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1 **Growth, temperature and density relationships of North Sea**

2 **cod**

3

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11

12 **Abstract**

13 This study presents an analysis of the relationship between ambient temperature, cod density,
14 fishing mortality, prey fish biomass and growth of North Sea cod (*Gadus morhua*) as estimated
15 from survey catches during the period from 1983 to 2006. Growth of young cod was positively
16 related to temperature, but though temperature has increased, distribution of 1-year olds has
17 changed concurrently, and no increase in length at age 1 has occurred. Growth from age 1 to 2 has
18 decreased as ambient biomass of sandeel and density of cod has decreased whereas growth of cod
19 older than 2 years decreased with increasing density of cod and increased with increasing biomass
20 of demersal fish prey. Though growth of juveniles was strongly positively correlated to ambient
21 temperature, no indication of direct temperature limitation of growth of older North Sea cod was
22 found.

23

24 Key words: Growth, cod, prey abundance, temperature, North Sea

25

26 **Introduction**

27 The scope for somatic growth of fish is determined by temperature and food abundance (Brett
28 1979). This has led to the expectation that growth rate is likely to increase if a stock experiences
29 increased temperatures (Brander 1995; Dutil et al. 1999) as food-unlimited growth is positively
30 related to temperature below a certain level (Jobling 1988; Björnsson and Steinarsson 2002). In
31 North Atlantic cod (*Gadus morhua*) stocks, the expectation of increased growth with increasing
32 temperature is supported by a high correlation between average ambient temperature of the stock
33 and size at age (Brander 1995; Campana et al. 1995). However, an analysis of the relationship
34 between temperature and length at age in the North Atlantic does not reveal whether temperature
35 acts directly on growth or indirectly through increasing food abundance. It remains an open
36 question whether the relationship is retained locally and whether it affects growth up to a certain
37 age only or is present throughout the lifetime of the fish. These aspects have important implications
38 for management. Predictions of the effect of altered growth rates on exploitation rates have mostly
39 focused on the beneficial effect of sustained growth increases on maximum sustainable yield
40 (Steinarsson and Stefánsson 1996; Rätz and Lloret 2003). However, if increased growth is only
41 exhibited by juveniles, the beneficial effect may be at least partly abated by the decreased efficiency
42 of technical measures aimed at limiting catches of juveniles (Pinhorn and Halliday 2001). If
43 increased growth of juveniles is furthermore followed by a decreased growth of old fish as seen in
44 Northeast Arctic cod (Michalsen et al. 1998), the combined effect may be a decrease in the level of
45 mortality the stock can sustain.

46 A stock which is currently facing the combined challenges of climatic changes, unsustainable
47 exploitation and a decrease in the biomass of important fish prey is the North Sea cod stock. Over
48 the past 20 years, recruitment has decreased severely, possibly due to a combination of a declining
49 spawning stock biomass, increasing temperatures and changes in the zooplankton community

50 (O'Brien et al. 2000; Beaugrand et al. 2003). In addition to this, the stock has moved northwards
51 within the North Sea (Hedger et al. 2004; Perry et al. 2005; Rindorf and Lewy 2006), a movement
52 which seems to be caused by poorer recruitment in southern areas (Rindorf and Lewy 2006). The
53 shift in distribution may have decreased average growth rate, as growth in northern areas is slower
54 than in southern areas (Graham 1934; Daan 1974; Rijnsdorp et al. 1991). Furthermore, the
55 distributional change may have limited the effect of the general increase in temperatures over this
56 period (O'Brien et al. 2000), possibly abating any effect of temperature on growth, as there does not
57 appear to be a clear correlation between average North Sea bottom temperature and weight of adult
58 North Sea cod in the commercial catch (Clark et al. 2003). This suggests that the effect of
59 temperature on growth has been limited thus far. Four of the most important fish prey of North Sea
60 cod, namely Norway pout, sandeel, young whiting and young herring (Kikkert 1993), have
61 decreased severely since the year 2000 (ICES 2005, 2006).

62 This study had three objectives: firstly, to investigate the changes in growth of North Sea cod
63 over the past 20 years, secondly to determine if the observed changes were related to temperature
64 and thirdly to determine whether growth was likely to be limited by prey fish biomass, cod density
65 or fishing mortality. The shape of the relationship between growth and these variables depends on
66 the life stage. Temperature thus affects growth of small cod differently from growth of large cod
67 (Björnsson and Steinarsson 2002) and ontogenetic changes in diet composition (Kikkert 1993) leads
68 to differences between life stages in the effect of the biomass of a specific prey. Therefore, the
69 study was divided into three: an analysis of juvenile cod feeding mainly on invertebrates, an
70 analysis of cod in the transition period between an invertebrate dominated diet and a piscivorous
71 diet and an analysis of predominantly piscivorous cod.

72 **Methods**

73 **Study area**

74 The study area was confined to the area of the North Sea within 51°N and 62°N latitude and
75 4°W and 9°E longitude (Fig. 1). The areas northeast of 57.5°N and 8°E and areas deeper than 200 m
76 were not sampled by the surveys and therefore excluded from the analyses. |

77 **Survey data**

78 Data on cod, clupeids and demersal fish prey were derived from catches in the English and
79 Scottish Groundfish Surveys (August/September 1983 to 1990) and in the ICES International
80 Bottom Trawl Survey (ICES International Bottom Trawl Survey Database, February 1983 to 2006
81 and August/September 1991 to 2005). The surveys use demersal trawls to sample the abundance of
82 fish. Total catch and length composition of the majority of species is recorded in each haul. Haul
83 duration generally varies between 0.5 and 1 hour, and all catch rates are standardised to hourly
84 values. On average, two trawl hauls are conducted within each ICES statistical rectangle (0.5°
85 latitude times 1° longitude, Fig. 1). The sampling intensity and spatial coverage of the 3rd quarter
86 surveys increased in 1991, and areas just off the coasts on the eastern side of the North Sea were not
87 covered in the 3rd quarter prior to this year. Additionally, the English Groundfish Survey used a
88 Granton Trawl up to 1992. This trawl has been shown to have a low efficiency in catching small
89 fish (Lewy et al. 2004).

90 Cod age-length keys were estimated using the method suggested by Rindorf and Lewy
91 (Rindorf and Lewy 2001; Gerritsen et al. 2006). Age-length keys were estimated separately for each
92 of 8 ICES roundfish sampling areas (ICES 1996, Fig. 1) where the number of fish aged was
93 sufficient (Appendix). For the remaining areas, a common age-length key was estimated for
94 combined two-roundfish areas (1 and 3, 2 and 4, 5 and 6 and 7 and 8). If this did not result in a

95 sufficient number of observations, a common age-length key for the entire North Sea was used.
96 Details of the estimation can be found in the Appendix. All fish ages were measured in years from
97 February in the year of spawning and hence the age of a cod with one winter ring caught in
98 September will be 1.5 years.

99 **Length at age**

100 The mean length at age a in a year y and season s , $\bar{l}_{a,y,s}$, was calculated by first estimating the
101 average length of the age group within each statistical rectangle r , $\bar{l}_{a,y,s,r}$. $\bar{l}_{a,y,s}$ was then estimated as
102 the average of $\bar{l}_{a,y,s,r}$ weighted by the average number of cod of age a caught per haul in rectangle r
103 in year y and season s , $n_{a,y,s,r}$. In cases where $\sum_r n_{a,y,s,r} < 10$, no mean length at age was estimated.

104 **Density and fishing mortality**

105 To investigate density dependent growth, an index of the density of age-group a in a given
106 year and season, $N_{a,y,s}$, was estimated by averaging the catch rate of age group a in each rectangle,
107 $n_{a,y,s,r}$, over all rectangles. This survey based index was chosen rather than assessment based
108 estimates as the latter provides an estimate of the number of fish once a year only and thus would
109 not reflect changes from winter to summer.

110 Size selective fishing mortality affects length at age in some stocks (Hanson and Chouinard
111 1992; Riget and Engelstoft 1998; Sinclair et al. 2002a). To investigate whether increased fishing
112 mortality is followed by a change in length at age, fishing mortality of age a in year y , $F_{a,y}$, was
113 taken from the most recent stock assessment, including discard mortalities of cod (ICES 2006). This
114 provided estimates for the period 1983 to 2005.

115 **Estimation of amount of prey available**

116 Three prey categories were considered: sandeel, clupeids and demersal fish. These prey types
117 together constitute more than 40%, on average, of the stomach content of cod of age 2 and older
118 (Fig. 2, Kikkert 1993). Though other prey types are also important to cod, no data were available to
119 measure their abundance on the resolution of ICES statistical rectangles. A biomass index of
120 clupeid and demersal prey fish was estimated from survey trawl catches. The fish biomass in the
121 length range 5 to 15 cm caught per survey trawl hour was used. The lower length limit was used as
122 the catchability of fish below this limit was considered highly variable. The upper limit corresponds
123 roughly to the maximum prey size in medium to large sized cod (Kikkert 1993). As weight of the
124 individual fish caught was not measured, biomass of clupeids and demersal fish within this size
125 range was estimated from the length distribution by assuming that weight of a fish of length l was
126 equal to $0.01l^3$. An index of the biomass of prey category j in rectangle r , quarter q and year y ,
127 $B_{j,y,q,r}$, was estimated as the average biomass caught per haul of this category. Flatfish were
128 excluded as they are not a major prey of North Sea cod (with the possible exception of dab
129 (*Limanda limanda*))(Kikkert 1993).

130 Two indices of average prey fish biomass were calculated: one was a North Sea average and
131 the other was an estimate of the ambient prey biomass of each age group. The latter estimate
132 accounts for differences in the spatial overlap between prey and predator whereas the former does
133 not. The North Sea average biomass index in year y and season s , $B_{j,NS,y,s}$, of clupeids ($j=clupeid$)
134 and demersal fish ($j=demersal$) was estimated as the average of the biomass index in the given year
135 and season and the biomass index estimated 6 months earlier, where the biomass index of a given
136 year and season was estimated as the average of all rectangles sampled. Ambient or cod-weighted
137 biomass is an index of the ambient biomass of prey to an average cod of a given age. It is obtained
138 by weighting the indices of prey biomass within a rectangle by the proportion of cod of a given age

139 which are present in the rectangle. This produces an index of the current ambient prey biomass.
140 However, to compare prey biomass indices with growth within the last 6 months, an estimate which
141 refers to the 6 months prior to the survey is required. This necessitates an assumption on the spatial
142 distribution of predators and prey in the time between the surveys. As an approximation, it was
143 decided to assume that the distribution of fish changed instantaneously on the 1st of June and the 1st
144 of December (midway between the surveys). Average ambient biomass indices, $B_{j,a,y,s}$, of clupeids
145 and demersal fish were estimated as the average of the current ambient prey biomass and that
146 experienced by the cohort 6 months earlier. The biomass indices of both clupeids and demersal fish
147 are likely to be biased by the change in spatial coverage and survey gear around 1991.

148 Sandeels are poorly represented in survey trawls, and the biomass index of sandeel in the
149 water column was therefore estimated from commercial catches per day in the Danish sandeel
150 fishery from 1983 to 2005 (Appendix). The total biomass of sandeel caught per day was used
151 directly as an estimate of available prey. No correction for the size distribution was necessary as
152 sandeels are generally smaller than 15 cm in the North Sea. Unfortunately, not all areas are fished in
153 every year and to achieve full spatial coverage of the estimates throughout the period, it was
154 necessary to assume that the spatial distribution of sandeel remained constant over the years.
155 Further, the sandeel biomass available in squares which were fished by less than 5 boats over the
156 entire period was assumed to be zero (or at least negligible compared to that in other squares) as
157 was the sandeel biomass available from September to March, the period when sandeel are buried in
158 the sediment most of the time (Winslade 1974). 2nd and 3rd quarter estimates were produced. The 2nd
159 quarter biomass index consists mainly of sandeels 1-year old and older whereas the 3rd quarter
160 index may include young of the year. To use this information, indices of sandeel biomass available
161 in the 2nd and 3rd quarter ($B_{s2,NS,y,summer}$ and $B_{s3,NS,y,summer}$, respectively) was estimated separately by
162 averaging the biomass indices in the North Sea over statistical rectangles. Following the estimation

163 of the ambient biomass index of clupeids and demersal fish prey, the ambient or cod-weighted
164 biomass index of sandeel in the second and third quarter ($B_{s2,a,y,summer}$ and $B_{s3,a,y,summer}$, respectively)
165 was obtained by weighting the indices of sandeel biomass within a rectangle by the proportion of
166 cod of a given age which are present in the rectangle in the September survey. As sandeel were
167 assumed to be unavailable in winter, ambient and North Sea average sandeel biomass of cod in
168 February was zero. Note that if survey changes in 1991 bias all cod catches by a common factor, the
169 index of ambient sandeel biomass is unaffected by changes in gear (Appendix).

170 **Estimation of average temperature**

171 Bottom temperature data are not available on a monthly basis from all ICES statistical
172 rectangles in the North Sea. To achieve this kind of resolution, it is necessary to use predictions
173 from a hydrodynamic model. We used output from the ECOSMO model (Schrum et al. 2006)
174 which provides estimates of temperature with a horizontal resolution of 10 km, a vertical grid
175 spacing of 5 m at depths less than 40 m and a larger grid spacing below this level. The
176 hydrodynamic part of the model is based upon the non-linear primitive equation model HAMSOM
177 (HAMBURG Shelf Ocean Model, Schrum and Backhaus 1999). Several studies have demonstrated
178 the ability of model to provide realistic simulations of North Sea hydrodynamics (Schrum et al.
179 2000; Janssen et al. 2001; Janssen 2002). Though the model does not capture all weekly variations
180 (deviations of up to 2°C occur in a few cases), yearly average temperatures are accurately
181 reproduced as is the temporal development over the study period (Janssen et al. 2001). Average
182 temperature, T , in each year and rectangle was extracted for the months March to May, June to
183 August, September to November and December to February. The groups were selected to provide 3
184 month intervals prior to and after the surveys. Temperature estimates were not available for the area
185 north of 60°N or for the year 2005.

186 Two temperature estimates were calculated in each year and season: a North Sea average and
187 an estimate of average ambient temperature of a given age (Heesen and Daan 1994). The latter
188 estimate accounts for the spatial distribution of the age group whereas the former does not. Two
189 temporal scales were considered: for the comparison with average length of fish younger than 2
190 years, an accumulated average temperature over their entire life time was estimated starting from
191 the time of settling and for the comparison with growth rates of cod older than 1.5 years, estimates
192 of average North Sea temperature within the last 6 months were estimated.

193 The accumulated average temperature over the entire life time of juvenile cod was estimated
194 starting from the time of settling. Cod are at least partly demersal from June onwards in their first
195 year (Bromley and Kell 1995) and hence the average demersal lifetime temperature of 0.5-year olds
196 is the average temperature from the 1st of June to the 1st of September whereas that of 1-year olds is
197 the average from the 1st of June to the 1st of March and that of 1.5-year olds is the average from 1st
198 of June the previous year to 1st of September in the current year. The estimates of average lifetime
199 North Sea temperature were thus the average over all rectangles in 3, 9 and 15 months prior to the
200 survey for cod of age 0.5, 1 and 1.5 years, respectively. Life-time average North Sea temperatures
201 ($T_{L,NS,a,y,s}$) were estimated as the average temperature in this period for each age group and ambient
202 life time temperatures ($T_{L,a,y,s}$) were estimated as the weighted average, weighting the temperature
203 in each rectangle with the proportion of the age group caught in that rectangle (Appendix).

204 The half yearly North Sea average temperature, $T_{NS,y,s}$, was estimated as the average of the
205 temperatures estimated in the 6 months prior to the survey in year y and season s . Ambient or cod-
206 weighted temperature was estimated as the average ambient temperature in the period 0 to 3 months
207 and 3 to 6 months prior to the survey. Average ambient temperature in the period 0 to 3 months
208 prior to the survey was estimated by weighting the temperature rectangle r in that period by the
209 proportion of cod of age a caught in rectangle r in year y and season s . Average ambient

210 temperature in the period 3 to 6 months prior to the survey was estimated by weighting the
211 temperature rectangle r in that period by the proportion of cod of the same cohort caught in the
212 rectangle r in the previous survey (Appendix).

213 **Measuring growth of fish**

214 Growth of fish have been measured in several ways in the literature. Firstly, average length at age is
215 a simple measure but has the disadvantage of measuring integrated growth over the entire life span
216 of the fish. While this may not be a problem when examining growth of young individuals, average
217 length of an older fish depends heavily on the conditions experienced earlier in life and little on
218 recent growth. Average length is therefore suitable only for the detection of relationships between
219 recent growth conditions and growth of young fish. Another measure frequently used is specific
220 growth rate G (Jobling 1988; Björnsson and Steinarsson 2002):

221
222
223

$$224 \quad G = 100 \frac{\ln W_t - \ln W_{t-\Delta t}}{\Delta t}$$

225
226
227

228 where W_t is the weight of the fish at time t . This measure has the advantage of measuring growth in
229 the period between two observations directly and hence is preferable if size of a fish is measured at
230 more than one point in time. Unfortunately, G varies not only with recent growth conditions but
231 also with size of the fish (Jobling 1988; Björnsson and Steinarsson 2002) and growth estimates can
232 only be compared directly for a limited range of sizes. This is particularly inconvenient when

233 growth conditions act in a comparable way on growth of several age groups (e.g. growth of all ages
234 is enhanced at increased prey biomass). In this case, it is preferable to look at growth of all ages
235 simultaneously and a model in which the parameters remain constant with size is needed. One
236 model which fulfils this is the von Bertalanffy model. The von Bertalanffy equation describes
237 length of a fish as a function of age and three constants:

238

239

240

241 (1)
$$l_a = L_\infty \left(1 - e^{-K(a-a_0)}\right)$$

242

243

244

245 where l_a is average length of the fish at age a , L_∞ is the average maximum attainable length, K is
246 instantaneous average growth rate and a_0 is a constant referring to the theoretical length at $a=0$.

247 This model is clearly preferable if size at age of a cohort is estimated at several points in time. Note
248 also that inserting length at age from the von Bertalanffy model to estimate of specific growth rate
249 between age a and $a+\Delta a$ and rearranging, is it clear that G depends directly on age a , K , a_0 and the
250 time elapsed between measurements (Δa) but is unaffected by L_∞ . As the model includes three
251 parameters, it can only be estimated if several age groups are included in the analyses.

252 Based on these considerations, it was decided to estimate growth of juvenile cod (cod younger than
253 18 months) by average length at age directly, growth of cod in the transition period between an
254 invertebrate dominated diet and a piscivorous diet by specific growth rate G and growth of
255 predominantly piscivorous cod by the parameters K and L_∞ from the von Bertalanffy equation.

256 To examine the likely effect of the observed temperatures on growth of cod, food unlimited
257 growth rate G in the laboratory of cod of a particular size and ambient temperature was estimated
258 from models given in two studies of temperature limited growth rate of cod fed to satiation: Jobling
259 (1988) and Björnsson and Steinarsson (2002). Björnsson and Steinarsson used Icelandic cod
260 whereas Jobling combined results from experiments with Scottish coastal cod, Norwegian coastal
261 cod, North east arctic cod and North Sea cod (Edwards et al. 1972; Jones and Hislop 1978; Braaten
262 1984; Hawkins et al. 1985; Jobling 1988). Jobling described the relationship between growth rate
263 G , W and temperature T as

264

265

266

$$267 \ln G = 0.216 + 0.297T - 0.000583T^3 - 0.441 \ln W$$

268

269

270

271 whereas Björnsson and Steinarsson described the relationship as

272

273

274

$$275 G = 0.5735TW^{-0.1934-0.02001T}$$

276

277

278

279 As potential growth rates are estimated from both temperature and weight of the fish, observed
280 weight at age was estimated from the observed length at age as $W_{a,y,winter} = 0.0198\bar{l}_{a,y,winter}^{2.8571}$
281 and $W_{a,y,summer} = 0.0211\bar{l}_{a,y,summer}^{2.8571}$ for cod caught in the winter and summer surveys, respectively
282 (Coull et al. 1989). This observed weight was used to predict potential growth at a range of
283 temperatures for each age group.

284 **Growth of cod feeding mainly on invertebrates**

285 Average length of 0.5-, 1- and 1.5-year old cod was compared to life-time average ($T_{L,NS,a,y,s}$)
286 and ambient ($T_{L,a,y,s}$) temperature, the index of density ($\ln(N_{a,y,s})$) and fishing mortality ($F_{l,y}$, 1.5-
287 year olds only). The analyses were conducted using multiple linear regression models. The factors
288 were tested for effect on the natural log of the average length, $\ln(\bar{l}_{a,y,s})$. To account for catchability
289 changes due to changes in survey design, the intercept of the models for 0 and 1-year olds in
290 summer was allowed to differ between the periods before and after 1991.

291 **Growth in the transition period**

292 Somatic growth in the transition period was examined by estimating the yearly growth rates
293 from age 1 to age 2 and the half yearly growth rates from age 1.5 to age 2. Half-yearly ($g_{0.5,y}$) and
294 yearly ($g_{1,y}$) growth rates were estimated as

295

296

297

$$298 \quad g_{0.5,y} = \ln \bar{l}_{2,y,winter} - \ln \bar{l}_{1.5,y-1,summer}$$

299

300

301

302 and

303

304

305

306 $g_{1,y} = \ln \bar{l}_{2,y,winter} - \ln \bar{l}_{1,y-1,winter}$

307

308

309

310 These estimates are directly proportional to specific growth rate G . Growth in the transition period
311 was investigated by fitting linear regression models where the independent variables were North
312 Sea average and ambient temperature, average and ambient prey biomass index, log cod density
313 index and fishing mortality of 1-year olds in the previous year. In the model of $g_{1,y}$, average values
314 of the explanatory variable in the past year was used, except for the biomass index of demersal and
315 clupeid prey where the values referred to the period between summer and winter in both cases, as
316 the consumption of these prey types is low in the period before summer (Kikkert 1991). To account
317 for changes catchability due to changes in survey design, the intercept of the model of $g_{0.5,y}$ was
318 allowed to differ between the periods before and after 1991 as was the effect of the biomass index
319 of clupeid and demersal fish in both models. All effects were assumed to be linear and the error
320 around the relationship assumed to be normal distributed. The significance of explanatory variables
321 was determined by forward elimination.

322 **Growth of cod older than 2 years**

323 Growth of cod older than 2 years was examined through an analysis of the relationship between the
324 parameters in the von Bertalanffy model and temperature, density index, prey fish biomass indices
325 and fishing mortality. To facilitate the analyses, Eq. 1 was rearranged to describe the relationship
326 between length at age a , l_a , and length at age $a+\Delta a$, $l_{a+\Delta a}$. $l_{a+\Delta a}$ can be rearranged to

327 $l_{a+\Delta a} = L_\infty \left(1 - e^{-K(a+\Delta a - a_0)}\right) = L_\infty \left(1 - e^{-K\Delta a}\right) + e^{-K\Delta a} L_\infty \left(1 - e^{-K(a - a_0)}\right)$. Inserting $l_a = L_\infty \left(1 - e^{-K(a - a_0)}\right)$

328 (Eq. 1), we obtain

329

330

331

332 (2) $l_{a+\Delta a} = L_\infty \left(1 - e^{-\Delta a K}\right) + e^{-\Delta a K} l_a$

333

334

335

336 If age is measured in years and the time elapsed between the two measurements of average length

337 (Δa) is 0.5 year, Eq. 2 corresponds to comparing the length of a given cohort with that 6 months

338 earlier. We examined the length of fish of age 2.5 years up to age 5.5, avoiding the oldest groups

339 which contain both 6-year olds and older fish. If it is assumed that L_∞ remains constant while K

340 varies between years and ages, and that $\bar{l}_{a,y,s}$ derived from surveys provides an unbiased estimate of

341 l_a , Eq. 2 becomes

342

343

344

345
$$\bar{l}_{a,y,winter} = L_{\infty} \left(1 - e^{-0.5K_{a,y,s}}\right) + e^{-0.5K_{a,y,s}} \bar{l}_{a-0.5,y-1,summer}$$

346
$$\bar{l}_{a,y,summer} = L_{\infty} \left(1 - e^{-0.5K_{a,y,summer}}\right) + e^{-0.5K_{a,y,summer}} \bar{l}_{a-0.5,y,winter}$$

347

348

349

350 in winter and summer, respectively. This is a standard autoregressive model of order 1. L_{∞} was
 351 assumed to remain constant over the period while K was a linear function of the explanatory
 352 variables. An F-test of the significance of each explanatory variable was conducted by comparing
 353 the residual variation to that of a model where growth rate was constant for the same time range (the
 354 period included depends on the explanatory variables as not all variables were known in all years).
 355 The significance of explanatory variables was determined by forward elimination. The explanatory
 356 variables tested were season (s), average ($T_{NS,y,s}$) and ambient ($T_{a,y,s}$) temperature, average ($B_{j,NS,y,s}$)
 357 and ambient ($B_{j,a,y,s}$) prey biomass indices, fishing mortality ($F_{a-1,y-1}$ in winter and $F_{a-0.5,y}$ in
 358 summer) and the density index ($\ln N_{a,y,s}$). As density decreases with age, including the density index
 359 directly would provide a measure of the combined effect of age and density rather than the effect of
 360 density alone. To avoid this, $\ln N_{a,y,s}$ was expressed in units of standard deviations from the mean of
 361 the given age group and this standardised measure denoted $\ln N_{a,y,s}^*$. The parameters were estimated
 362 using the NLIN procedure in SAS[®] (SAS Institute Inc. 2001). Variance in length at age increased
 363 with the mean (correlation=0.69) whereas there was no correlation between average $\ln \bar{l}_{a,y}$ and the
 364 variance of this (correlation=0.02). The model was therefore fitted assuming the residuals of $\ln \bar{l}_{a,y}$
 365 to be normal distributed.

366 **Examination of residuals**

367 All residuals were tested from significant deviations from a normal distribution (Shapiro-Wilks
368 test), trends and autocorrelations (Pearson correlation coefficients).

369 **Results**

370 Less than 10 fish of an age group were caught on two occasions: 6+-year olds in the 3rd
371 quarter of 1986 and 4-year olds in the 3rd quarter of 1988. Average length was not estimated in
372 these cases.

373 Average length of age 0.5 cod increased significantly in the period before 1991
374 (correlation=0.84, P=0.0088, Fig. 3a). Though average length also increased after 1991, no
375 significant change was seen for cod of age 0.5 in this period, in age 1 over the entire period or in
376 age 1.5 in the period before and after 1991 (correlations=0.16, 0.09, 0.71 and -0.07, for age 0.5 after
377 1991, age 1 in the entire period and age 1.5 before and after 1991, respectively). In contrast to this,
378 average length of cod older than 18 months decreased over the period (correlations ranging from -
379 0.30 to -0.62, ages 2 years and above, significant for all ages except age 6+, Fig. 3). From 1983 to
380 the end of the time series, this corresponded to a decrease in length at age of 10% and 13%, on
381 average, in the first and third quarter, respectively.

382 **Trends in North Sea average and ambient values**

383 There was no significant trend in the biomass indices for either North Sea average clupeid,
384 demersal or sandeel fish prey (All correlations with year >-0.63 and <0.16, P>0.05, Fig. 4).
385 However, there has been a drastic decrease in the biomass of demersal fish from 2000 to 2005,
386 reaching all time lows in 2004 and 2005 (Fig. 4). Changes in distribution of cod into areas of
387 unknown (presumably low) and low sandeel biomass led to a negative trend in the ambient biomass
388 of sandeel of all age groups (correlation between year and $B_{s2,a,y,summer}$ ranged from -0.31 to -0.61,

389 $P < 0.05$ for all ages but age 2.5 and between year and $B_{s3,a,y,summer}$ from -0.15 to -0.58, $P < 0.05$ for all
390 ages above 3.5).

391 The average North Sea temperature increased significantly in the 6 months before and after
392 the 1st quarter survey (correlations=0.53 and 0.48, $P=0.0127$ and 0.0235, respectively). With the
393 exception of cod younger than 2.5 years, half-yearly ambient temperatures were significantly colder
394 than the average (Table 1) and the differences amounted to as much as 1°C for some ages. Further,
395 though both average and ambient temperature increased for all ages except age 1 in summer, the
396 increase in ambient temperature was only significant for ages 0.5, 1 and 4.

397 The potential growth rate estimated by Jobling's method reaches its maximum at a higher
398 temperature than growth rate estimated by Björnsson and Steinarsson's method, and as a result of
399 this, the two models predict markedly different effects of temperature (Fig. 5). Whereas temperature
400 is predicted to account for less than 10% changes in growth of North Sea cod older than 1 year
401 using Björnsson and Steinarsson's model, Joblings method predicts a decrease of up to 50% within
402 the temperature range experienced (between 6 to 12°C, Fig. 5). Both models predict a large effect
403 on temperature on growth of the youngest age group (0.5-year olds).

404 **Growth within the first 18 months**

405 Average length of juvenile cod was highly correlated to average lifetime temperature (Fig. 6;
406 Table 2) while the effect of fishing mortality was insignificant. The correlations with North Sea
407 average temperature and the density index were always less significant than that with average
408 ambient temperature (Table 2). After including the effect of ambient life time temperature ($T_{L,a,y,s}$),
409 the final models of average length became

410

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412

413 $\ln \hat{l}_{0.5,y < 1991, summer} = 1.99^{(0.14)} + 0.032^{(0.012)} T_{L,0.5,y,summer}$

414 $\ln \hat{l}_{0.5,y \geq 1991, summer} = 1.85^{(0.12)} + 0.032^{(0.012)} T_{L,0.5,y,summer}$

415 $\ln \hat{l}_{1,y, winter} = 1.78^{(0.24)} + 0.108^{(0.023)} T_{L,1,y, winter}$

416 $\ln \hat{l}_{1.5,y < 1991, summer} = 2.70^{(0.17)} + 0.065^{(0.017)} T_{L,1.5,y, summer}$

417 $\ln \hat{l}_{1.5,y \geq 1991, summer} = 2.66^{(0.17)} + 0.065^{(0.017)} T_{L,1.5,y, summer}$

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420

421 where values in parentheses denotes standard error of the estimates ($r^2=0.48$, 0.53 and 0.53 for ages
422 0.5, 1 and 1.5, respectively). The effect of the index of density on length of 1 and 1.5-year olds was
423 no longer significant after the effect of ambient temperature was included in the model ($P=0.3409$
424 and 0.1148, respectively). The effect of temperature in the model of 0.5 year olds was significantly
425 lower than that in the model of 1-year olds ($P=0.0034$), whereas the difference between 1.5-year
426 olds and the other age groups was not significant ($P=0.1128$ and 0.1327, for age 0.5 and 1,
427 respectively). Inspecting the residuals, the relationship between log length and lifetime ambient
428 temperature appeared to decelerate. This was modelled by letting log length be a second degree
429 polynomial in temperature. The second degree term was significantly different from zero
430 ($P=0.0173$) and the resulting model became:

431

432

433

434 $\ln \hat{l}_{1,y,winter} = -4.38^{(2.36)} + 1.34^{(0.47)} T_{L,1,y,winter} - 0.061^{(0.023)} T_{L,1,y,winter}^2$

435

436

437

438 ($r^2=0.66$). The distribution of the residuals was not significantly different from a normal distribution

439 for any of the ages and no significant trends or autocorrelations in residuals were found.

440 **Growth in the transition period**

441 Growth in the transition period was significantly positively related to the index of cod density

442 and the sandeel biomass index in the 2nd or 3rd quarter (table 3, fig. 7). The correlation with ambient

443 sandeel biomass index was higher than that with North Sea average sandeel biomass index for both

444 quarters and growth rates, indicating that the change in overlap with sandeel was important. After

445 including the effect which had the highest correlation with growth rate in the models, the remaining

446 effects (including temperature) became insignificant and the resulting models were

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450 $g_{0.5,y} = 0.12^{(0.02)} + 0.0025^{(0.0008)} B_{s2,1,y-1,summer}$

451 $g_{1,y} = 0.51^{(0.04)} + 0.052^{0.019} \ln N_{2,y,winter}$

452

453

454

455 ($r^2= 0.34$ and 0.26 , respectively). The distribution of the residuals did not differ significantly from a

456 normal distribution and no significant trends or autocorrelations in residuals were found. The effects

457 of cod density and sandeel 3rd quarter biomass indices became insignificant when the other
 458 parameters were added (P=0.6288 and 0.9034, respectively) as did the difference between the
 459 period before and after 1991 (P=0.5341). Unfortunately, the cod density index was positively
 460 correlated to all sandeel biomass indices (table 3), which renders it difficult to determine which of
 461 the two factors is the most important one.

462 **Von Bertalanffy growth analyses**

463 After including the highly significant (P=0.0007) seasonal change in K in the model, the
 464 effect of the ambient demersal fish biomass index had the most significant effect (P=0.0039).
 465 Including this factor, no other variables maintained a significant effect. However, the cod density
 466 index was only marginally significant (P=0.0977) and inspecting the residuals, there appeared to be
 467 an effect of the density index in winter whereas no effect was seen in summer. Restricting the effect
 468 of density to affect only growth from summer to winter, the effect passed the significance level
 469 (P=0.0331). After including this parameter, none of the remaining variables retained a significant
 470 effect (P>0.15). The model of K became

$$474 \hat{K}_{a,y<1991,winter} = 0.142^{(0.037)} + 0.59^{(0.28)} B_{demersal,a,y,winter} - 0.020^{(0.011)} (\ln N_{a,y,winter}^*)$$

$$475 \hat{K}_{a,y\geq 1991,winter} = 0.142^{(0.037)} + 0.18^{(0.07)} B_{demersal,a,y,winter} - 0.020^{(0.011)} (\ln N_{a,y,winter}^*)$$

$$476 \hat{K}_{a,y<1991,summer} = 0.104^{(0.025)} + 0.59^{(0.28)} B_{demersal,a,y,summer}$$

$$477 \hat{K}_{a,y\geq 1991,summer} = 0.104^{(0.025)} + 0.18^{(0.07)} B_{demersal,a,y,summer}$$

$$478 L_{\infty} = 151^{(25)}$$

479

480

481

482 ($r^2=0.16$). Though the effects of season, the biomass index of demersal fish and the density index
483 were significant, the proportion of the variation which could be attributed to these factors was
484 small, each explaining only 7.1%, 6.4% and 2.5% of the unexplained variation, respectively. There
485 was no trend in the residuals and the distribution of the residuals did not deviate significantly from a
486 normal distribution. The residuals were neither significantly autocorrelated for a given age and a lag
487 of 1 year nor for a given cohort and a lag of 1 year. However, the residuals within a year of adjacent
488 age groups were significantly positively correlated (correlation=0.23, $P=0.0152$) and residuals of a
489 given cohort was significantly negatively correlated to that of the same cohort 6 months earlier
490 (correlation=-0.35, $P<0.0001$). Residuals were not correlated to age (correlation=0.01, $P=0.8675$)
491 which should have been the case if length at age of older ages was biased due to decreasing
492 catchability of very large fish (Godø et al. 1999).

493 ***Discussion***

494 Growth of cod within their first 1.5 years of life was highly dependent on temperature.
495 Though the increase in average temperature seen over the period could therefore potentially have
496 increased growth rates, this effect was abated by a change in the distribution of juveniles, and no
497 increase in ambient temperatures or growth of cod of age 1 and 1.5 could be detected. Growth of
498 older ages was not related to temperature. Instead, growth in the transition period between a diet
499 dominated by invertebrates and a diet dominated by fish was positively related to cod density and
500 sandeel biomass whereas growth of older cod was positively related to biomass of demersal fish
501 prey and negatively related to cod density. Both growth of juveniles, transition cod and cod older
502 than 2 years showed higher correlations with ambient estimates of temperature and prey biomass

503 than North Sea average values, demonstrating the importance of including the effect of changes in
504 distribution of prey and predator.

505 The increase in juvenile length with increasing temperature appeared to be caused by an effect
506 on growth during at least the first 12 months. Had growth been affected only up to age 0.5, the
507 effect of life time temperature should have decreased as age increased. In contrast to this, the effect
508 of temperature increased significantly from age 0.5 to age 1 indicating that the positive effect
509 persisted in the second half year of life. Similar positive relationships between growth of juveniles
510 and temperature have been found in Irish cod, Northeast Arctic cod and Placentia Bay cod
511 (Michalsen et al. 1998; Armstrong et al. 2004; Mello and Rose 2005), perhaps indicating that
512 temperature dependent growth of immature fish is the cause of the high correlation between
513 ambient temperature and length at age 4 detected by Brander (1995). The negative effect of density
514 on length of 1.5-year olds did not persist after the effect of temperature was taken into account. This
515 confirms the earlier results by van Alphen and Heesen (1984) and Rijnsdorp et al. (1991) who
516 detected no link between length at age 1 and density based on data from 1968 to 1989.

517 Growth of cod in the transition phase was significantly correlated to both ambient sandeel
518 biomass and cod density, but as the two time series were highly correlated, it is difficult to
519 determine which of the two had the most important effect. The positive effect of increasing density
520 on growth could seem counterintuitive and may lead to the conclusion that ambient sandeel biomass
521 was the causal factor. However, positive relationships between density and feeding success have
522 been recorded in other fish feeding on schooling or patchy prey (Major 1978; Pitcher et al. 1982). If
523 cod switch from feeding on invertebrates to feeding on patchily distributed tightly schooling
524 sandeel, it may be an advantage to forage in groups. Hence the explanation for the similarity of the
525 two effects may be that they work together to produce changes in growth.

526 Growth of cod older than 2 years showed clear seasonal differences with the autumn estimate
527 of K being 50% higher than the spring estimate. A similar seasonal pattern was seen in cod off
528 Newfoundland (Mello and Rose 2005). The difference in growth in the study of Newfoundland cod
529 was linked to temperature and the seasonally variable predation on capelin (*Mallotus villosus*). In
530 the current study, no effect of temperature could be found and the demersal fish biomass index
531 could not explain the difference between seasons. As the spring period encompasses the spawning
532 period of North Sea cod (Daan et al. 1990), the seasonal difference may be linked to a trade off
533 between using the available energy for reproduction or for growth. Growth in both seasons was
534 positively related to increasing biomass of demersal fish but independent of the biomass of sandeel
535 or clupeids. As sandeels constitute less than 8% of the diet of these age groups (Fig. 2), the lack of
536 effect on growth of old cod is not unexpected. However, the same argument cannot be made for
537 clupeids. Though they generally contribute less to the diet than demersal fish, their contribution is
538 as high as 30% in some age groups (Fig. 2). Possibly, the catchability of pelagic fish to the demersal
539 trawl used in the surveys varies to an extent where any underlying relationship becomes
540 undetectable. Alternatively, the changes in clupeid biomass over the period have been too small for
541 any serious effects on growth to occur. Growth of cod and prey fish abundance is significantly
542 correlated in both Icelandic cod (Steinarsson and Stefánsson 1996), Northeast Arctic cod (Jørgensen
543 1992) and cod on the Newfoundland and Labrador shelves (Krohn et al. 1997; Mello and Rose
544 2005). However, the proportion of the variation in growth which can be explained by temperature
545 and prey abundance is often low (24% and 23% in Northeast Arctic cod and cod off Newfoundland,
546 respectively (Jørgensen 1992; Krohn et al. 1997)). These figures include a substantial effect of
547 temperature and hence the proportion which can be attributed to prey biomass is only a fraction of
548 this. Hence the 6.4% of the variation in growth which could be attributed to demersal fish biomass
549 would appear to be a level comparable to that seen in other stocks, in spite of the fact that the diet of

550 North Sea cod differs from that of these stocks. North Sea cod consumes a variety of fish prey and
551 only occasionally does a single prey species account for more than 30% of the weight of the
552 stomach content (Kikkert 1993), whereas capelin accounts for up to 50%, 69% and 85% of the
553 stomach content in the Icelandic, North East Arctic and Newfoundland stocks, respectively (Pálsson
554 1983; Mehl 1989; Lilly 1991).

555 Though temperature has increased over the period, there was no evidence of an increase in
556 growth of cod older than 2 years as predicted by the relationship between temperature and food
557 unlimited growth given by Jobling (1988). A similar lack of effect of temperature on growth of
558 older cod was seen in the Northeast Arctic where average length at age 7 decreased as temperature
559 increased (Michalsen et al. 1998) and in Placentia Bay, where growth of cod age 8 and 9 decreased
560 with temperature (Mello and Rose 2005). In contrast to this, there was a positive effect of
561 temperature on growth of Northwest Atlantic cod stocks experiencing average temperatures
562 between 0°C and 3°C (Krohn et al. 1997; Riget and Engelstoft 1998; Swain et al. 2003). No effect
563 of temperature was found on growth of the 4X stock on the Scotian shelf, where average
564 temperature (6.8°C) approached that in the North Sea. Assuming that the relationship between food
565 unlimited growth and temperature estimated for Icelandic cod by Björnsson and Steinarsson (2002)
566 can be generalised to all cod stocks, an increase in temperature from 8 to 9°C should result in a
567 change in growth rate of less than 6% (Fig. 5). In comparison, an increase in temperature from 2 to
568 3°C should result in an increase in growth rate of more than 25%. Hence, the discrepancy between
569 the conclusions on the effect of temperature in cold and warm water stocks is not surprising.

570 Increased density was followed by decreased autumn growth of North Sea cod older than 2
571 years. The results confirm earlier results by Macer (1983) and van Alphen and Heesen (1984), who
572 found density dependent growth in cod of age 3 and ages 2, 3 and 4, respectively. The fact that the
573 effect could only be detected in the second half of the year may indicate that intra-specific

574 competition for prey or habitat acts mainly within the autumn period. Houghton and Flatman (1980)
575 found decreased growth rate of cod in the west central North Sea at high densities based on weight
576 at age in commercial catches, but growth within this and other areas was later examined by
577 Bromley (1989), who concluded that no evidence of density dependent growth could be detected
578 within local areas. He suggested that the causal relationship between density and growth in the
579 North Sea could be acting through changes in distribution. If this is the case, the coinciding
580 decrease in abundance and shift in distribution into slow growth areas seen in later years (Perry et
581 al. 2005; Andrews et al. 2006; Rindorf and Lewy 2006) should result in a positive correlation
582 between density and growth in contrast to the negative correlation found in cod older than 2 years.
583 Decreased growth at high densities has been found in the Southern Gulf of St. Lawrence cod
584 (Sinclair et al. 2002*b*), in two out of four stocks on the Labrador and Newfoundland shelves (Swain
585 et al. 2003), Irish Sea cod (Armstrong et al. 2004) and North east Arctic cod (Michalsen et al.
586 1998). Though an affect appeared to be present in Irish Sea cod, temperature and recruitment is
587 highly correlated in this stock, and it remains unclear whether the results are caused by the
588 combined links between density and temperature and temperature and growth (Armstrong et al.
589 2004). The density dependent decrease in growth rate of juvenile Northeast Arctic cod occurs
590 through changes in distribution as large yearclasses experience lower ambient temperatures and
591 hence achieve lower growth rates (Michalsen et al. 1998). Hence, there does not appear to be a
592 general presence or absence of density dependence in all stocks, and the presence of similar or
593 opposing trends stress the need to examine several variables when attempting to determine the
594 effects on growth of cod.

595 Negative correlations between size selective fishing mortality and size at age exist in Southern
596 Gulf of St. Lawrence cod (Sinclair et al. 2002*a*) and the West Greenland stock (Riget and Engelstoft
597 1998), but no such effect was seen in the North Sea. However, the number of partially recruited age

598 groups is higher in the Southern Gulf of St. Lawrence than in the North Sea (Pinhorn and Halliday
599 2001) leaving a greater time span for effects to occur. In the North Sea, size selective fishing has the
600 potential to affect mainly cod at age 1.5 (the only partially recruited age group (Pinhorn and
601 Halliday 2001)). Even so, length at this age was uncorrelated to fishing mortality. Though there is
602 always a possibility that this result is caused by poor quality of the assessment of the stock, we also
603 investigated the correlation between length at age and the minimum mesh size regulations and
604 obtained the same result (results not shown). As natural mortality of this age group is about four
605 times the fishing mortality (ICES 2006), the effect of size selective fishing mortality may be
606 masked by the much larger effect of size selective predation mortality. Further, results in the
607 literature of investigations of the effect of fishing mortality are not unanimous. Size at age in the
608 stock in the Northern Gulf of St. Lawrence appears to be unaffected by fishing mortality (Dutil et
609 al. 1999), in spite of the significant relationships seen in the adjacent Southern Gulf of St. Lawrence
610 stock (Hanson and Chouinard 1992; Sinclair et al. 2002a). However, of the 12 stocks examined by
611 Pinhorn and Halliday (2001), only the southern Gulf of St. Lawrence stock, the Northeast Arctic
612 stock, the Iceland stock and the Labrador stock are partially recruited to the fishery for more than 5
613 years (Pinhorn and Halliday 2001), and hence have potential to exhibit severely decreased size at
614 age as a result of size selective fishing mortality. Of these stocks, the Northeast Arctic stock shows
615 no evidence of a decrease in length at high fishing mortalities. Rather, high fishing mortality seems
616 to be accompanied by large size at age, perhaps due to density dependent effects on both (Marshall
617 et al. 2004). Another stock experiencing high fishing mortalities, the Irish cod stock, showed a
618 similar lack of relationship between size at age and fishing mortality (Armstrong et al. 2004) and
619 hence the lack of effect in the North Sea does not appear to be unique.

620 The positive correlation between residuals from the von Bertalanffy model within a given
621 year indicates that yearly changes in growth conditions affect all age groups similarly. However, the

622 result may also be caused by the statistical correlation introduced by the sampling procedure which
623 combines age-length keys with length distributions. This appeared to be the more likely reason as
624 correlations between residuals were only significant for ages 4.5 and 5.5 when age groups were
625 analysed separately and the problem of statistical correlation increases with increasing length
626 overlap of the age groups. The negative correlation between the residuals and those of the same
627 cohort 6 months earlier indicates that a larger than expected size in a given survey is generally
628 followed by smaller than expected size in the subsequent survey. This could be a result of sampling
629 errors if an estimate of large size at one age is in some cases caused by sampling errors alone. The
630 subsequent survey will then tend to find fish that are smaller than expected. When analysed for each
631 age separately, the correlations were significant only for fish of age 3, 5 and 5.5, two of which are
632 hampered by low catch rates (5 and 5.5 year olds). This may indicate that the problem is linked to
633 the higher sampling error of these ages. The residuals were not significantly correlated with those
634 from the same cohort 1 year earlier, indicating that between cohort differences in growth rates were
635 either small or swamped by yearly differences. Autocorrelation in the residuals results in a lower
636 number of degrees of freedom than the number of observations and as reducing the number of
637 degrees of freedom results in higher probability estimates, the probability levels given here should
638 be taken as minimum estimates. The r^2 values are, however, unaffected by this problem.

639 Though the von Bertalanffy growth parameters did not exhibit any trend over the past 20
640 years, this does not rule out growth changes in a longer time perspective. The confidence limit of
641 the estimate of L_∞ obtained here were wide and included the estimates of 110.8^(2.8) and 118.7^(5.6) cm
642 presented by Daan (1974) for southern and northern North Sea cod, respectively, in the period 1968
643 to 1972. Reanalysing his data using model (2), the difference between the northern and southern
644 parts in L_∞ and K are insignificant ($P=0.2374$ and 0.1654 , respectively) and a fit using data from
645 both areas results in the estimates $L_\infty=113.6^{(4.7)}$ cm and $K=0.300^{(0.033)}$. Fixing L_∞ at this value and

646 using the present data results in an estimate of K of $0.241^{(0.010)}$ which is not significantly different
647 from the value estimated from Daans data ($P=0.0871$). Even earlier than the investigation by Daan
648 are the data from Graham on length of cod in the southeastern North Sea (Graham 1934). Using his
649 estimates of length at ages 1.5 to 6.5 in March and September of 1991 to 1927 and fixing L_{∞} to
650 113.6 cm results in an estimate of $K=0.219^{(0.020)}$. This value is significantly different from that
651 obtained from Daans data ($P=0.0358$) but not from the estimate derived in the present study
652 ($P=0.3252$). Hence there may have been an increase in growth rate from the early 20th century to the
653 1970s, but the current growth rate seems to have decreased to a value between the two historical
654 estimates.

655 This study has shown a decrease in length at age of fish older than 1.5 years over the past 23
656 years. This appeared to be caused by a decrease in growth of cod in the transition phase as length at
657 age of cod younger than 2 years has increased slightly with increasing temperatures and growth
658 rates of fish older than 2 years showed no trend over the period. The decreased growth in the
659 transition phase appeared to be linked either to decreasing ambient sandeel biomass, decreasing cod
660 density or both. However, as ambient sandeel biomass is highly dependent on the distribution of
661 cod the coinciding trends may be also be caused by a shift in the dominance of southern
662 aggregations towards a dominance of northern aggregations. Cod aggregations within the central
663 North Sea do not differ genetically (Hutchinson et al. 2001), but this does not necessarily imply that
664 northern and southern aggregations do not have individual characteristics. As cod in different areas
665 have different scopes for growth (Andrews et al. 2006), the change in growth rate could be the
666 result of a change either in the proportion of the stock which reside in fast-growth areas or in the
667 proportion of the number of cod recruited in a number of relatively stationary sub-stocks in fast-
668 growth areas. If the latter situation occurs, temporal changes in growth caused by changes in
669 distribution may not be reversible unless the relative importance of the different aggregations is

670 restored. In conclusion, there does not appear to be scope for increased growth of cod older than 2
671 years with increasing temperatures. Rather, as increasing temperatures tend to lead to a more
672 northerly distribution (Perry et al. 2005; Rindorf and Lewy 2006), growth rate of North Sea cod
673 may further decrease if temperatures continue to be above the long term average as ambient sandeel
674 biomass and cod density are both negatively related to this factor (O'Brien et al. 2000; Rindorf and
675 Lewy 2006). Furthermore, increased growth of juveniles as temperatures increase may lead to a
676 higher fishing mortality on age 1 cod (Pinhorn and Halliday 2001) and hence further aggravate the
677 severe decrease in recruitment to the North Sea cod stock due to the combined effects of poor
678 recruitment success and a severe decrease in spawner biomass.

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833 **Appendix**

834 **Estimation of age-length keys**

835 Age-length keys were estimated by the method described by Rindorf and Lewy (2001). This
836 method utilises the smoothness of length at age distributions to provide more accurate estimates of
837 age at length than traditional methods. The number of fish observed of a given age in a sample is
838 assumed to be multinomial distributed, but the variance may exceed that of this distribution. In the
839 present study, length at age was assumed to be normal distributed. Analyses were also performed
840 based on the assumption of gamma distributed length at age, but these analyses provided poorer fits
841 to the observed age at length.

842 Age at length is analysed by comparing the proportion of fish at length l which are of age a ,
843 $p_{a,l}$, with the proportion of fish which are of age a or older, $p_{a+,l}$. This is equivalent to estimating the
844 probability that a fish of a given length is of age a given that the fish is of age a or older. The
845 variable analysed is the continuation ratio logit:

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849
$$\log\left(\frac{p_{a,l}}{p_{a+,l}}\right)$$

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851

852

853 The continuation logit can be used to estimate the probability of being of age group a at

854 length l , $\hat{p}_{a,l}$, (Rindorf and Lewy 2001):

855

856

857

$$\hat{p}_{1,l} = \left(\frac{\hat{p}_{1,l}}{\hat{p}_{1+,l}} \right)$$

858

$$\hat{p}_{a,l} = \left(\frac{\hat{p}_{a,l}}{\hat{p}_{a+,l}} \right) * \left(1 - \sum_{j=1}^{a-1} \hat{p}_j \right) \quad , \quad a > 1$$

859

860

861

862 The model analysed in this study was that appropriate for individuals with normal distributed length
863 at age (Rindorf and Lewy 2001):

864

865

866

$$\log \left(\frac{p_a}{p_{a+}} \right) = b_{a,y,q,ro} + c_{a,y,q,ro} l + d_{a,y,q,ro} l^2$$

867

868

869

870

871 where b , c and d are parameters to be estimated in the model and indices y , q and ro denotes year,
872 quarter and each of 8 ICES roundfish areas (Fig. 1), respectively. Overdispersion was allowed by
873 estimating scale by the Pearson statistic. The number of parameters estimated varies as the number
874 of roundfish area-year-quarter combinations which fulfil the data requirement varies between ages.

875 The model was used to predict the proportion of fish of each age at a given length, year, quarter and
876 roundfish area. The proportion of fish which were age a was set to zero outside the length range in
877 which age a was observed to avoid extrapolating small probabilities outside the realistic length span
878 of the age group. Fish larger than the maximum size aged were assigned to the plus group.
879 Combinations of age, year, quarter and roundfish area where less than 5 fish of that age or older, on
880 average, were aged in each length group were not used to predict the proportion at age. In these
881 roundfish areas, a regional model was used to predict the proportion at age. This model analysed the
882 age at length of regions based on two adjacent roundfish areas (areas 1 and 3, 2 and 4, 5 and 6 or 7
883 and 8, ICES 1996). The parameters b , c and d were estimated using all data (i.e. both data from the
884 sparsely sampled roundfish areas and from other areas) and were allowed to vary with age, year,
885 quarter and region. If the regional data did not fulfil the data requirements, the parameters estimated
886 for the entire North Sea were used to estimate the proportion at age:

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889

$$890 \log\left(\frac{p_a}{p_{a+}}\right) = b_{a,y,q} + c_{a,y,q}l + d_{a,y,q}l^2$$

891
892
893

894 The resulting age-length key is a result of the combined proportions at age from these different
895 spatial scales. Hence, the age-length key for a given location may be based on roundfish area data
896 for the youngest age groups whereas North Sea scale data are used for the older age groups.

897 **Estimation of sandeel biomass indices**

898 The biomass of sandeel caught per day in a statistical rectangle r in a given year y and quarter
899 q increases with size of the fishing vessel (ICES 1995), and the biomass available to a vessel of
900 gross tonnage GT , $CPUE_{GT,y,q,r}$, was modelled as

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904
$$\ln(CPUE_{GT,y,q,r}) = \alpha_{q,r} + \beta_{y,q} + \gamma_q \ln(GT)$$

905

906

907

908 The parameters α , β and γ were estimated using general linear models assuming a normal error
909 distribution of $\ln(CPUE_{GT,y,q,r})$. A total of more than 100 000 Danish logbook records of catches of
910 sandeel per day were used. A standard vessel size of 200 GT was used to estimate and index of the
911 sandeel biomass in a given square and year in the second ($B_{s2,y,r}$) and third ($B_{s3,y,r}$) quarter:

912

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914

915
$$B_{s2,y,r} = \exp(\alpha_{2,r} + \beta_{y,2})200^{\gamma_2}$$

916
$$B_{s3,y,r} = \exp(\alpha_{3,r} + \beta_{y,3})200^{\gamma_3}$$

917

918 This model was used to estimate sandeel biomass indices in the years 1983 to 2005 in the 2nd
 919 quarter and 1983 and 2004 in the 3rd quarter. Due to catch restrictions, the number of logbook
 920 records in the 3rd quarter of 2005 was too low to allow the estimation of reliable sandeel biomass
 921 indices. Note that if survey changes in 1991 bias all catches by a common factor, the estimated
 922 ambient sandeel biomass index is unaffected by changes in gear:

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924

925

$$926 \quad B_{s2,a,y,s} = \frac{1}{\sum_r ca_{a,1} n_{a,y,q,r}} \sum_r ca_{a,1} n_{a,y,s,r} B_{s2,y,r} = \frac{1}{\sum_r ca_{a,2} n_{a,y,s,r}} \sum_r ca_{a,2} n_{a,y,s,r} B_{s2,y,r}$$

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930 where $ca_{a,1}$ and $ca_{a,2}$ is the catchability of cod age a to the survey before and after 1991,
 931 respectively and $n_{a,y,s,r}$ is the number of cod of age a caught in an average haul in rectangle r in year
 932 y and quarter q .

933 **Estimation of average life time ambient temperature**

934 The estimation of average life time ambient temperature posed a special problem as the distribution
 935 of fish younger than 1 year is not necessarily well reflected by the distribution of 0.5-year olds in
 936 the 3rd quarter survey. It was therefore decided to assume that the distribution of 1-year olds in the
 937 1st quarter survey reflected that of the cohort up to age 1 for fish of age 1 and 1.5. The estimates of
 938 average lifetime ambient temperatures were therefore:

939

940

941

$$942 \quad T_{L,0.5,y} = \frac{1}{\sum_r n_{0.5,y,s,r}} \sum_r n_{0.5,y,s,r} T_{6-8,y,r}$$

$$943 \quad T_{L,1,y} = \frac{1}{3 \sum_r n_{1,y,s,r}} \sum_r n_{1,y,s,r} (T_{6-8,y-1,r} + T_{9-11,y-1,r} + T_{12-2,y,r})$$

$$944 \quad T_{L,1.5,y} = \frac{1}{5 \sum_r n_{1,y,s,r}} \sum_r n_{1,y,s,r} (T_{6-8,y-1,r} + T_{9-11,y-1,r} + T_{12-2,y,r} + T_{3-5,y,r}) + \frac{1}{5 \sum_r n_{1.5,y,s,r}} \sum_r n_{1.5,y,s,r} T_{6-8,y,r}$$

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948 where $T_{6-8,y,r}$ $T_{9-11,y,r}$ $T_{12-2,y,r}$ and $T_{3-5,y,r}$ denotes the average temperature in year y in rectangle sq in
 949 the months June to August, September to November, December the previous year to February the
 950 current year and March to May, respectively and $n_{a,y,s,r}$ is the number of cod of age a caught in an
 951 average haul in rectangle r in year y and quarter q . The estimates of ambient temperature are
 952 unaffected by the changes in survey gear as is ambient sandeel biomass index.
 953 Ambient temperature within the last 6 months was estimated as

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955

956

$$957 \quad T_{a,y,winter} = \frac{1}{2 \sum_r n_{a-0.5,y-1,summer,r}} \sum_r n_{a-0.5,y-1,summer,r} T_{9-11,y-1,r} + \frac{1}{2 \sum_r n_{a,y,winter,r}} \sum_r n_{a,y,winter,r} T_{12-2,y,r}$$

$$958 \quad T_{a,y,summer} = \frac{1}{2 \sum_r n_{a-0.5,y,winter,r}} \sum_r n_{a-0.5,y,winter,r} T_{3-5,y,r} + \frac{1}{2 \sum_r n_{a,y,summer,r}} \sum_r n_{a,y,summer,r} T_{6-8,y,r}$$

960

961 Tables

962 Table 1. Relationship between halfyearly average North Sea temperature ($T_{NS,y,s}$) and ambient
 963 temperatures ($T_{a,y,s}$). Values in bold are significantly different from 0 at the 5% (*), 1% (**) or
 964 0.1% (***) level.

Age	September to February		March to August	
	Correlation ¹	Difference ²	Correlation ¹	Difference ²
1	0.73***	-0.07	0.63**	-0.03
2	0.76***	0.29*	0.90***	-0.41***
3	0.94***	-0.26***	0.90***	-0.49***
4	0.91***	-0.37***	0.86***	-0.73***
5	0.78***	-0.54***	0.83***	-0.97***
6+	0.81***	-0.69***	0.79***	-1.14***

965 ¹Correlation between ambient temperature and North Sea average temperature

966 ²Average difference between ambient temperature and North Sea average temperature ($T_{a,y,s}$ -

967 $T_{NS,y,s}$)

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970

971 Table 2. Correlation between ln(average length at age of juveniles) and half yearly average North

972 Sea temperature ($T_{NS,y,s}$), ambient temperatures ($T_{a,y,s}$), log density ($\ln(N_{a,y,s})$) and fishing

973 mortality ($F_{a,y}$). Values in bold are significant at the 5% level

Age	0.5	1	1.5
$T_{L,a,y,s}$	0.60**	0.73***	0.63**
$T_{L,NS,a,y,s}$	0.47*	0.35	0.24
$\ln(N_{a,y,s})$	0.20	-0.41*	-0.41*
$F_{a,y}$			-0.06

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977

978 Table 3. Correlation between North Sea average and ambient sandeel biomass in the second and
 979 third quarter ($B_{s2,NS,y-1,summer}$, $B_{s2,1.5,y-1,summer}$, $B_{s3,NS,y-1,summer}$ and $B_{s3,1.5,y-1,summer}$, respectively), cod
 980 density ($\ln(N_{2,y,winter})$) and half yearly ($g_{0.5,y}$) and yearly ($g_{1,y}$) growth rate of cod and between
 981 explanatory values and density in the transition period. Explanatory values which were not
 982 significantly correlated to one of the two measures of growth rate as either ambient or North Sea
 983 average values are not listed. Values in bold are significant at the 5% level.

984

Age	$\ln(N_{2,y,winter})$	$B_{s2,NS,y-1,summer}$	$B_{s2,1.5,y-1,summer}$	$B_{s3,NS,y-1,summer}$	$B_{s3,1.5,y-1,summer}$
$g_{0.5,y}$	0.49*	0.58**	0.50*	0.24	0.09
$g_{1,y}$	0.51*	0.38	0.30	0.43*	0.31
$\ln(N_{2,y,winter})$		0.75***	0.62**	0.65**	0.53*

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989 Figure captions

990

991 Fig. 1. Map of the study area. Small rectangles indicates ICES statistical rectangles, Black lines
992 indicate areas used to estimate age-length keys (ICES Roundfish areas).

993

994 Fig. 2. Food composition in cod stomachs (data from Kikkert (1993)). Herring and Sprat (white),
995 gadoids (grey) and sandeel (black). Left column within tick marks represents winter (4th and 1st
996 quarter) values, right column represents summer (2nd and 3rd quarter) values.

997

998 Fig. 3. Average length of selected age groups of cod. a: 0-groups in the 3rd quarter (▲) and 1-groups
999 in the 1st (◇) and 3rd quarter (◆). Symbols not connected indicate change of survey design. b and c:
1000 Cod age 2 (×), 3 (□), 4 (△), 5 (+) and 6 (*) in the 1st (b) and 3rd quarter (c).

1001

1002 Fig. 4. Temporal development in prey biomass indices and density index of cod. Sandeel in the 2nd
1003 quarter (a), clupeid fish prey in the 1st (b) quarter, other fish prey in the 1st (c) quarter and density
1004 index of cod (d). Average in the North Sea (×) and ambient prey biomass of cod age 2 (□) and 4
1005 (△) (a, b and c) and density of age 2 (□) and 4 (△)(d).

1006

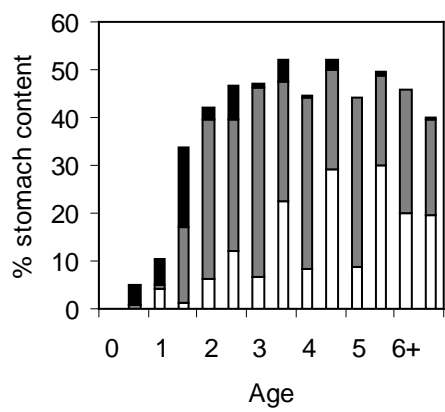
1007 Fig. 5. Temperature and growth according to the model suggested by Björnsson and Steinarsson
1008 (2002)(a) and Jobling (1988)(b). a: Growth relative to maximum for the given age. Black indicates
1009 95-100% of max growth, grey shades represent 5% levels of deteriorating growth. Area within
1010 white lines represents temperatures experienced in the period from 1983 to 2005. b: Temperature
1011 and growth relative to maximum. Note that all size groups exhibit the same relationship between
1012 temperature and relative growth in this model.

1013

1014 Fig. 6. Average ln(length) of cod age 0.5 year (a), 1 year (b) and 1.5 (c) years as a function of
1015 average life time ambient temperature. Period before (◇) and after (×) 1991 (a and c) and entire
1016 periods (◇)(b). Broken lines are regressions for the period before 1991. Lines are linear regressions
1017 for the period after 1991 (a and c) and the entire period (b).

1018

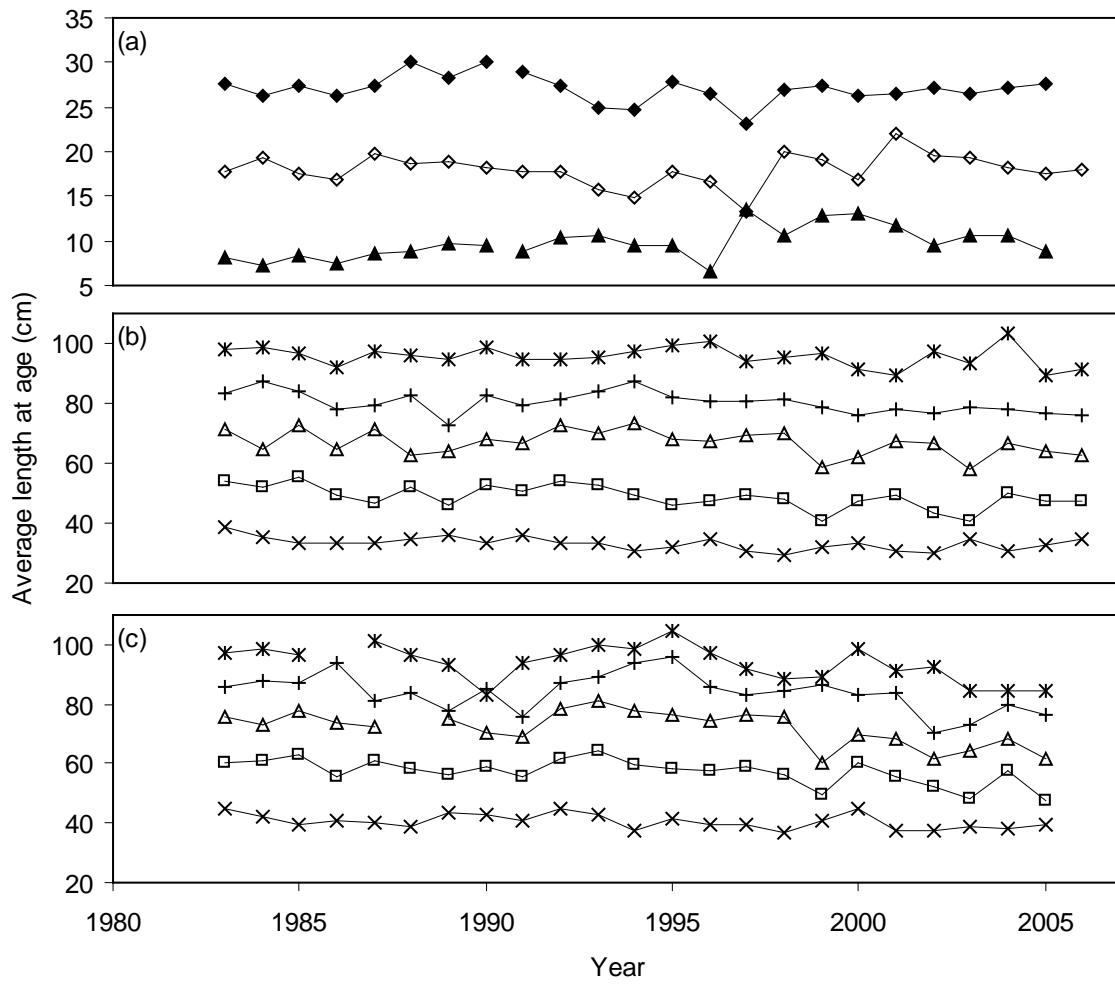
1019 Fig. 7. Growth rate during the transition period as a function of density (a) and residuals around a
1020 linear relationship between density and growth rate as a function of ambient sandeel biomass (b).
1021 Half yearly growth rate $g_{0.5,y}$ (\diamond) and yearly growth rate $g_{1,y}$ (\square). Ambient sandeel biomass are
1022 values taken for the 2nd ($B_{s2,1,y-1,summer}$) and 3rd ($B_{s3,1,y-1,summer}$) quarter for $g_{0.5,y}$ and $g_{1,y}$,
1023 respectively. Lines are linear regressions for $g_{0.5,y}$ (solid) and $g_{1,y}$ (broken).
1024



1028

1029 Fig. 2

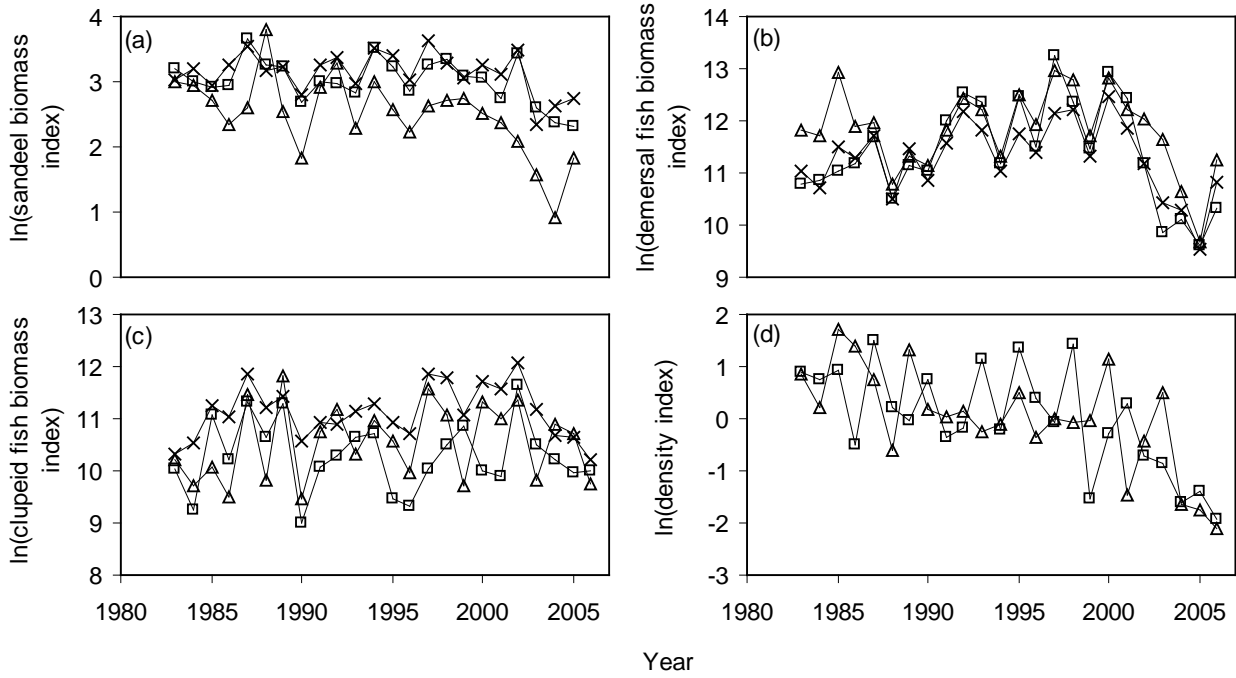
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1032 Fig. 3

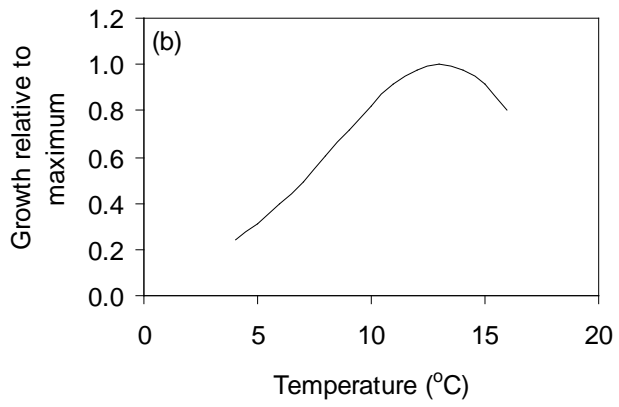
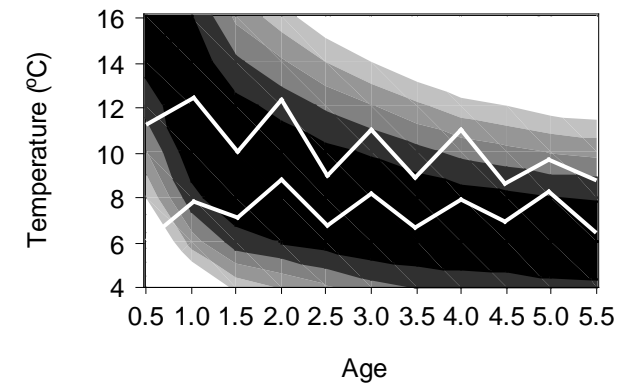
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1035 Fig. 4

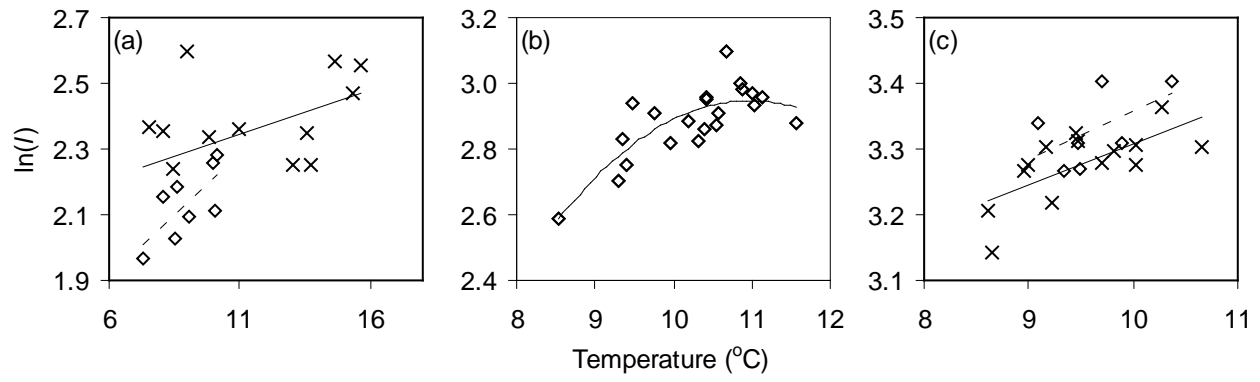
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1038 Fig. 5

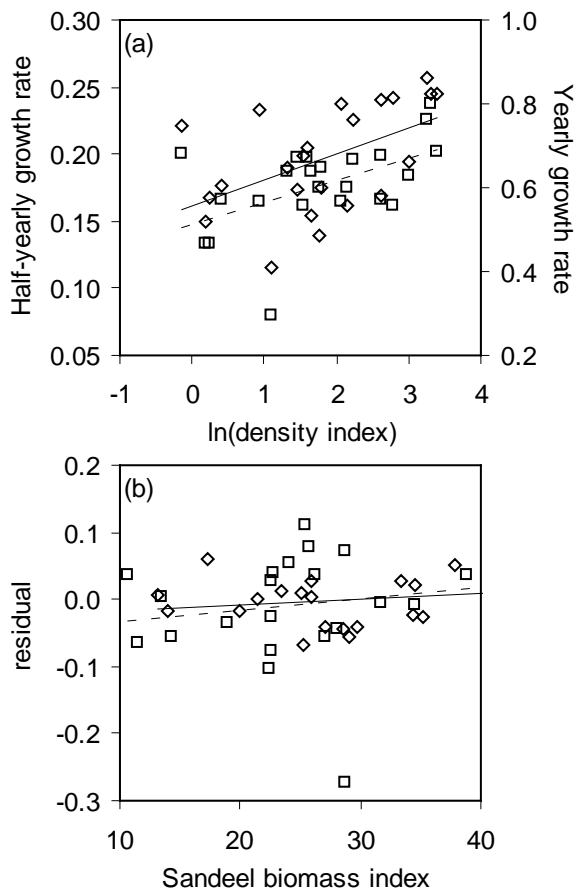
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1041 Fig. 6

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1044 Fig. 7

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