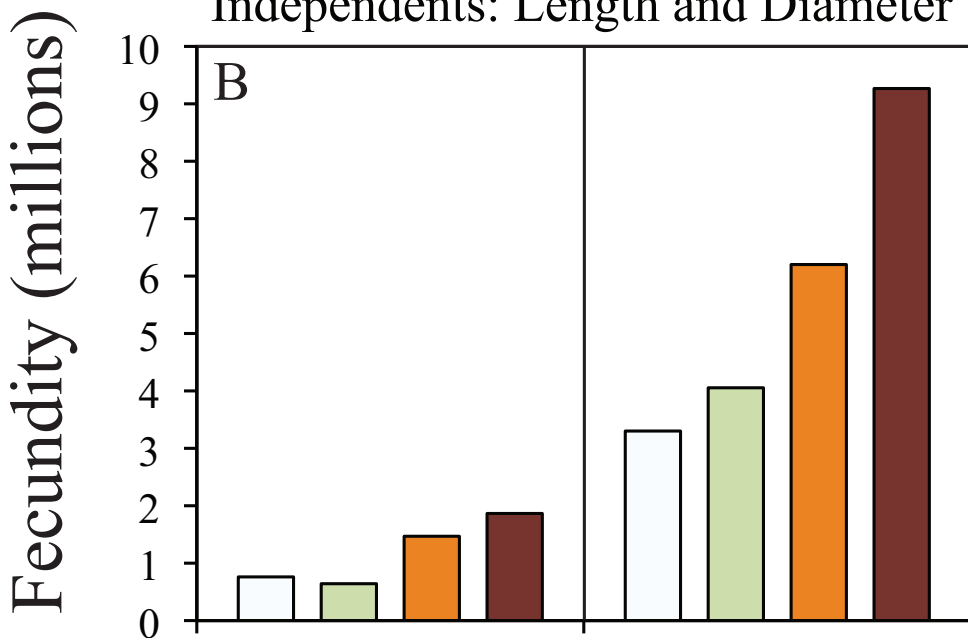


Figure 4

### Independent: Length



### Independents: Length and Diameter



### Independents: Length, Diameter and K

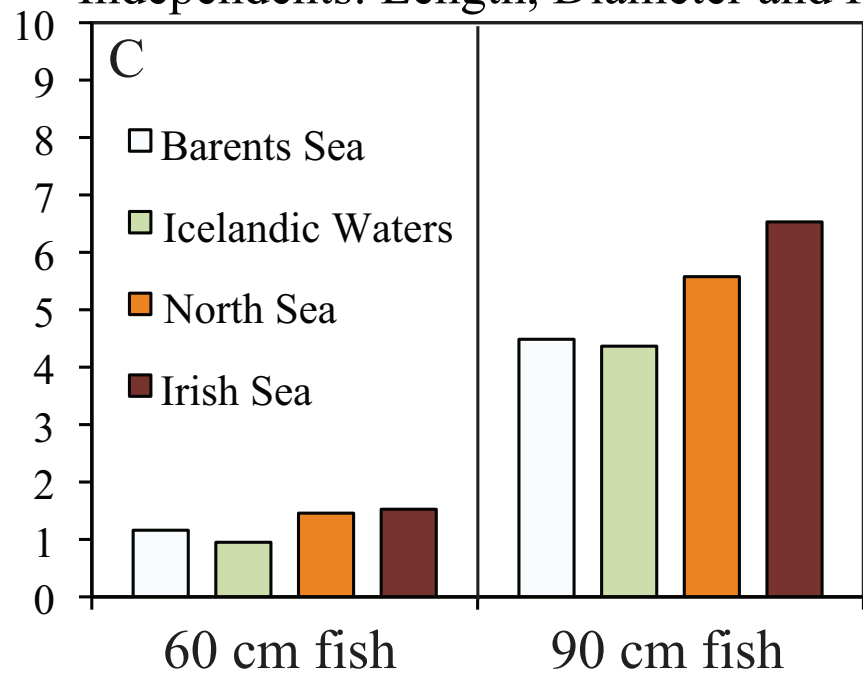


Figure 5 4

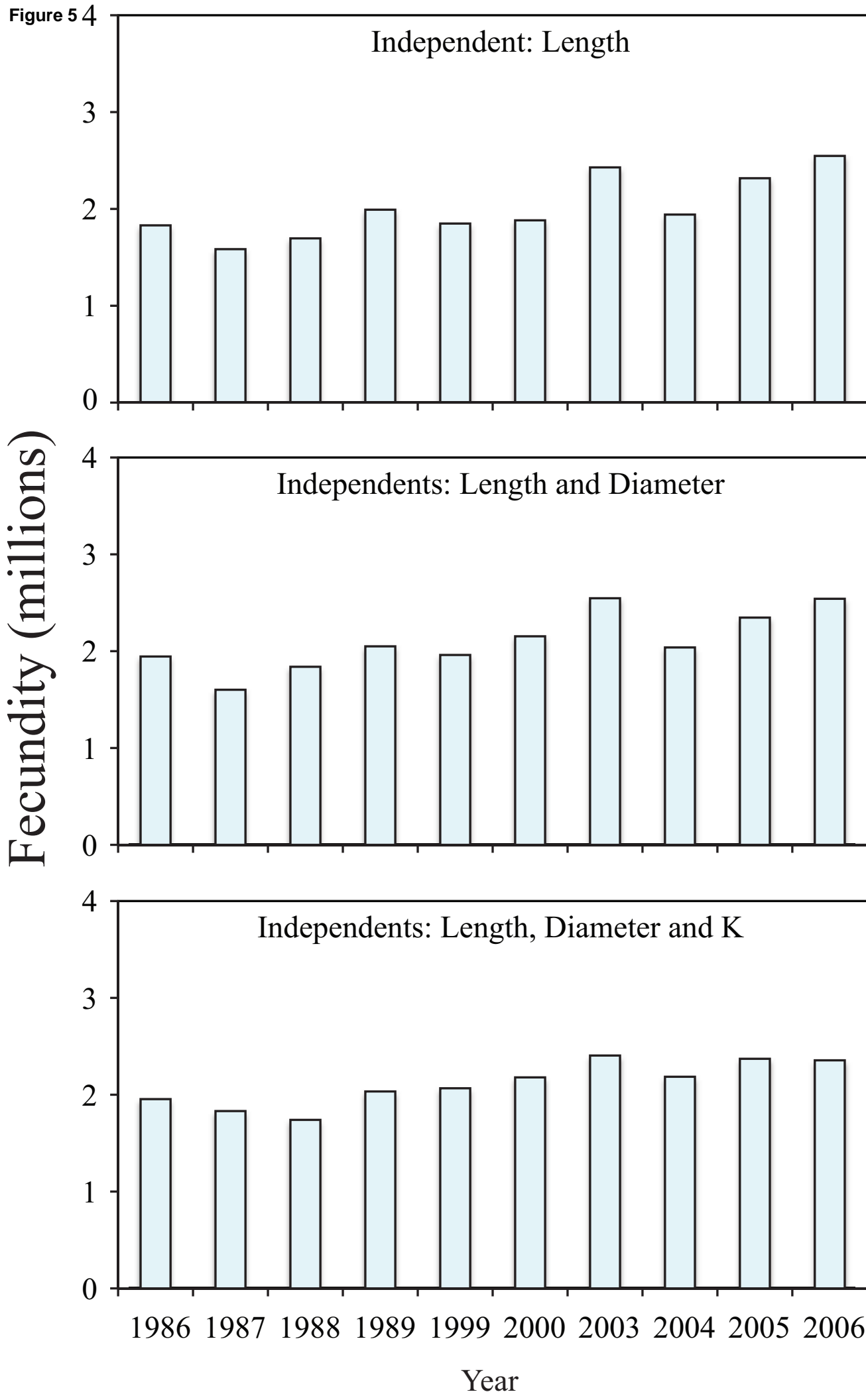
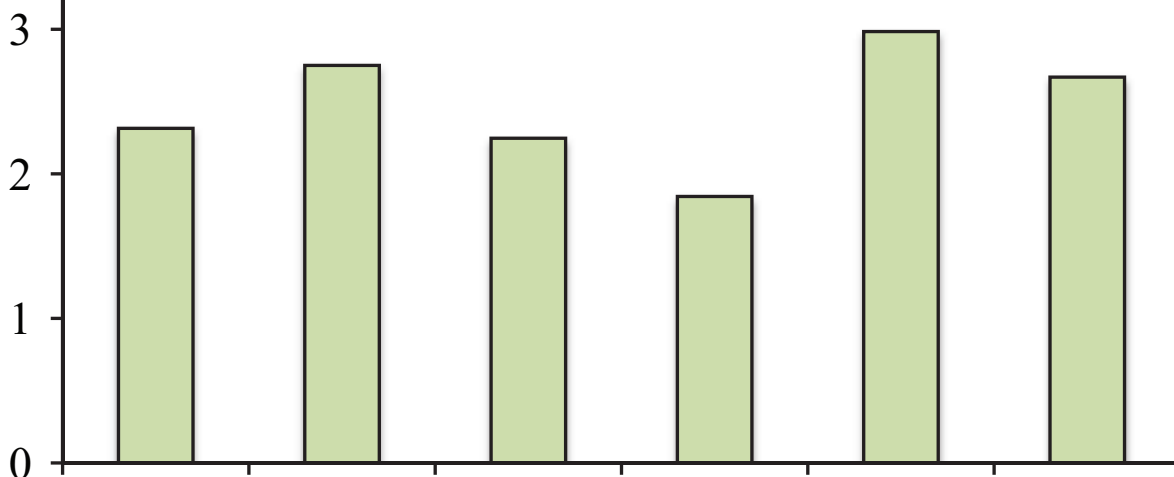


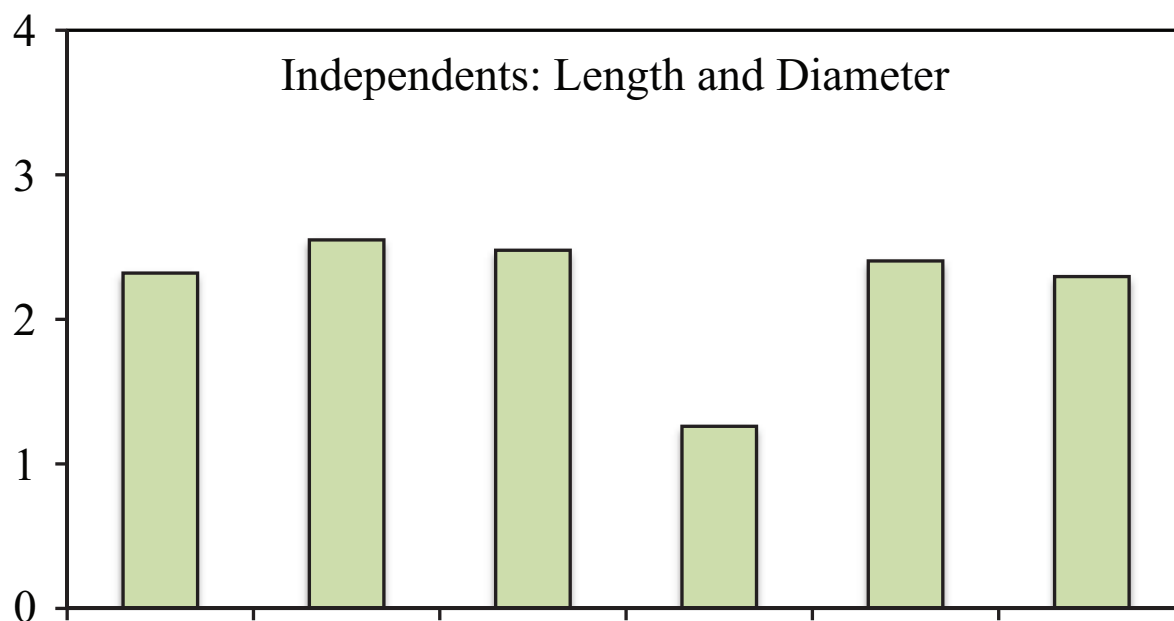
Figure 64

Fecundity (millions)

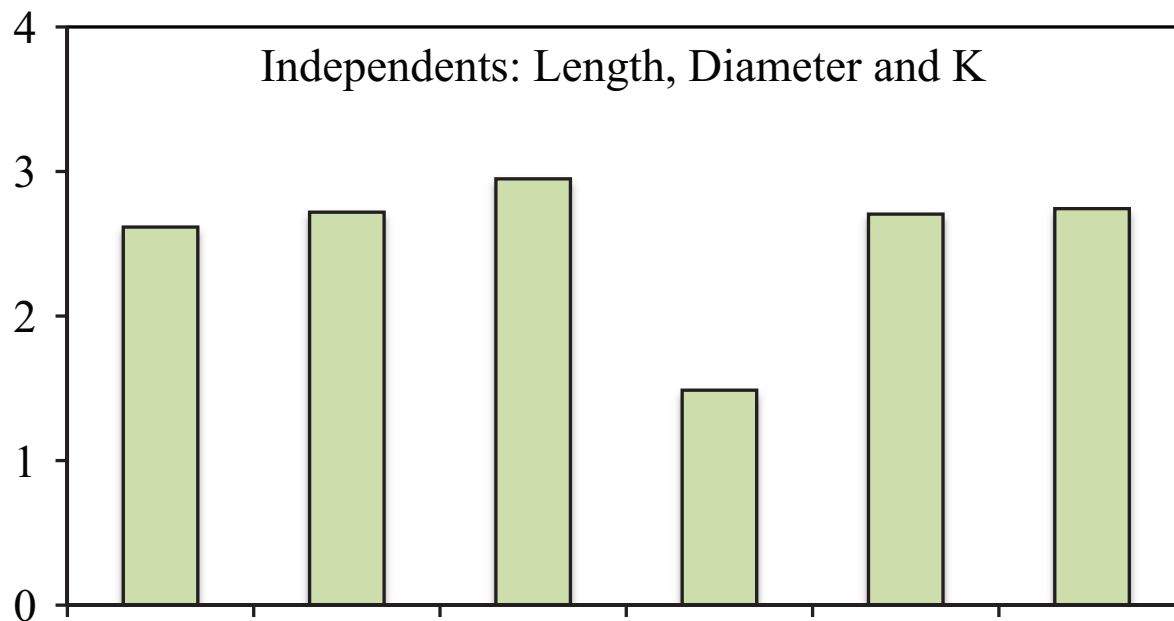
Independent: Length



Independents: Length and Diameter



Independents: Length, Diameter and K



1995 1996 1997 1998 1999 2000

Year



Figure 7

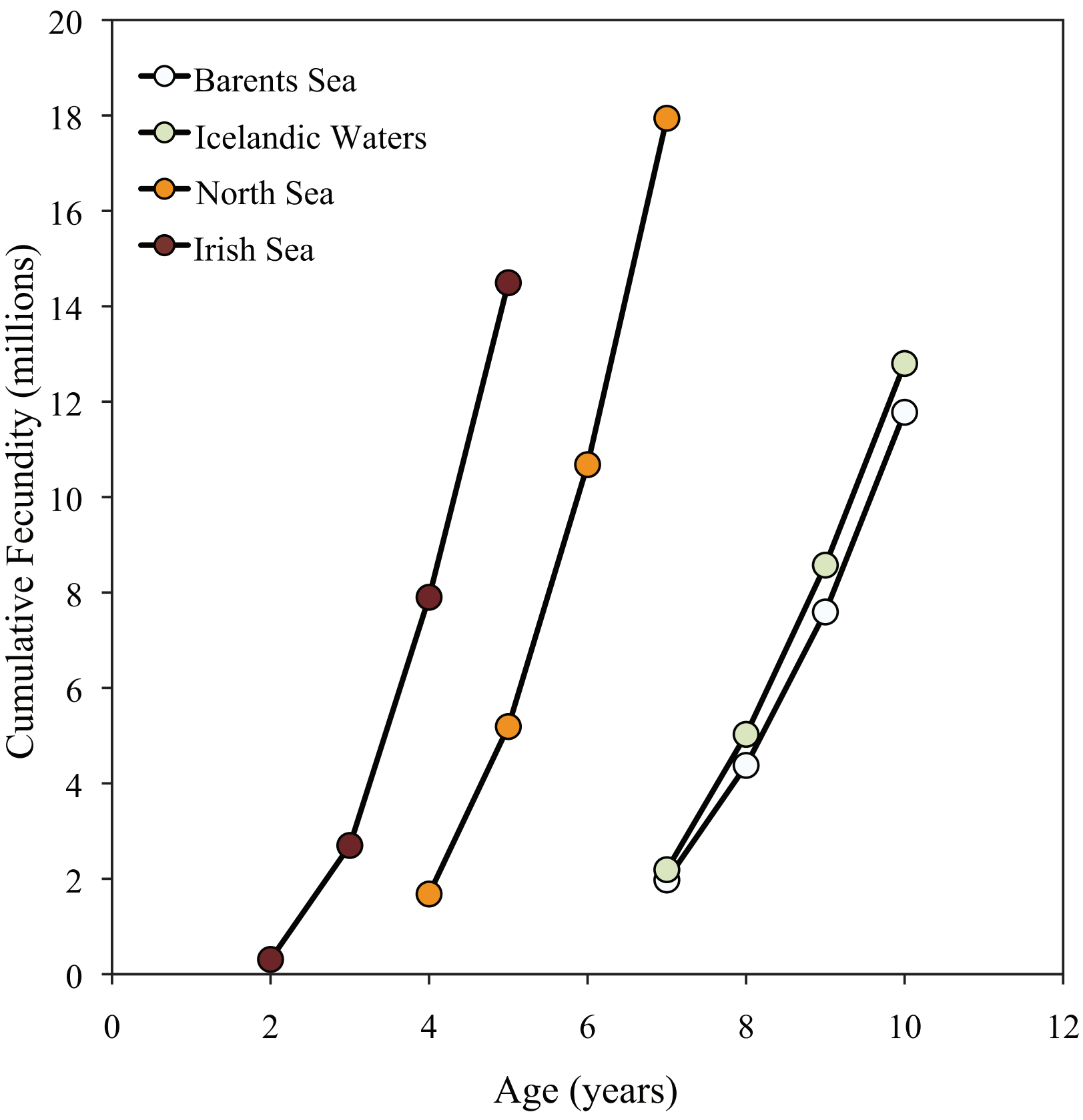


Table 1. Length, condition, and mean oocyte diameter for the sampled fish.

Stock	Year	N	Fulton's K				Length (cm)				Mean oocyte diameter ( $\mu\text{m}$ )			
			Mean	SD	Min	Max	Mean	SD	Min	Max	Mean	SD	Min	Max
<b>Barents Sea</b>														
	1986	29	0.90	0.126	0.67	1.21	81.8	15.4	55.0	122.0	646	69	467	789
	1987	20	0.73	0.094	0.57	0.91	64.1	8.3	52.0	82.0	679	71	444	784
	1988	49	0.89	0.094	0.73	1.21	79.6	19.4	50.0	122.0	681	64	532	799
	1989	110	0.90	0.084	0.64	1.14	84.5	22.1	50.0	126.0	619	62	465	763
	1999	90	0.87	0.066	0.71	1.04	85.2	9.7	67.5	121.0	648	62	469	813
	2000	79	0.89	0.078	0.75	1.16	80.8	9.4	57.0	101.0	692	62	548	832
	2003	48	0.95	0.095	0.78	1.17	84.9	14.7	58.5	117.0	629	71	468	773
	2004	51	0.87	0.105	0.68	1.09	86.1	16.1	63.0	121.0	627	51	502	744
	2005	45	0.91	0.113	0.74	1.27	89.7	13.4	63.0	123.0	620	68	408	726
	2006	78	0.95	0.108	0.71	1.38	86.2	16.9	54.0	120.0	603	73	373	715
	<b>Total</b>	<b>599</b>	<b>0.89</b>	<b>0.060</b>	<b>0.73</b>	<b>0.95</b>	<b>82.3</b>	<b>7.0</b>	<b>64.1</b>	<b>89.7</b>	<b>644</b>	<b>30</b>	<b>603</b>	<b>692</b>
<b>Icelandic Waters</b>														
	1995	263	1.08	0.16	0.46	1.49	94.2	11.9	67.0	125.0	619	56	477	786
	1996	159	1.06	0.18	0.73	1.59	91.1	18.2	57.0	133.0	567	70	423	766
	1997	141	1.13	0.19	0.80	1.60	95.9	11.4	67.0	128.0	696	74	519	849
	1998	92	1.03	0.14	0.68	1.35	98.1	15.7	59.0	129.0	493	64	380	675
	1999	101	1.05	0.17	0.75	1.46	94.4	18.2	59.0	133.0	509	73	355	721
	2000	96	1.00	0.17	0.72	1.57	87.6	15.0	63.0	131.0	534	74	407	782
	<b>Total</b>	<b>852</b>	<b>1.06</b>	<b>0.04</b>	<b>1.00</b>	<b>1.13</b>	<b>93.6</b>	<b>3.7</b>	<b>87.6</b>	<b>98.1</b>	<b>570</b>	<b>76</b>	<b>493</b>	<b>696</b>
<b>North Sea</b>														
	2003	42	1.12	0.15	0.87	1.74	68.9	17.9	34.0	115.0	540	126	355	793
	2004	39	1.14	0.14	0.85	1.42	69.5	15.8	36.0	113.0	605	107	393	792
	<b>Total</b>	<b>81</b>	<b>1.13</b>	<b>0.01</b>	<b>1.12</b>	<b>1.14</b>	<b>69.2</b>	<b>0.4</b>	<b>68.9</b>	<b>69.5</b>	<b>573</b>	<b>46</b>	<b>540</b>	<b>605</b>
<b>Irish Sea</b>														
	2003	18	1.13	0.06	1.02	1.26	45.8	6.7	39.0	68.3	658	47	569	723
	2004	33	1.41	0.18	1.14	1.98	63.5	13.4	45.0	92.0	686	64	526	789
	<b>Total</b>	<b>51</b>	<b>1.27</b>	<b>0.19</b>	<b>1.13</b>	<b>1.41</b>	<b>54.6</b>	<b>12.5</b>	<b>45.8</b>	<b>63.5</b>	<b>672</b>	<b>20</b>	<b>658</b>	<b>686</b>

Table 2. Age and length at 50 % mature for the Barents Sea cod, Icelandic cod, North Sea cod, and Irish Sea cod females. Data for Icelandic cod taken from Marteinsdóttir and Begg (2002).

<b>Stock Period</b>	<b>Barents Sea 1981-2002</b>	<b>Icelandic waters 1985-1999</b>	<b>North Sea 1981-2002</b>	<b>Irish Sea 2003-2004</b>
<b>A<sub>50</sub> (years)</b>	7.2	6.6	3.8	1.6
<b>L<sub>50</sub> (cm)</b>	78	76	62	36

Table 3. Potential fecundity regressions split by stock and year using length, mean oocyte diameter and condition as independent variables. All regressions and regression coefficients (except mean oocyte diameter for Irish Sea cod) were significant with  $P \leq 0.001$ . For calculation of fecundity (F) from the regression coefficients the following equation should be used:  $F = e^a \text{ Length}^b \text{ Diameter}^c \text{ Condition}^d$

### Barents Sea

A	Total	1986	1987	1988	1989	1999	2000	2003	2004	2005	2006
Intercept (a)	-15.526	-17.049	-16.664	-16.580	-13.965	-15.364	-15.802	-13.966	-15.290	-14.343	-14.912
Length (b)	3.702	4.029	3.908	3.904	3.344	3.646	3.751	3.390	3.641	3.465	3.616
r <sup>2</sup>	0.860	0.892	0.787	0.915	0.923	0.745	0.767	0.835	0.869	0.810	0.853

B	Total	1986	1987	1988	1989	1999	2000	2003	2004	2005	2006
Intercept (a)	-7.460	-11.822	-6.858	-11.742	-7.028	-10.071	-9.012	-6.751	-7.352	-9.822	-6.493
Length (b)	3.620	4.153	3.363	3.822	3.311	3.647	3.651	3.260	3.717	3.531	3.589
Diameter (c)	-1.193	-0.893	-1.158	-0.687	-1.058	-0.819	-0.972	-1.032	-1.286	-0.750	-1.298
r <sup>2</sup>	0.889	0.903	0.825	0.917	0.936	0.772	0.795	0.866	0.888	0.829	0.899

C	Total	1986	1987	1988	1989	1999	2000	2003	2004	2005	2006
Intercept (a)	-6.884	-8.911	-8.188	-12.831	-6.795	-9.077	-8.499	-4.092	-3.775	-7.845	-6.980
Length (b)	3.335	3.612	3.372	3.440	3.268	3.354	3.617	2.971	3.241	3.201	3.325
Diameter (c)	-1.059	-0.951	-0.921	-0.223	-1.036	-0.731	-0.998	-1.235	-1.482	-0.807	-1.024
Condition (d)	1.620	1.383	0.793	2.264	1.626	1.917	1.617	1.301	1.410	1.324	1.576
r <sup>2</sup>	0.937	0.942	0.850	0.964	0.963	0.861	0.873	0.899	0.926	0.895	0.944

### Icelandic waters

A	Total	1995	1996	1997	1998	1999	2000
Intercept (a)	-18.305	-18.692	-17.495	-19.494	-23.294	-16.869	-18.759
Length (b)	4.386	4.457	4.223	4.633	5.455	4.099	4.505
r <sup>2</sup>	0.832	0.805	0.909	0.746	0.837	0.877	0.859

B	Total	1995	1996	1997	1998	1999	2000
Intercept (a)	-14.524	-14.383	-13.612	-14.679	-12.301	-11.223	-12.854
Length (b)	4.544	4.573	4.462	4.725	5.504	4.313	4.702
Diameter (c)	-0.707	-0.753	-0.782	-0.800	-1.811	-1.063	-1.082
r <sup>2</sup>	0.852	0.816	0.917	0.762	0.889	0.905	0.890

C	Total	1995	1996	1997	1998	1999	2000
Intercept (a)	-9.392	-9.518	-9.275	-7.281	-6.868	-8.520	-6.604
Length (b)	3.759	3.773	3.842	3.593	4.673	3.695	3.606
Diameter (c)	-0.968	-0.958	-1.037	-1.168	-2.081	-1.057	-1.294
Condition (d)	1.458	1.318	1.265	1.573	1.754	1.414	1.564
r <sup>2</sup>	0.907	0.889	0.945	0.876	0.925	0.951	0.940

**North Sea**

<b>A</b>	<b>Total</b>	<b>2003</b>	<b>2004</b>
<b>Intercept (a)</b>	-13.777	-13.454	-14.343
<b>Length (b)</b>	3.476	3.426	3.580
<b>r<sup>2</sup></b>	0.880	0.879	0.915

<b>B</b>	<b>Total</b>	<b>2003</b>	<b>2004</b>
<b>Intercept (a)</b>	-8.829	-7.623	-12.556
<b>Length (b)</b>	3.553	3.510	3.605
<b>Diameter (c)</b>	-0.834	-0.987	-0.296
<b>r<sup>2</sup></b>	0.916	0.931	0.917

<b>C</b>	<b>Total</b>	<b>2003</b>	<b>2004</b>
<b>Intercept (a)</b>	-6.886	-5.562	-10.679
<b>Length (b)</b>	3.309	3.216	3.426
<b>Diameter (c)</b>	-1.001	-1.143	-0.492
<b>Condition (d)</b>	1.262	1.395	1.061
<b>r<sup>2</sup></b>	0.937	0.952	0.935

**Irish Sea**

<b>A</b>	<b>Total</b>	<b>2003</b>	<b>2004</b>
<b>Intercept (a)</b>	-15.430	-13.206	-14.881
<b>Length (b)</b>	3.911	3.312	3.786
<b>r<sup>2</sup></b>	0.930	0.808	0.895

<b>B</b>	<b>Total</b>	<b>2003</b>	<b>2004</b>
<b>Intercept (a)</b>	-13.403	-7.771	-13.886
<b>Length (b)</b>	3.953	3.427	3.806
<b>Diameter (c)</b>	-0.338	-0.906	-0.166
<b>r<sup>2</sup></b>	0.930	0.816	0.892

<b>C</b>	<b>Total</b>	<b>2003</b>	<b>2004</b>
<b>Intercept (a)</b>	-9.403	-6.935	-10.338
<b>Length (b)</b>	3.585	3.468	3.727
<b>Diameter (c)</b>	-0.779	-1.071	-0.746
<b>Condition (d)</b>	1.352	0.641	1.690
<b>r<sup>2</sup></b>	0.957	0.808	0.947

Table 4. Model output on relative fecundity (eggs g<sup>-1</sup>) by stock and class. Values calculated from regression models using length and mean oocyte diameter as independent variables. For calculating output a mean oocyte diameter of 600 µm was used.

<b>Length</b>	<b>Barents Sea</b>	<b>Icelandic waters</b>	<b>North Sea</b>	<b>Irish Sea</b>
60 cm	416	354	615	677
90 cm	497	532	711	892
100 cm	521	591	738	