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*Published in:*  
Canadian Journal of Fisheries and Aquatic Sciences

*Link to article, DOI:*  
[10.1139/F08-086](https://doi.org/10.1139/F08-086)

*Publication date:*  
2008

*Document Version*  
Peer reviewed version

[Link back to DTU Orbit](#)

*Citation (APA):*  
Rindorf, A., & Andersen, B. S. (2008). Do North Sea cod (*Gadus morhua*) fisheries maintain high catch rates at low stock size? *Canadian Journal of Fisheries and Aquatic Sciences*, 65(9), 1800-1813. DOI: 10.1139/F08-086

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1 **Do North Sea cod fisheries maintain high catch rates at**  
2 **low stock size?**

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9 Key words: Density dependence, catchability, aggregation, North Sea cod

10

11 **Abstract:** This study presents an investigation of the relationship between stock size of North Sea  
12 cod and catch rates in seven commercial fishing fleets. The shape of the relationship was estimated  
13 using a new model allowing both density dependent changes in catchability and bias in the  
14 assessment biomass estimates. Catchability in fisheries targeting a mixed species composition either  
15 remained constant or decreased with decreasing stock size whereas catchability in targeted cod  
16 fisheries increased with decreasing stock size. However, even in the cases where catchability  
17 increased, the change was insufficient to compensate for the decrease in stock size and catch rates  
18 of all fleets decreased. Two factors which could lead to non-constant catchability were investigated:  
19 the presence of a decoupling between stock size and density in high density areas, and the presence  
20 of concurrent shifts in the spatial distribution of the cod stock and the cod fishery. No evidence of  
21 the former was found but there was a northern shift in the spatial distribution of both effort and the  
22 cod stock.

23

## 24 **Introduction**

25           The stability of any exploited stock relies on the relationship between stock size and  
26 harvest rate. If harvest rate decreases with declining stock size, year to year variation in stock size is  
27 decreased and limited harvesting has a stabilising effect. In contrast, if harvest rate increases with  
28 declining stock size, any decrease in stock size is aggravated as the stock is further diminished by  
29 exploitation, and the probability of collapse of the stock is increased. Harvest rate in fish stocks is  
30 usually regulated by restricting total landings, effort exerted and a number of technical measures  
31 such as gear type and mesh size. The restriction of fishing effort is based on the implicit assumption  
32 that catchability is constant. However, catchability in several fisheries increases with decreasing  
33 stock size (Rose and Leggett 1991; Rose and Kulka 1999; Swain et al. 1994), presumably by  
34 targeting local areas where density remains high (Paloheimo and Dicke 1964; Crecco and Overholtz  
35 1990; Rose and Leggett 1991). The increase in catchability often leads to an increase in harvest rate  
36 as catch rate remains high (hyperstable) at low stock size giving the fishing fleet the potential to  
37 destabilise a small stock further. Knowledge of the presence or absence of a relationship between  
38 stock size and catchability is thus crucial when attempting to predict the effect of different effort  
39 management measures, a task which is required on a yearly basis for a great number of exploited  
40 stocks. Accuracy in the predictions is particularly important at low stock sizes, a situation in which  
41 data quality may be deteriorating due to misreporting and low catch rates in surveys.

42           A stock which is currently at a historic low due to the combined effect of fishing and  
43 changing climatic conditions is the North Sea cod (*Gadus morhua*) stock (O'Brien et al. 2000;  
44 Beaugrand et al. 2003; ICES 2006). In addition to the severe decline in stock size, the stock has  
45 exhibited changes in spatial distribution and is now distributed more northerly than previously  
46 (Perry et al. 2005; Rindorf and Lewy 2006). Furthermore, the area inhabited by juvenile cod seems  
47 to have contracted as stock size decreased (Blanchard et al. 2005). The stock would thus appear to

48 have the potential to exhibit a highly undesirable combination of decreasing stock size and  
49 increasing catchability due to a contraction and change in location of the inhabited area. However, it  
50 has not yet been investigated whether catchability in the commercial fisheries has actually changed  
51 or whether any changes can be linked to a relatively constant density of cod in high density areas.  
52 This problem is particularly relevant as catch rates of cod are now regulated through limitations of  
53 both total catch and effort.

54 The objective of this study was to investigate the relationship between stock size and  
55 catchability of North Sea cod. The study was divided into three parts: Firstly, the relationship  
56 between stock size and catch rate in seven commercial fisheries was investigated to determine  
57 whether catchability changed with stock size. Secondly, the relationship between the change in the  
58 spatial distribution of cod and fishing effort was examined to determine whether cod related  
59 fisheries have followed the northwards shift in distribution of the population or has retained its  
60 historic distribution. Finally, the relationship between stock size and survey catch rates in high  
61 density areas was investigated to determine whether the presence of a relationship between  
62 catchability and stock size could be explained by constant high densities in these areas.

## 63 **Materials and methods**

### 64 **Stock size**

65 Stock size of North Sea (ICES areas IV, IIIA and IIVD) cod is estimated each year by  
66 ICES (ICES 2006). The biological assessment is based on reported landings, estimates of discard  
67 and age compositions of both landings and discards. In addition, catch rates in the 1<sup>st</sup> and 3<sup>rd</sup> quarter  
68 International Bottom Trawl Surveys (IBTS) are used to tune the assessment. In recent years,  
69 concern about the reliability of the reported total landings has led to the adoption of a modified  
70 assessment where total landings in the years 2000 to 2005 are adjusted by a yearly factor accounting

71 for unaccounted mortality due to e.g. unreported landings. This factor is determined by a  
72 comparison between stock numbers and catch rates in the IBTS. Commercial catch rates are not  
73 used to tune the cod assessment, and though they contribute to total landings, it is unlikely that the  
74 catch rate of an individual fleet will affect the assessment. Hence commercial catch rates can be  
75 compared directly to assessment derived estimates of stock biomass without introducing a bias in  
76 the analyses whereas catch rates in the IBTS surveys are intrinsically linked to the assessment and  
77 therefore can not be used to determine the actual relationship between stock size and survey catch  
78 rates.

#### 79 **Catch and effort data**

80 The catch in numbers per hour of each agegroup taken by two English fleets (English trawlers and  
81 English seiners) were derived from the assessment report (ICES 2006). These catch rates include  
82 discard estimates (ICES 2006) and hence provide direct estimates of catches rather than just  
83 landings. Estimates of biomass caught per unit effort were derived from catch numbers multiplied  
84 by the weight at age in landings (also given in ICES 2006). The catch per unit effort of English  
85 trawlers was available for the years from 1978 to 2005 whereas catch per unit effort of English  
86 seiners was only available up to 2001. Later years were therefore excluded from the analyses for  
87 this fleet. Though catch per unit effort of three Scottish fleets are also given in the reports, previous  
88 analyses (Cook and Armstrong 1985) has demonstrated that a historical change in the areas fished  
89 has led to severe changes in catchability of Scottish fleets. Hence, the differences seen in  
90 catchability are not directly related to stock size and these fleets were not examined.

91       Effort and cod landings of five Danish fleets (small trawlers, large trawlers, small  
92 gillnetters, large gillnetters and Danish seiners) was estimated from a combination of vessel data,  
93 sales slips and official logbook records. In addition to date and location of each trip, the Danish  
94 logbooks provide information on vessel size, gear used, mesh size, weight and value of landings by

95 species for each ICES statistical rectangle (1°W and 0.5°N, Fig. 1) and number of effort days for  
96 each fishing trip. Effort days are defined as days from the first fishing day to the day of entering the  
97 landing harbor. Both variables have been mandatory in the Danish logbooks since 1983. As a vessel  
98 can fish in several ICES rectangles during a trip, the effort of a trip is allocated to the ICES  
99 rectangle from which the highest catches (by value) were taken. Trips and vessels with missing or  
100 abnormal information and vessels with income below the economic criteria defining a fulltime  
101 fisherman were removed from the data set (Ulrich and Andersen 2004). Subsequently, the most  
102 important cod related fleets were defined from a combination of main gear deployed (type and mesh  
103 size) and vessel length (Table 1).

104           The trawl fisheries are mixed species fisheries targeting cod, other demersal fish species  
105 and Norway lobster (*Nephrops norvegicus*), species which are generally caught together. Including  
106 all fishing trips rather than merely trips catching cod has the advantage that trips which do not catch  
107 cod due to low abundance are included. Unfortunately, this means including trips operating in areas  
108 where cod could not have been caught even if abundance was high (uninhabitable areas). Though  
109 such areas may exist, cod has historically been abundant throughout the North Sea and the latter  
110 problem was therefore considered to be minor whereas the former problem had the potential to  
111 influence results greatly. Based on these considerations, it was decided to include all trawl and seine  
112 fishing trips regardless of whether cod was caught. In contrast to this, the gear type, deployment and  
113 choice of fishing area of the gillnet fisheries depends heavily on which species is the target. The  
114 target species or net type is not recorded in the official logbooks but retrospective analysis of the  
115 catch composition indicated that there was a clear separation between catches consisting primarily  
116 of cod and catches consisting of flatfish (Ulrich & Andersen, 2004). Therefore, a cod-directed  
117 fishing trip for the gillnet fleets was defined as a trip where the cod was the dominating species by  
118 value (Table 1). These trips covered over 90% of the total cod landings of gillnet fleets. This

119 method assured that catch rates were based on one gear type and deployment only but suffered the  
120 disadvantage that low catch rates are likely to lead to a categorisation of the trip as non-cod fishery  
121 and hence near-zero catch rates are likely to be discarded.

122 As estimates of discards are unfortunately not available at a disaggregated level for the  
123 Danish fleets, the average amount of cod caught per unit effort by a particular fleet in a given year  
124 and quarter was estimated as total landings (kg cod) divided by total effort. Only data from the  
125 North Sea proper (Fig. 1) in the years 1983 to 2005 were used.

### 126 **Survey catch per unit effort**

127 The catch at age in numbers per hour in the 1<sup>st</sup> quarter International Bottom Trawl Survey  
128 (IBTS) is given in the assessment report (ICES 2006). From this, the total weight of immature and  
129 mature cod caught per hour of trawling was estimated by multiplying catch in numbers at age by  
130 weight at age in the stock (also available in the assessment report) and maturity at age, and then  
131 summing over ages. Catch rate of all cod was estimated as the sum of immature and mature. In  
132 contrast to commercial catch per unit effort series, catch rate in 1<sup>st</sup> quarter IBTS survey was used to  
133 tune the assessment (ICES 2006) and this survey is therefore not independent of the assessment.  
134 Hence, the correlation between catch per hour in the IBTS was given for comparison but it was not  
135 attempted to estimate changes in catchability as the assessment was based on an assumption of  
136 constant survey catchability (ICES 2006).

### 137 **Cod density in high density areas**

138 If cod concentrate in high density areas as biomass decreases, catch rate in these areas will not  
139 be proportional to stock biomass. If these high density areas are then targeted by the fishery,  
140 hyperstability of catch rates will occur. To investigate whether a decoupling of local density and  
141 stock size occurred, cod density in high density areas was estimated from catch rates in the 1<sup>st</sup>



142 quarter IBTS survey (ICES International Bottom Trawl Survey Database, 1983 to 2005). The  
143 survey uses demersal trawls and length composition and total catch is recorded in each haul. Haul  
144 duration generally varies between 0.5 and 1 hour, and all catch rates are standardised to hourly  
145 values. On average, two trawl hauls are conducted within each ICES statistical rectangle (Fig. 1).  
146 Cod age-length keys were estimated using the method suggested by Rindorf and Lewy (Rindorf and  
147 Lewy 2001; Gerritsen et al. 2006; Rindorf et al. 2007). This method uses the correlation between  
148 length groups to determine smooth functions between length and the probability of being of a given  
149 age and is particularly useful to determine age length keys in cases with sparse sampling (Rindorf  
150 and Lewy 2001) as has been the case with larger cod in recent years. Number of each age group  
151 caught per hour was estimated by applying the estimated age length key to length distributions of  
152 the catch. Survey catch rate of mature cod and immature cod within each statistical rectangle (Fig.  
153 1) was estimated by multiplying survey catch rate in numbers at age by weight at age in the stock  
154 (given in ICES 2006) and maturity at age (ICES 2006) and then summing over agegroups. Total  
155 survey catch rate of cod was estimated by summing the catch rate of immature and mature cod.

156 High density areas were defined as the 10% of statistical rectangles which supported the  
157 highest average survey catch rates in a given year. These areas were selected for separately total and  
158 mature cod, and the average total and mature cod survey catch rate within these high density areas  
159 was estimated. Hence, the actual rectangles included were not necessarily the same in all years or  
160 for total and mature cod. This method was chosen to avoid the problems caused by using a spatially  
161 explicit area while the distribution of the stock is changing and the distribution of immature cod  
162 differs from that of mature.

### 163 **Catch composition**

164 The average proportion of the catch per unit effort of English fleets consisting of mature  
165 cod was estimated as the product of catch in numbers, mean weight and maturity at age as given in

166 ICES (2006) divided by the total catch. The Danish catches were not sampled for age within  
167 individual fleets and instead the distribution of the catch weight on commercial landing size classes  
168 of cod from 1987 to 2005 was used. These size classes were divided into immature (<2 kg), mature  
169 (>4 kg) and a mixture of mature and immature fish (2-4 kg) and correspond roughly to cod of age 1  
170 to 2, age 4+ and age 2 to 4, respectively. The proportion mature in these agegroups are <0.05, >0.62  
171 and 0.05-0.62 (ICES 2006).

## 172 **Comparisons of catch per day and stock biomass**

173 We used a flexible model to describe the relationship between catch rates and stock size:

174

175

176

$$177 \quad U = aB^{(1+b)} + c \quad (1)$$

178

179

180

181 where  $U$  is catch rate,  $B$  is stock size and  $a$ ,  $b$  and  $c$  are constants. This model includes increasing  
182 catchability at decreasing stock size ( $b < 0$  and/or  $c > 0$ ), decreasing catchability at decreasing stock  
183 size ( $b > 0$  and/or  $c < 0$ ) as well as constant catchability ( $b = c = 0$ ) (Fig. 2). As a special case, it includes  
184 the power function often used in the literature ( $c = 0$ ,  $b \neq 0$ ) (Bannerot and Austin 1983; Harley et al.  
185 2001). Furthermore, it includes the case where density remains relatively constant in areas  
186 unavailable to fishing (e.g. refugia) even when biomass is severely reduced. This leads to catch  
187 rates reaching zero at a biomass greater than zero ( $c < 0$ ). Assuming  $b = 0$  for simplicity, the biomass  
188 of fish in refugia is  $-\frac{c}{a}$  as

189

190

191

192 
$$U = a\left(B + \frac{c}{a}\right) = aB + c \quad (2)$$

193

194

195

196 Further, the model includes the case where the true amount of fish,  $B'$ , corresponds to the amount  
197 estimated scientifically ( $B$ ) plus a bias of  $\frac{c}{a}$ . The bias term may be either positive or negative,  
198 corresponding to scientific under- and over-estimation of biomass, respectively. Underestimation  
199 could be the result if a constant amount of fish were unavailable to scientific surveys but remained  
200 available to commercial fishing. This could occur if fish residing in areas with large rocks or around  
201 wrecks were unavailable to survey trawls but available to commercial fisheries using stationary gear  
202 such as hooks or gillnets. The commercial fishery then catches a constant proportion  $a$  of the true  
203 biomass per unit effort:

204

205

206

207 
$$U = aB' = aB + c \quad (3)$$

208

209

210

211 Note that the change in catch rate caused by the presence of refugia can not be separated from that

212 caused by over-estimation of the stock (both lead to  $c < 0$ ). An intercept smaller than zero should  
213 therefore be followed by detailed investigations before drawing conclusions regarding the state of  
214 the stock.

215 Equation (1), denoted the full model in the following has the advantage that the different  
216 models of catchability (power function, refuge and bias models) are nested and statistical testing is  
217 therefore straightforward. To our knowledge, no other studies have included all these models in a  
218 formal test. The full model (eq. 1) was used to analyse the relationship between catch per unit of  
219 effort in both commercial fleets and the high density area survey ( $U$ ) by replacing of  $B$  with either  
220 total ( $T$ ) or spawning stock biomass ( $S$ ) (both in units of  $10^9$  kg), depending on which of these  
221 exhibited the highest correlation with catch per unit effort. The parameters  $a$ ,  $b$  and  $c$  were  
222 estimated by minimising the residual variation (sum of squares) of the full model.

223 The residual variation of this model was compared to that of two reduced models, one with  
224  $b=0$  and another with  $c=0$ . If these reduced models both provided a significant increase in residual  
225 variation (F-test), the final model was equivalent to the full model and parameters  $a$ ,  $b$  and  $c$   
226 estimated. However, if setting either  $b=0$  or  $c=0$  led to no significant increase residual variation (F-  
227 test), the parameter ( $b$  or  $c$ ) with the lowest F-value (highest probability of being insignificant) was  
228 removed from the model. This reduced model was then compared to a model where  $b=c=0$ , and if  
229 this reduction did not deteriorate the fit of the model significantly (F-test), the final model was  
230 reduced to  $U = aB$ . The procedure is based on the assumption that the error in stock and spawning  
231 biomass derived from the assessment is zero or at least negligible compared to that in catch rate. As  
232 the assessment is based on total catches, the age composition of catches and survey catch rates and  
233 hence integrates information from several sources, this assumption appeared reasonable. The  
234 parameters of non-linear models ( $b \neq 0$ ) were estimated using the NLIN procedure in SAS<sup>®</sup> whereas  
235 linear models ( $b=0$ ) were estimated using the GLM procedure in the same programme (SAS

236 Institute Inc. 2001). Residuals were tested for trends (Pearson correlation with year) and  
237 autocorrelation, and their distribution tested for significant differences from a normal distribution  
238 (Shapiro-Wilks test).

239           Unfortunately, restrictive quota regulations may lead to misreporting of both effort, catch,  
240 area fished and even vessel size if the catch is brought ashore by another vessel. This may lead to  
241 both bias and variation in the estimated catch rates – bias if the catch is not reported at all and  
242 variation if the catch is landed by another vessel or reported as being from another area. Hence both  
243 bias and variation may occur in years with restrictive quotas (according to ICES (2006), the years  
244 from 2001 and onwards). They will express themselves as either consistent directional deviations  
245 from the average relationship between catch rates and stock size or as increases in the variation  
246 around the relationship in years with restrictive quotas. Furthermore, technical improvements in  
247 fishing power are likely to have occurred over the time span of the study. An increase in fishing  
248 power should express itself as an increase in catchability over time. The residuals were therefore  
249 examined to determine whether trends or increases in variance occurred.

#### 250 **Distribution of survey catch rates and Danish fishing effort**

251           The spatial distribution of the Danish cod-related fishing effort was compared to the spatial  
252 distribution of the survey catch of mature cod per hour through an investigation of the relationship  
253 between the centre of gravity of survey catch rates and effort of each fleet in each year and quarter.  
254 As catch per day in the Danish fleets consisted of a high proportion of mature fish and was  
255 furthermore highly correlated to spawning stock biomass (see results), the centre of gravity of effort  
256 was only compared to the centre of gravity of survey catch rate of mature cod. The centre of gravity  
257 of mature cod was estimated from the average catch of mature cod per hour in the IBTS in each  
258 statistical rectangle in the 1<sup>st</sup> quarter of 1983 to 2006 and the 3<sup>rd</sup> quarter of 1991 to 2005. The 3<sup>rd</sup>  
259 quarter survey was initiated in 1991 and thus covers only part of the period. The centre of gravity in

260 a given year and quarter was estimated as the average latitude and longitude weighted by the natural  
261 log of  $(1 + \text{the average catch of mature fish (in kg) in each statistical rectangle, } sr \text{ (} 0.5^\circ \text{ latitude}$   
262  $\text{times } 1^\circ \text{ longitude)})$ ,  $\ln(C_{sr} + 1)$ . This estimate of the centre was used for survey catches to obtain a  
263 homogenous error structure (Rindorf and Lewy 2006). To avoid bias due to differences in survey  
264 coverage, only rectangles fished in at least 80% of the years were used. This resulted in 169 and 161  
265 rectangles in the 1<sup>st</sup> and 3<sup>rd</sup> quarter, respectively. The centre of gravity of cod-related fishing effort  
266 of a particular fleet in each year and quarter was estimated as the average latitude and longitude  
267 weighted by days fished in each statistical rectangle. The Pearson correlation coefficients between  
268 the coordinates (latitude and longitude) of survey and effort centres of gravity were estimated.

## 269 **Results**

### 270 **Development in stock size, effort and catch per unit effort**

271         Though a slight increase in biomass was observed in the late 1990's, this was followed by  
272 decline, and both total and spawning stock biomass has decreased severely over the past 25 years  
273 (Fig. 3). Effort has decreased contemporaneously, in particular over the past 10 years (Pearson  
274 correlations coefficients between year (1994-2005) and effort < -0.68 (P < 0.05) for all fleets except  
275 Danish large trawlers, Fig. 4) and in 2005, the effort of most fleets was less than 25% of the  
276 maximum recorded since 1983, the exceptions being Danish small (45%) and large (77%) trawlers.  
277 The majority of the reduction of effort can be explained by a reduction in the number of vessels.  
278 Catch per unit effort series of most fleets show similar temporal patterns (Fig. 4).

### 279 **Catch composition**

280         More than 80% of the English catch per unit effort consisted of immature cod, whereas the  
281 Danish catch generally consisted of a greater proportion of mature than immature cod (Fig. 5).  
282 Around 40% of gillnet and seine catches consisted of mature cod and another 40% of a mixture of

283 mature and immature cod, while the proportion of mature and mixed mature and immature in  
284 Danish trawl catches was intermediate between these values and those of the English fleets.

### 285 **Comparisons of catch per unit effort and total stock and spawning stock biomass**

286 As expected from the catch composition, spawning stock biomass showed the highest  
287 correlation with catch per day for Danish fleets whereas total stock biomass showed the highest  
288 correlation to English fleets (Table 2). Note that in this table, 36 correlation analyses are performed  
289 (not including the IBTS). If the significance level is set to 5%, 5% on average will be termed  
290 significant due to type 1 error (detecting significant relationships where none exists). When  
291 examining 36 correlations, there is thus a greater than 5% probability of detecting up to 4  
292 correlations significant at the 5% level (binomial probability  $>0.05$ ,  $B(36, 0.05)$ ). At the 1% level,  
293 this is decreased to a greater than 5% probability of detecting 1 or 2 significant correlations whereas  
294 at a significance level of 0.1%, the probability of detecting 1 or more significant correlations by  
295 type 1 error is 0.035. Therefore, four comparisons should be expected to be significant at the 5%  
296 level, two at the 1% level and none at the 0.1% level by type 1 error alone. In contrast to this, 26  
297 correlations were significant at the 0.1% level for both total stock and spawning biomass and further  
298 30 and 32 comparisons were significant at the 1 and 5% level, respectively. Thus the number of  
299 significant relationships greatly exceeds that expected by type 1 error.

300 Eq. (1) was fitted to English catch per unit effort using total stock biomass as the  
301 independent variable and to Danish catch per unit effort using spawning stock biomass as the  
302 independent variable as these combinations showed the highest correlation (Table 2). The Danish  
303 seiners showed low correlations with both total and spawning stock biomass (Fig. 6, Table 2) and  
304 were excluded from further analyses. The parameter  $b$  was significantly different from zero in five  
305 cases: English seiners, Danish small gillnetters in the 1<sup>st</sup> and 3<sup>rd</sup> quarter and Danish large gillnetters  
306 in the 1<sup>st</sup> and 3<sup>rd</sup> quarter (Table 3). In the English seiners,  $b$  was larger than zero (the exponent was

307 larger than 1) indicating increased catchability at large stock sizes (Table 3, Fig. 7). In contrast to  
308 this, the value of  $b$  found for Danish gillnetters was negative in all cases (the exponent was less than  
309 1). The intercept was only significantly different from zero in two cases: Danish small trawlers in  
310 the 3<sup>rd</sup> quarter and English seiners (Table 3). Danish small trawlers showed negative intercepts in  
311 both quarters, but only the 3<sup>rd</sup> quarter value was significantly different from zero, indicating a  
312 decrease in catchability at low stock sizes (Fig. 7). The intercept of English seiners was positive and  
313 hence this fleet tended to retain catch rates at a certain minimum level in spite of decreases in stock  
314 size corresponding to an increase in catchability at low stock sizes (Fig. 7). In summary,  
315 catchability decreased with decreasing spawning stock biomass for Danish small trawlers in the 3<sup>rd</sup>  
316 quarter but increased with decreasing spawning stock biomass for Danish gillnet fleets. Catchability  
317 of English seiners decreased with decreasing biomass, though this pattern seemed to reverse at low  
318 stock sizes (Fig. 7). However, as the amount of data in the area where catchability supposedly  
319 increases was limited, firm conclusions on this would require additional estimates of catch per unit  
320 effort at low stock size.

321         The distribution of the residuals did not differ significantly from a normal distribution for  
322 any fleets except for Danish small trawlers and gillnetters in quarter 1, English trawlers and the high  
323 density surveys catch rates of total and spawning cod ( $P=0.0002$ ,  $P=0.0111$ ,  $P<0.0001$ ,  $P=0.0394$   
324 and  $P=0.0003$ , respectively). Only English trawlers exhibited significant trends in the residuals  
325 ( $P>0.05$ , Table 3, Fig. 8). There does thus not appear to have been a general decrease in reported  
326 catch per unit effort as a result of reporting only part of the landings but all of the effort. Neither  
327 was there any indication of increased catchability due to technical improvements in any fleets  
328 except the English trawl fleet. Only Danish small gillnetters in the 1<sup>st</sup> quarter exhibited significant  
329 autocorrelation of the residuals (correlation=0.48,  $P=0.0212$ ).



330 **Comparison between high density survey catch rates and total and spawning stock biomass**

331 First quarter survey catch rates in high density areas were highly correlated to both total  
332 stock biomass and spawning stock biomass (Fig. 9, Table 2). There was no indication of a non-  
333 linear relationship as survey catch rates were proportional to the assessment estimates of biomass  
334 (Table 3).

335 **Comparison of centres of gravity of survey catches and commercial effort**

336 Latitude of the centre of gravity of survey catches of mature cod increased significantly in  
337 both the 1<sup>st</sup> and 3<sup>rd</sup> quarter (Table 4) indicating a northern shift in distribution. Contemporary to the  
338 shift in centre of gravity of survey catches, effort of all five Danish fleets moved northeastwards in  
339 the first quarter (Table 4). The pattern was less clear in the 3<sup>rd</sup> quarter, as Danish trawlers moved  
340 south while Danish small gillnetters moved north. There was a general trend towards operating in  
341 more eastern waters in the 3<sup>rd</sup> quarter in recent years (Table 4). Effort centres of gravity were  
342 closely related to survey centres of gravity for the Danish gillnet and Danish seine fleets in the 1<sup>st</sup>  
343 quarter whereas effort centres of gravity of the remaining fleets were only weakly (but positively)  
344 related to survey centres of gravity in the same period (Table 4). In contrast to this, the correlation  
345 between effort and survey centres of gravity in the 3<sup>rd</sup> quarter was only significantly positive for  
346 latitude of large trawlers and small gillnetters (Table 4). Hence, there was evidence that effort  
347 followed cod distribution in the 1<sup>st</sup> quarter which is the traditional period among fishermen for  
348 targeting cod (pers. obs.), whereas there was only a tendency for effort to follow the latitude of cod  
349 distribution in two fleets in the 3<sup>rd</sup> quarter. Note that as table 4 examines 44 correlation analyses, 5  
350 should be significant at the 5% level, 2 at the 1% level and none at the 0.1% level by type 1 error  
351 alone (binomial probability  $>0.05$ ,  $B(44, \alpha)$ ). However, of the 44 comparisons, 24 were significant  
352 at the 5% level, 20 at the 1% level and 12 at the 0.1% level (Table 4), a much higher number than  
353 would be expected by chance.

## 354 **Discussion**

355           We found no evidence of the presence of refuges, of concentration in high density areas or  
356 of constant bias in the scientific stock assessment. All fleets except one exhibited a clear  
357 relationship between catch rates and either total or spawning stock biomass. Catchability of several  
358 fleets changed with stock size and in two cases, the relationship between catchability and stock size  
359 was monotonically decreasing (corresponding to hyperstability of catch rates). However, in spite of  
360 this negative relationship, the fleets were unable to compensate for the severe decrease in biomass  
361 and catch rate of all fleets decreased as biomass diminished. Except from a barely significantly  
362 positive intercept for English seiners, there was no evidence from any of the fleets of positive  
363 intercepts corresponding to scientific underestimation of stock size. Further, only one fleet exhibited  
364 a significantly negative intercept corresponding to either fishing outside refuges or scientific  
365 overestimation of the stock.

366           Density in high density areas was tightly related to stock size in the North Sea and there  
367 was no evidence of non-proportionality. The lack of aggregation rendered the trawl fleets unable to  
368 maintain constant high densities and, generally, catchability remained constant in these fleets.  
369 Gillnetters often target fish around wrecks and rocks, areas which may support dense fish  
370 aggregations (Gregory and Anderson 1997) and which are unavailable to demersal trawl gears. In  
371 spite of this, catch rates of gillnetters showed a high degree of agreement with trawl catch rates  
372 indicating that density in trawlable and non-trawlable areas co-varied. This agreement may even  
373 have increased in later years as the development of more flexible ground gears has allowed the use  
374 of towed gears on bottom substrates previously unavailable to trawlers. The co-occurrence of a  
375 northern shift in the spatial distribution of gillnet fishing effort and survey catch rates in the main  
376 fishing season also suggests that gillnet catch rates agree with survey catch rates. In contrast, the  
377 distribution of the stock in the 3<sup>rd</sup> quarter inferred from survey catch rates was not generally related

378 to the distribution of effort, indicating either that factors other than cod distribution affects the  
379 distribution of effort in this period or that the shorter time period contained less contrast in the  
380 centres.

381           Persistent high densities in some areas in spite of decreases in stock biomass have been  
382 found in studies of cod both in the northern Gulf of St. Lawrence and northern cod (NAFO areas  
383 3Pn4RS and 2J3KL, respectively) (Rose and Leggett 1991; Rose and Kulka 1999). Presumably as a  
384 result of this decoupling of local density and stock size, the catchability of the cod related trawl  
385 fishery increased in both stocks as stock size declined (Rose and Leggett 1991; Rose and Kulka  
386 1999). Why the aggregative behaviour of North Sea cod differs from that of cod in other areas  
387 remains unknown. Possibly, the North Sea has fewer low-quality habitats as growth rates in this  
388 area have historically been high compared to other areas (Brander 1995). In any event, there was no  
389 evidence of aggregation or of increasing trawl catchability at low stock size.

390           Fleets with a diverse landing composition such as trawlers showed either no or positive  
391 relationships between catchability and stock size whereas specialised cod-directed fleets such as  
392 gillnetters showed negative relationships. This corresponds with what is expected from random  
393 sampling (trawling) and oversampling of high density areas resulting from cod being the target  
394 species (gillnetters). Contrasting results have been seen in other studies of catchability and stock  
395 size of cod as some authors have found inverse relationships between both commercial and survey  
396 catchability and stock size (Winters and Wheeler 1985; Rose and Leggett 1991; Swain et al. 1994)  
397 whereas others found no significant relationships, be it positive or negative (Harley et al. 2001,  
398 Hanchet et al. 2005). Though other authors have suggested that one common pattern for all fleets  
399 targeting a given species should exist (Harley et al. 2001), this seems unlikely as the tendency for  
400 catchability to increase at low stock size is increased by both the aggregative behaviour of the target  
401 species and the degree to which the fishery targets local high density areas (Paloheimo and Dickie

402 1964; Hilborn and Walters 1992; Gaertner and Dreyfus-Leon 2004). The difference between the  
403 conclusions reached may reflect both differences in the aggregative behaviour of the stocks as well  
404 as in the motivation or ability of fishermen to target high density areas. However, the pattern of  
405 constant catchability in mixed species fisheries and increasing catchability with decreasing stock  
406 size in targeted fisheries seen here is likely to be general.

407         The results obtained here can not necessarily be generalised to all North Sea fishing fleets.  
408 Targeting behaviour and hence catchability is influenced by physical constraints such as vessel type  
409 and size, restrictions imposed by management regulation, vessel interactions, information sharing as  
410 well as skipper skills (Gillis et al. 1993; Gillis and Peterman 1998; Gaertner and Dreyfus-Leon  
411 2004) and variation in these decision parameters between fleets and among fishermen within a fleet  
412 will create both temporal and spatial diversity in catchability. Though it cannot be generalised to all  
413 fisheries, the analysis does, however, present the first thorough multi-fleet analyses of North Sea  
414 cod related fisheries and the fleets together cover a significant proportion of the cod landings.

415         The increased catchability of gillnetters at low stock size could be the result of either an  
416 increased aggregation of cod in non-trawlable areas, a correlation between effort allocation and  
417 catchability of individual vessels, a gear saturation effect at high stock sizes or a relationship  
418 between catch rates and effort recorded as cod-targeted. Increased aggregation in non-trawlable  
419 areas seems unlikely as there is a fair agreement between gillnet effort distribution and survey catch  
420 rate distribution, indicating that the two gear types provide comparable estimates of spatial  
421 distribution and therefore most likely also of temporal distribution. A correlation between effort  
422 allocation and catchability of individual vessels could occur if individual differences in cod catch  
423 rates exists due to e.g. differences in skipper skills and gillnetters with low catch rates switch to  
424 other fisheries at low stock size. This would lead to an increase in catchability as less efficient  
425 vessels shift to other species or leave the fishery. Another explanation for changes in catchability

426 which are unrelated to aggregation of the target species could be gear saturation. This would occur  
427 if gillnets become more visible and hence are more easily avoided once some cod have been  
428 entangled. To reveal whether this occurs would require detailed studies of density and avoidance  
429 behaviour around set nets. Lastly, a relationship between catch rates and effort recorded as cod-  
430 targeted could be an artefact caused by the exclusion of gillnet fishing trips where cod was not the  
431 main economic species in the landing. Using this method, the gillnet fleet can maintain apparently  
432 stable catch rates at low stock size, as only those trips where sufficient cod were caught to obtain  
433 the majority of the landing value will be included in the estimate of catch per unit effort. Though  
434 this problems seem to arise due to the definition of cod directed fishing effort, using all fishing  
435 effort as done for the trawl fleets is not without problems either. In this case, one obtains an over-  
436 occurrence of low or zero catches of cod (corresponding to an overestimation of effort) as trawl  
437 trips performed in areas uninhabitable by cod and with different gear deployment are included. This  
438 problem is likely to increase as cod stock size decreases and more restrictive catch quotas decrease  
439 the motivation to target cod. Nevertheless, we believe the definitions used (targeted gillnet fishery  
440 and non-targeted trawl and seine fishery) present the least bias among the two alternatives, given  
441 that the actual species targeted is unknown.

442           The low correlation between stock size and catch rates observed in Danish seiners may be  
443 caused by several factors. Firstly, over 90% of the Danish seine vessels have been decommissioned  
444 during the study period (>500 in 1983 to 47 vessels in 2005), primarily due to a combination of a  
445 dramatic decline in the quotas of both cod and other target species and a lack of cod in the southern  
446 part of the North Sea where the majority of the Danish seine fleet traditionally had their home  
447 harbour. Most likely, the decommissioning has caused a permanent loss of the least efficient vessels  
448 (low catchability vessels) from the fishery. Furthermore, the Danish seine fishery in contrast to the  
449 other Danish fisheries investigated is primarily a summer fishery and catch success depends heavily

450 on weather conditions.

451           The residuals show no evidence of increased catchability (technical creep) or increased  
452 misreporting in later years. The fishery has been severely reduced since the implementation of the  
453 North Sea cod recovery plan in 2001 and this could have caused both bias and increased variation in  
454 reported catch rates within this period. They should have expressed themselves as either consistent  
455 directional deviations from the average relationship between catch rates and stock size or as  
456 increases in the variation around the relationship in years with restrictive quotas. Nevertheless, there  
457 was no tendency for variation in the residuals to increase or exhibit trends in later years (Fig. 8).  
458 Furthermore, there was only minor changes in the parameters of the models if the years from 2001  
459 onwards were excluded from the estimation procedure (results not shown), and hence the results  
460 given here did not appear to be greatly biased by misreporting in later years.

461           As catch per unit effort of the modelled fleets was highly correlated to stock biomass, the  
462 fleets fulfil two of the requirements to an abundance estimate (unbiased residuals and high  
463 correlation). These catch per unit effort series may thus be the solution to the need for industry-  
464 based series of North Sea cod abundance as a supplement to survey series described by Horwood et  
465 al. (2006). However, for these series to be reliable, it must be assured that discard, misreporting of  
466 effort and catch and fishing power does not increase in the future.

467           A central question from a management point of view is whether any of the fleets examined  
468 here would seriously diminish the population if not regulated restrictively. Assuming that the total  
469 landings of each fleet provide reliable estimates of catches, this problem is evident by the observed  
470 increase in catch divided by total stock biomass as stock biomass decreased up to the year 2000  
471 (Fig. 10). Note that catch of a fleet divided by total stock size is proportional to the partial fishing  
472 mortality induced by that fleet if the ratio between average weight of cod in the catch and in the  
473 stock remains constant. The severe decrease in total allowable catch appears to have reduced at least

474 official landings per biomass by about 50% whereas the regulations prior to this period does not  
475 appear to have reduced fishing mortality. Though ICES suggests that the decrease in the observed  
476 fishing mortality may partly have been abated by a larger unspecified mortality in later years (ICES  
477 2006), Horwood et al. (2006) estimated a decrease in cod fishing effort of 37% from 2000 to 2004.  
478 The discrepancy between these two estimates of cannot be explained at present. However, it is clear  
479 that in the absence of the severe reductions in total allowable catch, there would have been a further  
480 increase in fishing mortality as stock size decreased, thereby accelerating the decline of the already  
481 threatened cod stock.

## 482 **Acknowledgements**

483 This work was funded by the national project REX1 (funded by the Danish Ministry of Food,  
484 Agriculture and Fishery), and of the EU project CAFÉ (Capacity, F and Effort). The results and  
485 conclusions drawn do not necessarily reflect the views of the sponsors. Clara Ulrich and two  
486 anonymous referees provided valuable comments on an earlier draft.

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552 Table 1. Definition of Danish cod fishing fleets and cod related fisheries.

Fleet	Vessel length (m)	Gear	Mesh size (mm)	Target species*	Avg. % of total Danish cod landings**
Danish small trawlers	0-20	OTB/Pair trawl	90 -140	-	5%
Danish large trawlers	20-40	OTB/Pair trawl	90 -140	-	16%
Danish small gillnetters	0-20	Gillnet and line	90- 200	Cod	36%
Danish large gillnetters	20-40	Gillnet and line	90- 200	Cod	9%
Danish Seine	All	Danish and Scottish seine	90 – 150	-	16%

553 \*Defined as the most important species by value, -=not defined. \*\* Based on landings statistics

554 from 1990 to 2005

555

556 Table 2. Correlation between catch per unit effort and total stock biomass (*T*), spawning stock  
557 biomass (*S*) from stock assessment and total and mature cod survey catch rate within high density  
558 areas. Values in parentheses denote probability of no correlation. Significant correlations ( $P < 0.05$ )  
559 are in bold.

	Quarter	Stock		High density survey	
		<i>T</i>	<i>S</i>	<i>Total cod</i>	<i>Mature cod</i>
Danish small trawlers	1	<b>0.60</b> <sup>(0.0023)</sup>	<b>0.77</b> <sup>(&lt;0.0001)</sup>	<b>0.72</b> <sup>(&lt;0.0001)</sup>	<b>0.53</b> <sup>(0.0089)</sup>
Danish small trawlers	3	<b>0.77</b> <sup>(&lt;0.0001)</sup>	<b>0.84</b> <sup>(&lt;0.0001)</sup>		
Danish large trawlers	1	<b>0.69</b> <sup>(0.0002)</sup>	<b>0.80</b> <sup>(&lt;0.0001)</sup>	<b>0.84</b> <sup>(&lt;0.0001)</sup>	<b>0.68</b> <sup>(0.0003)</sup>
Danish large trawlers	3	<b>0.62</b> <sup>(0.0014)</sup>	<b>0.81</b> <sup>(&lt;0.0001)</sup>		
English trawlers	All	<b>0.67</b> <sup>(&lt;0.0001)</sup>	<b>0.53</b> <sup>(0.0037)</sup>		
Danish small gillnetters	1	<b>0.83</b> <sup>(&lt;0.0001)</sup>	<b>0.90</b> <sup>(&lt;0.0001)</sup>	<b>0.77</b> <sup>(&lt;0.0001)</sup>	<b>0.67</b> <sup>(0.0005)</sup>
Danish small gillnetters	3	<b>0.80</b> <sup>(&lt;0.0001)</sup>	<b>0.86</b> <sup>(&lt;0.0001)</sup>		
Danish large gillnetters	1	<b>0.73</b> <sup>(&lt;0.0001)</sup>	<b>0.85</b> <sup>(&lt;0.0001)</sup>	<b>0.77</b> <sup>(&lt;0.0001)</sup>	<b>0.74</b> <sup>(&lt;0.0001)</sup>
Danish large gillnetters	3	<b>0.81</b> <sup>(&lt;0.0001)</sup>	<b>0.77</b> <sup>(&lt;0.0001)</sup>		
Danish seine	1	0.29 <sup>(0.1831)</sup>	0.189 <sup>(0.3757)</sup>	0.34 <sup>(0.1168)</sup>	0.17 <sup>(0.4447)</sup>
Danish seine	3	<b>0.42</b> <sup>(0.0484)</sup>	<b>0.42</b> <sup>(0.0489)</sup>		
English seiners	All	<b>0.91</b> <sup>(&lt;0.0001)</sup>	<b>0.79</b> <sup>(&lt;0.0001)</sup>		
IBTS	1	<b>0.88</b> <sup>(&lt;0.0001)</sup>	<b>0.88</b> <sup>(&lt;0.0001)</sup>		
High density survey	1	<b>0.85</b> <sup>(&lt;0.0001)</sup>	<b>0.77</b> <sup>(&lt;0.0001)</sup>		

560

561

Table 3. Probability of the parameters  $b$  and  $c$  being zero and final models (including only significant parameters) of catch per unit effort ( $U$ ) in either  $\text{kg} \cdot \text{day}^{-1}$  (Danish fleets) or  $\text{kg} \cdot \text{hour}^{-1}$  (English fleets and surveys) as a function of total stock ( $T$ ) or spawning stock ( $S$ ) biomass (both in  $10^9$  kg). Probabilities significant at the 0.05-level are in bold. Values in parentheses denote standard error of the estimates.

Fleet	$P(b=0 c \neq 0)$	$P(c=0 b \neq 0)$	$\dagger: P(b=0 c=0)$ or $\dagger: P(c=0 b=0)$	Final model	$r^2$
<b>Quarter 1</b>					
Danish small trawlers	0.5063	0.2734	0.1980 $\dagger$	$U = 4.91^{(0.42)} S$	0.56
Danish large trawlers	0.3060	0.4954	0.2689 $\dagger$	$U = 5.05^{(0.33)} S$	0.64
Danish small gillnetters	0.2803	0.8825	<b>&lt;0.0001</b> $\dagger$	$U = 4.55^{(0.81)} S^{0.62^{(0.07)}}$	0.81
Danish large gillnetters	0.5242	0.9724	<b>0.0124</b> $\dagger$	$U = 8.26^{(2.12)} S^{0.71^{(0.10)}}$	0.73
Total cod survey catch rate in high density areas	0.5413	0.8036	0.1295 $\dagger$	$U = 0.348^{(0.017)} T$	0.72
Mature cod survey catch rate in high density areas	0.4357	0.5130	0.6177 $\dagger$	$U = 0.772^{(0.052)} S$	0.61
<b>Quarter 3</b>					
Danish small trawlers	0.7541	0.5770	<b>0.0488</b> $\dagger$	$U = 4.53^{(0.65)} S - 0.110^{(0.054)}$	0.70
Danish large trawlers	0.1071	0.2624	0.1090 $\dagger$	$U = 3.38^{(0.23)} S$	0.64
Danish small gillnetters	0.6435	0.7493	<b>0.0004</b> $\dagger$	$U = 3.61^{(0.77)} S^{0.62^{(0.09)}}$	0.75
Danish large gillnetters	0.7017	0.7069	<b>0.0009</b> $\dagger$	$U = 4.27^{(1.14)} S^{0.56^{(0.11)}}$	0.60

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**Yearly average**

English trawlers	0.5300	0.7296	0.1892 <sup>†</sup>	$U = 0.117^{(0.009)}T$	0.43
English seiners	<b>&lt;0.0001</b>	<b>0.0449</b>	-	$U = 0.205^{(0.014)}T^{2.54^{(0.29)}}$ $+ 0.021^{(0.009)}$	0.93

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569 Table 4. Trends (Pearson correlation coefficient with year) in latitude north (*lat*) and longitude east  
570 (*lon*) of effort centre of gravity and correlation between survey and effort centre of gravity. Values  
571 in parentheses denote probability of no correlation. Significant correlations are in bold.

Fleet	Trend				Correlation between survey and effort centre			
	Quarter 1		Quarter 3		Quarter 1		Quarter 3 <sup>a</sup>	
	<i>lat</i>	<i>lon</i>	<i>lat</i>	<i>lon</i>	<i>Lat</i>	<i>Lon</i>	<i>lat</i>	<i>Lon</i>
Danish small trawlers	<b>0.60</b> (0.0026)	<b>0.43</b> (0.0398)	<b>-0.66</b> (0.0006)	<b>0.67</b> (0.0005)	0.25 (0.2478)	0.02 (0.9234)	-0.34 (0.2218)	-0.02 (0.9566)
Danish large trawlers	<b>0.48</b> (0.0217)	0.41 (0.0539)	0.03 (0.9088)	<b>0.43</b> (0.0406)	0.37 (0.0795)	0.27 (0.2200)	<b>0.69</b> (0.0040)	0.17 (0.5534)
Danish small gillnetters	<b>0.65</b> (0.0007)	<b>0.97</b> (<0.0001)	<b>0.50</b> (0.0153)	<b>0.88</b> (<0.0001)	<b>0.63</b> (0.0014)	<b>0.59</b> (0.0030)	<b>0.72</b> (0.0028)	0.30 (0.2728)
Danish large gillnetters	<b>0.68</b> (0.0004)	<b>0.78</b> (<0.0001)	-0.19 (0.3877)	<b>0.80</b> (<0.0001)	<b>0.61</b> (0.0019)	<b>0.73</b> (<0.0001)	-0.02 (0.9563)	0.51 (0.0522)
Danish seine	<b>0.77</b> (<0.0001)	0.29 (0.1855)	0.05 (0.8109)	-0.11 (0.6021)	<b>0.74</b> (<0.0001)	0.41 (0.0538)	0.49 (0.0611)	0.35 (0.1991)
Survey	<b>0.73</b> (<0.0001)	<b>0.55</b> (0.0050)	<b>0.76</b> (0.0011)a	0.23 (0.4103)a				

572 <sup>a</sup>Based on data from 1991 to 2005

573

572 **Figure captions**

573 Fig. 1. Study area. Small rectangles are ICES statistical rectangles.

574 Fig. 2. Relationship between catch per unit effort ( $U$ ) and biomass ( $B$ ) (a) and catchability ( $U/B$ ) (b)

575 for different parameterisations of the model  $U = aB^{(1+b)} + c$ . ■:  $b=c=0$ ; ▲:  $b=0, c>0$ ; ◆:  $b=0, c<0$ ;

576 ■:  $0<b<1; c=0$  and □:  $b>0, c=0$ .

577 Fig. 3. Temporal development in North Sea cod total stock biomass (solid line) and spawning stock  
578 biomass (broken line).

579 Fig. 4. Temporal development in yearly effort (a and b) and yearly average catch per unit effort (c  
580 and d) of the seven fleets examined. Right axis refers to Danish fleets, left axes to English fleets. a

581 and c: Danish small trawlers (+), Danish large trawlers (■), and English trawlers (▲). b and d:

582 Danish small gillnetters (▲), Danish large gillnetters (×), Danish seine (■) and English seine (+).

583 Fig. 5. Cod catch composition of the different fleets (yearly average by weight). Mature (■), mixed

584 mature and immature (■) and immature (□) cod. A: Danish small trawlers, B: Danish large

585 trawlers, C: Danish small gillnetters, D: Danish large gillnetters, E: Danish seine, F: English

586 trawlers and G: English seine.

587 Fig. 6. Relationship between catch per unit effort and stock biomass (a and b) or spawning stock

588 biomass (c, d, e, f and g). Values for Danish fleets refer to the 1<sup>st</sup> quarter. English trawlers (a),

589 English seiners (b), Danish small trawlers (c), Danish large trawlers (d), Danish small gillnetters (e),

590 Danish large gillnetters (f) and Danish seine (g). Lines are fitted models (se Table 3) for all fleets

591 except Danish seiners where a linear regression was used (no model was fitted for this fleet).

592 Fig. 7. Relationship between catchability and stock biomass (a and b) or spawning stock biomass (c,

593 d, e, f and g). English trawlers (a), English seiners (b), Danish small trawlers in the first quarter (c),

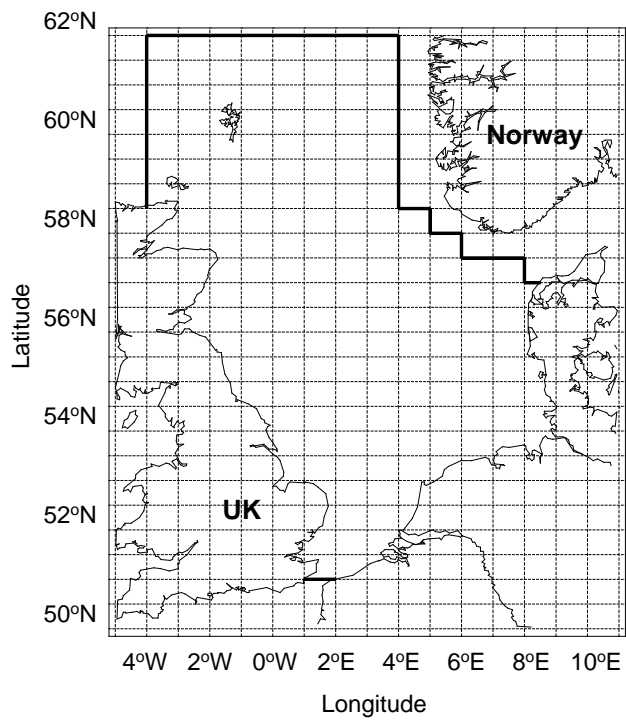


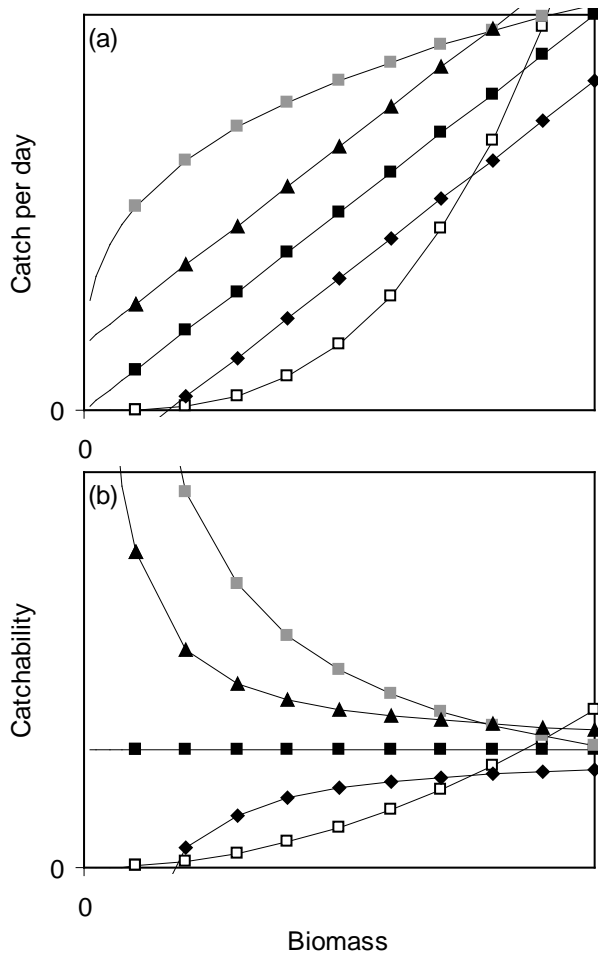
594 Danish small trawlers in the third quarter (d), Danish small gillnetters in the first quarter (e) and  
595 Danish large gillnetters in the first quarter (f). Lines are catchabilities estimated as predicted catch  
596 per unit effort from fitted models (se Table 3) divided by biomass.

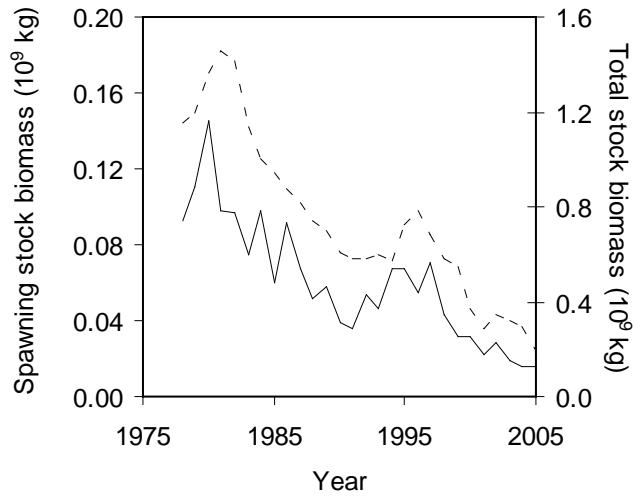
597 Fig. 8. Residuals of fitted models (observed catch per unit effort-model predicted catch per unit  
598 effort). a: English trawlers (▲) and seiners (△), b: Danish small (△) and large (▲) trawlers and c:  
599 Danish small (△) and large (▲) gillnetters.

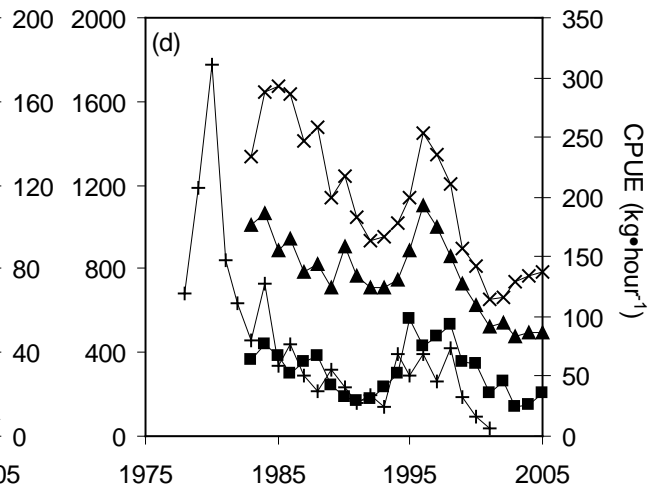
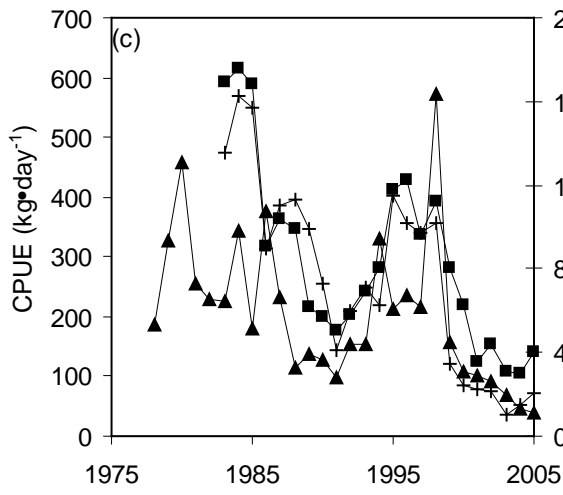
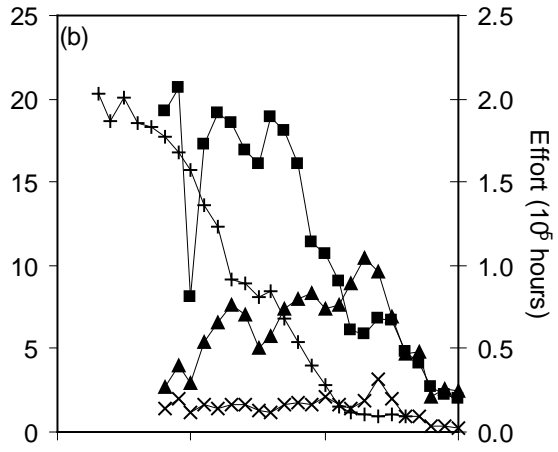
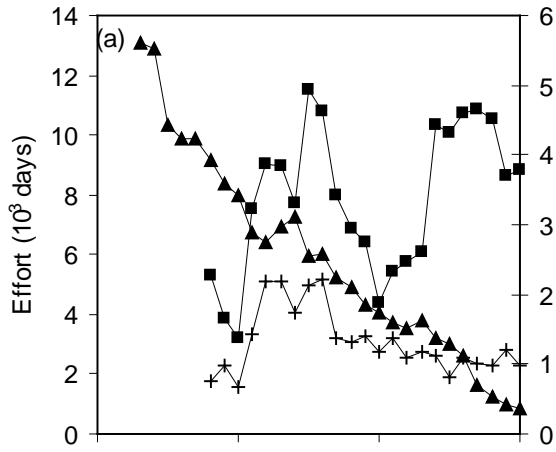
600 Fig. 9. Relationship between survey catch rate of all (a) and mature (b) cod in high density areas  
601 and total stock (a) and spawning stock biomass (b). Lines are fitted models (se Table 3).

602 Fig. 10. Relationship between harvest rate (yearly landings/stock biomass) and stock biomass. a:  
603 English (△ and ▲) and Scottish (□ and ■) landings and b: Danish (△ and ▲) and other  
604 international (□ and ■) landings. Solid and empty symbols denote the period before and after the  
605 introduction of restrictive quotas in 2001, respectively. Lines are linear regressions for the period  
606 before 2001.









Year

