

Technical University of Denmark



Do North Sea cod (*Gadus morhua*) fisheries maintain high catch rates at low stock size?

Rindorf, Anna; Andersen, Bo Sølgaard

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

DTU Library

Technical Information Center of Denmark

General rights

Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from the public portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain
- You may freely distribute the URL identifying the publication in the public portal

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

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

3 **Anna Rindorf^{1*} and Bo Sølgaard Andersen²**

4 ¹Danish Technical University, Danish Institute for Fisheries Research, Charlottenlund Castle,
5 DK2920 Charlottenlund, Denmark, Email: ar@difres.dk

6 ²Danish Technical University, Danish Institute for Fisheries Research, The North Sea Centre, P.O.
7 Box 101, DK9850 Hirtshals, Denmark, Email: bsa@difres.dk

8 *Corresponding author. Telephone: +45 33 96 33 59, fax: +45 33 96 33 33

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 1st and 3rd 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 1st 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 1st 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 1st

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[®] 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 1st quarter of 1983 to 2006 and the 3rd quarter of 1991 to 2005. The 3rd
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 1st and 3rd 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 1st and 3rd quarter and Danish large gillnetters
306 in the 1st and 3rd 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 3rd quarter and English seiners (Table 3). Danish small trawlers showed negative intercepts in
311 both quarters, but only the 3rd 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 3rd
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 1st 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 1st and 3rd 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 3rd 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 3rd 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 1st
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 3rd 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 1st 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 3rd 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 3rd 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.

487 **References**

- 488 Bannerot, S. P., and Austin, C. B. 1983. Using frequency distributions of catch per unit effort to
489 measure fish abundance. *Trans. Am. Fish. Soc.* **112**: 608-617.
- 490 Beaugrand, G., Brander, K. M., Lindley, J. A., Souissi, S., and Reid, P. C. 2003. Plankton effect on
491 cod recruitment in the North Sea. *Nature* **426**: 661-664.
- 492 Blanchard, J. L., Mills, C., Jennings, S., Fox, C. J., Rackham, B. D., Eastwood, P. D., and O'Brien,
493 C. M. 2005. Distribution-abundance relationships for North Sea Atlantic cod (*Gadus*
494 *morhua*): observation versus theory. *Can. J. Fish. Aquat. Sci.* **62**: 2001-2009.
- 495 Brander, K. 1995. The effect of temperature on growth of Atlantic cod (*Gadus morhua* L.). *ICES J.*
496 *Mar. Sci.*, **52**: 1-10.

- 497 Cook, R. M., and Armstrong, D. W. 1985. Changes in catchability of cod, haddock, and whiting
498 associated with the Scottish seine-net fleet. *J. Cons. Int. Explor. Mer* **42**: 171-178.
- 499 Crecco, V., and Overholtz, W. J. 1990. Causes of density-dependent catchability for Georges Bank
500 haddock *Melanogrammus aeglefinus*. *Can. J. Fish. Aquat. Sci.* **47**: 385-394.
- 501 Gaertner, D. and Dreyfus-Leon, M. 2004. Analysis of non-linear relationships between catch per
502 unit effort and abundance in a tuna purse-seine fishery simulated with artificial neural
503 networks. *ICES J. Mar. Sci.* **61**: 812-820.
- 504 Gerritsen, H. D., McGrath, D., and Lordan, C. 2006. A simple method for comparing age-length
505 keys reveals significant regional differences within a single stock of haddock
506 (*Melanogrammus aeglefinus*). *ICES J. Mar. Sci.* **63**: 1096-1100.
- 507 Gillis, D. M., and Peterman, R. M. 1998. Implications of interference among fishing vessels and the
508 ideal free distribution to the interpretation of CPUE. *Can. J. Fish. Aquat. Sci.* **55**: 37-46.
- 509 Gillis, D. M., Peterman, R. M., and Tyler, A. V. 1993. Movement dynamics in a fishery: application
510 of the ideal free distribution to spatial allocation of effort, *Can. J. Fish. Aquat. Sci.* **50**: 323-
511 333.
- 512 Gregory, R. S., and Anderson, J. T. 1997. Substrate selection and use of protective cover by
513 juvenile Atlantic cod *Gadus morhua* in inshore waters of Newfoundland. *Mar. Ecol. Prog.*
514 *Ser.* **146**: 9-20.
- 515 Hanchet, S. M., Blackwell, R. G., and Dunn, A. 2005. Development and evaluation of catch per unit
516 effort indices for southern blue whiting (*Micromesistius australis*) on the Cambell Island
517 Rise, New Zealand. *ICES J. Mar. Sci.* **62**: 1131-1138.
- 518 Harley, S. J., Myers, R. A., and Dunn, A. 2001. Is catch-per-unit-effort proportional to abundance?
519 *Can. J. Fish. Aquat. Sci.* **58**: 1760-1772.
- 520 Hilborn, R., and Walters, C. J. 1992. Quantitative fisheries stock assessment: choice, dynamics and

521 uncertainty. Chapman and Hall, New York.

522 Horwood, J., O'Brien, C., and Darby, C. 2006. North Sea cod recovery? ICES J. Mar. Sci. **63**: 961-
523 968.

524 ICES 2006. Report of the working group on the assessment of demersal stocks in the North Sea and
525 Skagerrak (WGNSSK). ICES CM 2006/ACFM:35

526 O'Brien, C. M., Fox, C. J., Planque, B., and Casey, J. 2000. Climate variability and North Sea cod.
527 Nature **404**: 142.

528 Paloheimo, J. E., and Dickie, L. M. 1964. Abundance and fishing success. Rapp. R-V. Reun. Cons.
529 Int. Explor. Mer **155**: 152-163.

530 Perry, A. L., Low, P. J., Ellis, J. R., and Reynolds, J. D. 2005. Climate change and distribution
531 shifts in marine fishes. Science **308**: 1912–1915.

532 Rindorf, A., and Lewy, P. 2001. Analyses of length and age distributions using continuation- ratio
533 logits. Can. J. Fish. Aquat. Sci. **58**: 1141-1152.

534 Rindorf, A., and Lewy, P. 2006. Warm, windy winters drive cod north and homing of spawners
535 keeps them there. J. Appl. Ecol. **43**: 445-453.

536 Rindorf, A., Jensen, H., and Schrum, C. 2007. Growth, temperature and density relationships of
537 North Sea cod. In press, Can. J. Fish. Aquat. Sci.

538 Rose, G. A., and Kulka, D. W. 1999. Hyperaggregation of fish and fisheries: how catch-per-unit-
539 effort increased as the northern cod (*Gadus morhua*) declined. Can. J. Fish. Aquat. Sci. **56**
540 (**S1**): 118-127.

541 Rose, G. A., and Leggett, W. C. 1991. Effects of biomass-range interactions on catchability of
542 migratory demersal fish by mobile fisheries: An example of Atlantic cod (*Gadus morhua*).
543 Can. J. Fish. Aquat. Sci. **48**: 843-848.

544 SAS Institute Inc. 2001. SAS version 8.12 [computer program]. SAS Institute Inc., Cary, North

- 545 Carolina.
- 546 Swain, D. P., Nielsen, G. A., Sinclair, A. F., and Chouinard, G. A. 1994. Changes in catchability of
547 Atlantic cod (*Gadus morhua*) to an otter-trawl fishery and research survey in the southern
548 Gulf of St Lawrence. ICES J. Mar. Sci. **51**: 493-504.
- 549 Winters, G. H., and Wheeler, J. P. 1985. Interaction between stock area, stock abundance, and
550 catchability coefficient. Can. J. Fish. Aquat. Sci. **42**: 989-998.
- 551 Ulrich, C., and Andersen, B. S. 2004. Dynamics of fisheries, and the flexibility of vessel activity in
552 Denmark between 1989 and 2001. ICES J. Mar. Sci. **61**: 308-322.

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	0.60 ^(0.0023)	0.77 ^(<0.0001)	0.72 ^(<0.0001)	0.53 ^(0.0089)
Danish small trawlers	3	0.77 ^(<0.0001)	0.84 ^(<0.0001)		
Danish large trawlers	1	0.69 ^(0.0002)	0.80 ^(<0.0001)	0.84 ^(<0.0001)	0.68 ^(0.0003)
Danish large trawlers	3	0.62 ^(0.0014)	0.81 ^(<0.0001)		
English trawlers	All	0.67 ^(<0.0001)	0.53 ^(0.0037)		
Danish small gillnetters	1	0.83 ^(<0.0001)	0.90 ^(<0.0001)	0.77 ^(<0.0001)	0.67 ^(0.0005)
Danish small gillnetters	3	0.80 ^(<0.0001)	0.86 ^(<0.0001)		
Danish large gillnetters	1	0.73 ^(<0.0001)	0.85 ^(<0.0001)	0.77 ^(<0.0001)	0.74 ^(<0.0001)
Danish large gillnetters	3	0.81 ^(<0.0001)	0.77 ^(<0.0001)		
Danish seine	1	0.29 ^(0.1831)	0.189 ^(0.3757)	0.34 ^(0.1168)	0.17 ^(0.4447)
Danish seine	3	0.42 ^(0.0484)	0.42 ^(0.0489)		
English seiners	All	0.91 ^(<0.0001)	0.79 ^(<0.0001)		
IBTS	1	0.88 ^(<0.0001)	0.88 ^(<0.0001)		
High density survey	1	0.85 ^(<0.0001)	0.77 ^(<0.0001)		

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
Quarter 1					
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	<0.0001 \dagger	$U = 4.55^{(0.81)} S^{0.62^{(0.07)}}$	0.81
Danish large gillnetters	0.5242	0.9724	0.0124 \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
Quarter 3					
Danish small trawlers	0.7541	0.5770	0.0488 \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	0.0004 \dagger	$U = 3.61^{(0.77)} S^{0.62^{(0.09)}}$	0.75
Danish large gillnetters	0.7017	0.7069	0.0009 \dagger	$U = 4.27^{(1.14)} S^{0.56^{(0.11)}}$	0.60

Yearly average

English trawlers	0.5300	0.7296	0.1892 [†]	$U = 0.117^{(0.009)}T$	0.43
English seiners	<0.0001	0.0449	-	$U = 0.205^{(0.014)}T^{2.54^{(0.29)}}$ $+ 0.021^{(0.009)}$	0.93

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

572 ^aBased 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 1st 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,

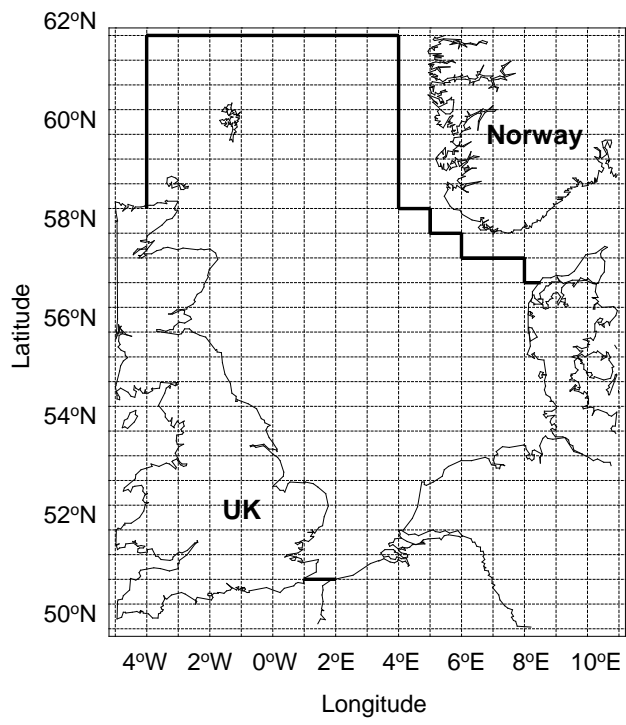
593 d, e, f and g). English trawlers (a), English seiners (b), Danish small trawlers in the first quarter (c),

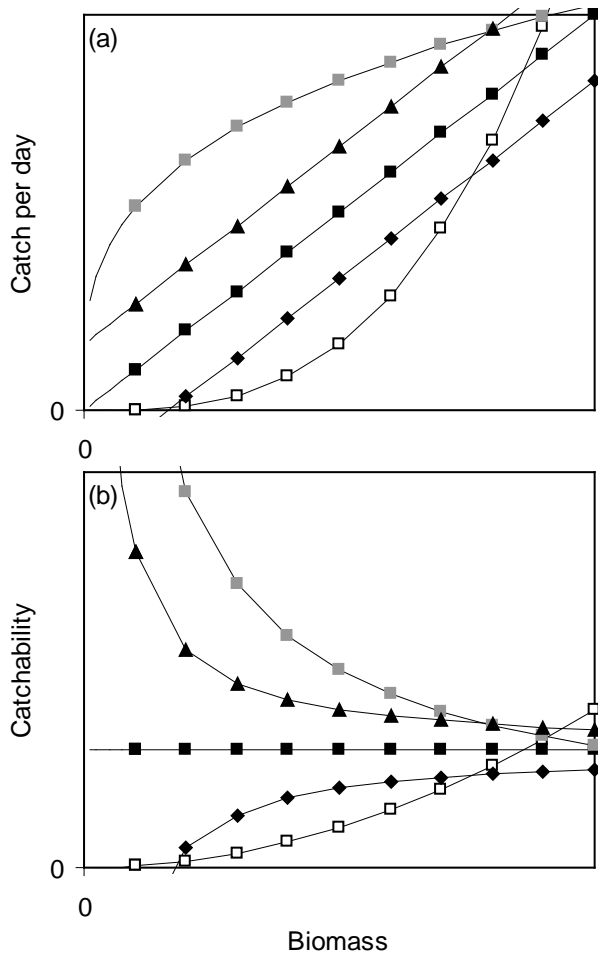
594 Danish small trawlers in the third quarter (d), Danish small gillnetters in the first quarter (e) and
595 Danish large gillnetters in the first quarter (f). Lines are catchabilities estimated as predicted catch
596 per unit effort from fitted models (se Table 3) divided by biomass.

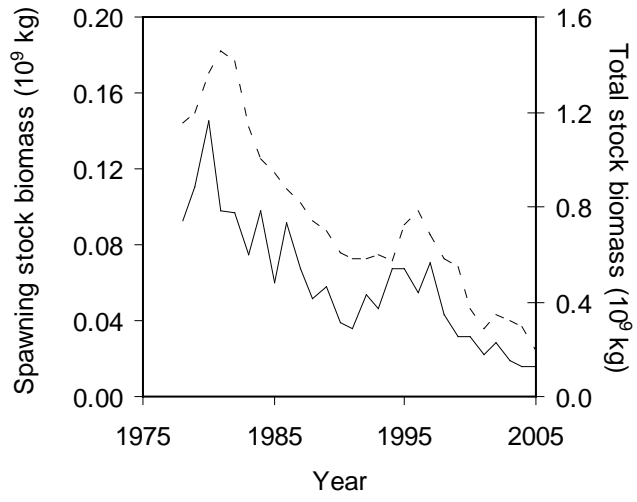
597 Fig. 8. Residuals of fitted models (observed catch per unit effort-model predicted catch per unit
598 effort). a: English trawlers (▲) and seiners (△), b: Danish small (△) and large (▲) trawlers and c:
599 Danish small (△) and large (▲) gillnetters.

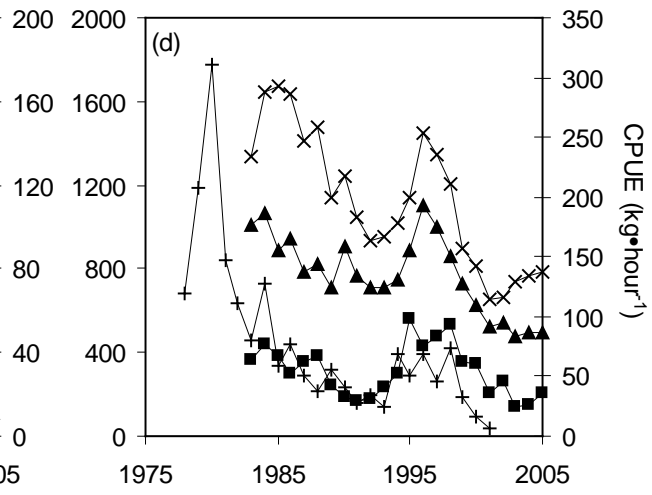
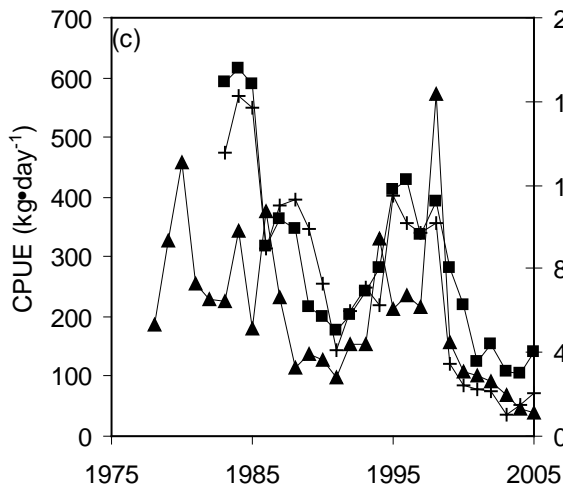
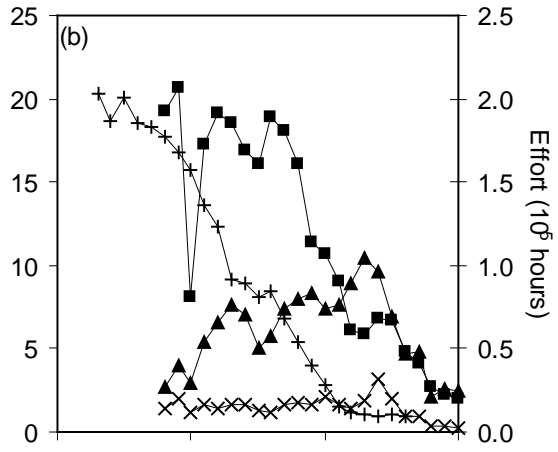
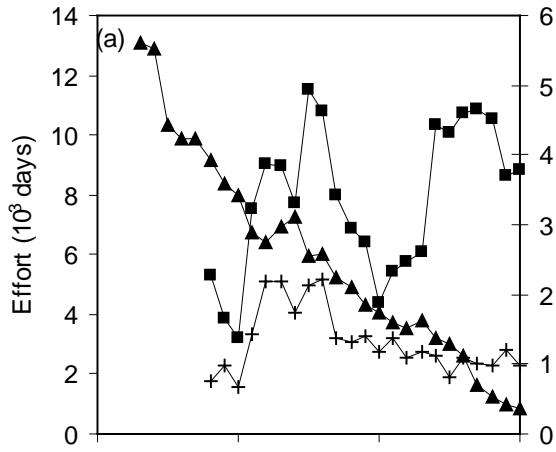
600 Fig. 9. Relationship between survey catch rate of all (a) and mature (b) cod in high density areas
601 and total stock (a) and spawning stock biomass (b). Lines are fitted models (se Table 3).

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

