Feeding and growth of Atlantic cod (Gadus morhua L.) in the eastern Baltic Sea under environmental change

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1 **Feeding and growth of Atlantic cod (*Gadus morhua* L.) in the Eastern Baltic Sea under**

2 **environmental change**

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21 <u>Running head:</u>   Environment and cod growth

22 <u>Key words:</u>   Environmental change, predation, bioenergetics modelling, growth,

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24

25   **Abstract:**

26   Five decades of stomach content data allowed detailed insight into the long-term development of

27   consumption, diet composition, and resulting somatic growth of *Gadus morhua* (Atlantic cod) in the

28   Eastern Baltic Sea. We show a recent reversal in the development of feeding level over body length,

29   resulting in present feeding levels of small cod that indicate severe growth limitation and increased

30   starvation-related mortality. For young cod, the low growth rate and high mortality rate is

31   manifested through a reduction in size-at-age. The low feeding levels are likely the result of a

32   decrease in benthic prey abundance due to increased hypoxic areas, while decreasing abundances

33   of pelagic species in the area of cod distribution have prevented a compensatory shift in prey. Our

34   study emphasizes that under the current ecosystem state, environmental forcing as well as the

35   decline of pelagic prey caused changes in consumption and growth rates of small cod in the Baltic

36   Sea. The food reduction is amplified by stunted growth leading to high densities of cod of smaller

37   size competing for the scarce resources. Under these conditions, the average growth rate is

38   negative, and only the individuals with feeding levels well above average will survive, though

39   growing slowly. These results suggest that the relation between consumption rate, somatic growth

40   and predator-prey population densities, as well as its consequences for species interactions and

41   ecosystem functioning, are strongly environmentally mediated and hence not stable under

42   environmental change.

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Introduction:

46

47 The somatic growth of consumers depends on the availability of suitable food items (Ursin, 1967;

48 Fretwell, 1987). Food deprivation leads to stunted growth (Deelder, 1951; Amundsen and

49 Klemetsen, 1988), and in the worst case to starvation (Dutil and Lambert, 2000). Reduced growth of

50 predatory fishes may also hamper the ontogenetic transition to an energetically more profitable,

51 piscivorous diet (Werner and Gilliam, 1984), because of insufficient mouth gape size (Werner, 1974)

52 and other attack capabilities such as fast-start swimming (Domenici and Blake, 1997). In this way,

53 decreased somatic growth can affect the structuring role of a predator in the ecosystem (Brooks *et*

54 *al.* 1965; Hall *et al.* 1976), as previously suitable prey species are released from predation.

55

56 Food restriction at population level can be ascribed to density-dependence, assuming that an

57 increase in predator density leads to a decrease in the amount of prey available per individual

58 predator (Murdoch, 1994; Turchin, 2003); reduced prey availability controlled by environmental

59 conditions or anthropogenic activities such as fisheries (Uzars, 1994; Neuenfeldt and Beyer, 2006;

60 ICES 2018), or a combination of the two processes. Furthermore, the effects of environmental

61 changes can be immediate, as for example hypoxia events (Diaz and Rosenberg, 2008), or changes

62 in predator-prey spatial overlap (Neuenfeldt and Beyer, 2006), while the effects of density-

63 dependence are often delayed (Murray, 1994). This interplay between environmental changes and

64 density-dependence in shaping the dynamics of marine fish predators and prey populations is

65 complex and difficult to unravel.

66

67 During the past four decades, the Baltic Sea ecosystem went through a major reorganization with

68 two alternative states separated by a transition period in 1988–1993 (Möllmann *et al.*, 2009). The

first state is characterized by high fish predator (Eastern Baltic cod, *Gadus morhua L.*, hereafter

simply referred to as cod) and low pelagic prey (sprat, *Sprattus sprattus L.*) abundances, and the

second by decreased cod and increased sprat abundances (Casini, 2013; Möllmann *et al.*, 2009). This

shift has been attributed to a combination of overfishing of cod intertwined with unfavorable

environmental conditions for cod reproduction and favorable conditions for sprat recruitment

(Casini, 2013; Alheit *et al.*, 2005). Since the end of the 1970s, the frequency of major inflows of saline

water to the brackish Baltic Sea has decreased drastically (Matthäus and Schinke, 1994). The lack of

renewed bottom water has led to massive environmental changes, in particular hypoxia in the

bottom water (Carstensen *et al.*, 2014), accentuated by high nutrient loading from land-based

sources (Österblom *et al.*, 2007), and consequently decreased productivity of benthic prey (Karlson

et al., 2002). Hypoxia is common rather than an exception since 2005 and nowadays also extends

into the main area of cod distribution (Casini *et al.*, 2016).

In this changed ecosystem, a shift of the cod stock size structure towards smaller sizes and decline

in maximum length have been observed and advocated to be due to a decline in growth (Svedäng

and Hornborg, 2014; Eero *et al.*, 2015; Orio *et al.*, 2017). However, the problematic age

determination of Eastern Baltic cod (Eero *et al.*, 2015) has prevented a confirmation of this theory

and therefore the mechanistic understanding of these observations.

Here, we investigate changes in the diet composition of the Eastern Baltic cod, its feeding levels and

consumption rates, and their consequences for growth and mortality over five decades using

stomach content data in combination with bioenergetics models. After the larval stage, cod

experiences two feeding modes. Small, post-settlement 4-16 cm cod mainly consume benthic

92   invertebrates (Hüssy, 1997), while larger individuals consume a mix of fish and benthic invertebrates

93   (Uzars, 1994; Neuenfeldt and Beyer, 2006; Pachur and Horbowy, 2013). We therefore examine the

94   ontogenetic development of diet composition and energy intake to identify life stages with critical

95   feeding conditions. Subsequently, we track the temporal dynamics in feeding levels and growth

96   during these sensitive life stages. Using empirical data and bioenergetics, we address the following

97   questions: (1) have size-specific feeding levels changed during the past five decades and which are

98   the likely causes? (2) what are the expected long-term changes in cod growth considering the

99   changes in feeding level (3) when during life history is the bottleneck for cod growth and survival?

100

101

102   **Material and Methods:**

103   *Stomach data*

104   About 120 000 stomachs of Atlantic cod in the Eastern Baltic Sea have been sampled by trawling

105   between 1963 and 2014 (Fig. 1). Sampling covered the distributional area of the Eastern Baltic cod

106   population (Bagge, 1994) except in the period 1995 to 2004, where sampling was limited to the

107   north-eastern part. Prey items in the stomachs were recorded at the highest possible taxonomic

108   resolution with total mass, and, where identifiable, number of individuals and lengths per prey

109   taxon. At least individual predator length was also recorded (except 1975 to 1979), and in later years

110   also predator weight (Huwer *et al.*, 2014; ICES, 2014a). The data are available at ICES (www.ices.dk).

111

112   Previous studies have shown that 15-40 % of cod stomachs are empty (Uzars, 1994; Neuenfeldt and

113   Beyer, 2003), which has an important impact on estimates of population-level mean consumption

114   rate. Whether or not a stomach is truly empty, or the fish has regurgitated the content during

trawling and processing, was deducted from the appearance of the gall bladder (ICES, 1991) since

the mid-1980s. In the stomach sampling for the last decade, cod with signs of regurgitation have

been replaced during sampling by randomly selected individuals of the same length and with

stomach contents (Huwer *et al.*, 2014). However, whether this practice has been the same for the

sampling between 1963 and 2005 is unknown. Exploratory analyses indicate, though, that in this

earlier period at least not all cod with signs of regurgitation have been discarded. Consequently,

temporal differences in the fraction of empty stomachs before and after 2005 are possibly a

sampling artefact, and the fraction probably being over-estimated from the data until 2005. This

means that calculated decreases in consumption rates after 2005 would be conservative estimates

since they were probably more pronounced in reality. Constant or increasing consumption rates

would, on the other hand, be difficult to verify, because any increase or constant levels of average

population-level consumption rates might be due to the lower observed fraction of empty stomachs

after 2005.

Consumption rates and feeding levels

Average daily energy consumption rates *C* (kJ d^{-1}) were estimated using the cylinder gastric

evacuation rate model (Andersen and Beyer, 2005a, b) by year and 1-cm predator length group for

cod between 20 and 80 cm total length, amounting to 109 000 stomachs in this size range from the

stomach database. Experienced temperature *T* was assumed constant at 5°C, corresponding roughly

to the average temperature experienced by cod in the Baltic Sea (Righton *et al.*, 2010). Note that

the focus in this study is to compare consumption rates in different periods. Although cod

experience varying temperature throughout the year, only significant trends in average

temperature regime for the cod in their preferred habitat might potentially bias our analyses. Such

138   trends have not been shown for the Baltic Sea. We assumed constant energy densities E_i for benthic

139   prey (3.5 kJ g^{-1}) and consumed fishes (*Clupea harengus L.* (herring) and sprat 5.5 kJ g^{-1}, cod 4.0 kJ g$^-$

140   ^{1} ;Pedersen and Hislop, 2001). *E* denotes the average energy densities (kJ g^{-1}) of the individually

141   observed total stomach contents *S* (g). Using the principle that consumption rate *C* (kJ d^{-1}) on

142   average over population and time equals evacuation rate (Pennington, 1985), and knowing cod total

143   length *L* (cm) and the basic evacuation rate parameter ρ_0 = 2.43 x 10^{-3}, we used the parametrization

144   of the cylinder model for cod presented in Andersen (2012):

145

146   $$C = 24\,\rho_0 L^{1.30} e^{0.083T} E^{0.15}\sqrt{S} \qquad\qquad (1)$$

147

148   Feeding level *f* is actual energy intake *C* expressed relative to maximum sustained energy intake

149   $C_{\max}$ (*f* = *C* / $C_{\max}$). The maximum intake $C_{\max}$ was obtained from Jobling (1988):

150

151   $$C_{\max} = 0.223 e^{(0.104T - 0.000112T^3)} W^{0.802} \qquad\qquad (2)$$

152

153   Where T is temperature (°C). The stomach data rarely specified cod weight *W* (g), so here a

154   relationship based on data from the Danish part of the Baltic International Trawl Survey covering

155   the cod distributional area (data on www.ices.dk) was used:

156

157   $$W = 6.838*10^{-3}\ L^{3.07} \qquad\qquad (3)$$

158

159   The condition of cod in the Eastern Baltic Sea has declined since 1990. We have not considered this

160   when calculating $C_{\max}$, and thus feeding level *f*, because the condition of the cod used by Jobling

161   (1988) to establish Eqn (2) is unknown. The assimilative capacity of fish is related to the structural

162   size (i.e., the body length) rather than the condition and hence the body mass (e.g. Andersen, 2001).

163   The consequence is that our estimates of $C_{\max}$ using eqn. (2) becomes lower, and thus f higher, when

164   condition declines because the body mass at specific length becomes lower. This further means that

165   our estimates of the temporal development of f are conservative – for example, the decline for small

166   cod is probably more pronounced than we find.

167

168   *Bioenergetics growth model*

169   We estimated the somatic growth rates P_B (kJ d^{-1}) from the observed feeding levels using a simplified

170   energy balance equation (Andersen and Riis-Vestergaard, 2003):

171

172     $$P_B = \kappa f C_{\max} - R_S - R_A \, , \qquad\qquad\qquad (4)$$

173

174   where net food conversion efficiency κ is described by a simple power function of food consumption

175   rate $\kappa = 0.426 \, (f C_{\max})^{0.109}$, and $R_S = 5.52 \, (0.001W)^{0.75} \, e^{0.08T}$ (Andersen and Riis-Vestergaard, 2003)

176   and R_A are standard metabolic rate and costs of swimming activity (kJ d^{-1}). R_A is determined by the

177   activity multiplier 1.25 (Hansson *et al.*, 1996) as $R_S + R_A = 1.25 \, R_S$. Due to the focus on juvenile cod,

178   gonadal maturation was assumed to be negligible in the bioenergetics growth model and set to 0.

179   Body mass (g) was determined iteratively as $W_{t+\Delta t} = W_t + P_{B,t} \, (0.057 L_t + 3.37)$. The energy to mass

180   conversion factor $0.057 L_t + 3.37$ (Pedersen and Hislop, 2001) was assumed to depend on length

181   only. Time increments Δt were in daily steps and length measured in cm. Length was calculated using

182   eqn. (3).

183

Observational data on catch per unit of effort and hypoxic areas

185   Indices of cod density in the first quarter of the year (calculated as catch per unit of effort, CPUE, in

186   numbers per hour; herein referred to as density) from the Baltic International Trawl Survey (BITS)

187   in ICES sub-divisions 25, 26 and 28 were retrieved from the ICES DATRAS database

188   (http://www.ices.dk/marine-data/data-portals/Pages/DATRAS.aspx). The indices are based on

189   bottom trawl hauls typically swept between 20 and 100 m depth, whereas hauls shallower than 20

190   m and deeper than 100 m are very rare (ICES, 2014b).

191

192   Time-series of total areas (km^2) of hypoxic bottoms (here taken as areas between 20 and 100 m

193   depth (Casini *et al*., 2016) with an oxygen concentration of < 1 ml l^{-1}, i.e. approx. 1.4 mg l^{-1}) by sub-

194   division (25, 26 and 28) were obtained from the Swedish Meteorological and Hydrological Institute

195   (SMHI, www.smhi.se). We used 1 ml l^{-1} as threshold for hypoxia to indicate failure in benthic

196   productivity (Karlson *et al*., 2002; Conley *et al*., 2009).

197

198

199   **Results:**

200   The data show a pronounced change in the average mass of prey in stomachs containing that prey

201   for all sizes of cod after the Baltic regime shift (Fig. 2). The mass of the benthic isopod *Saduria*

202   *entomon* in the stomachs in the period 1963-1988 was increasing constantly with increasing cod

203   size, while in the period 1994-2014, after the regime shift, the mass of *S. entomon* is rather constant

204   at a low level through cod ontogeny. The mass of the nekto-benthic crustacean *Mysis mixta*

205   increased slightly in the diet of cod < 35 cm, but decreased in the diet of cod > 35 cm after the

206   regime shift, although the biomass of this prey in the stomachs has been small throughout the entire

207 time-series. Sprat mass has also declined in the stomachs of small cod, with the decline becoming

208 more obvious with increasing cod size after the regime shift. The average mass of herring in the

209 stomachs of larger cod remained unchanged between the two periods, while herring mass in the

210 stomachs increased in the later period for cod between 25 cm and 35 cm. (Fig. 2). In the most recent

211 period, there is on average about twice as much cod in the stomach of cod > 40 cm than before the

212 regime shift. The mass of other prey, mainly benthic organisms and flatfish, in the cod stomachs

213 increased for cod > 50 cm after the regime shift.

214

215 The average daily consumption rate of 20-30 cm cod increased in the beginning of the time-series,

216 reached a maximum in 1990s and rapidly decreased in the early 2000s (Fig. 3). In contrast,

217 consumption of 30-40 cm cod showed an increasing trend during the whole time-series, except for

218 a slight decline in early 1990s (Fig. 3). This development is the same also for cod > 40 cm (not shown

219 here). In connection to the diet represented in Fig. 2, the decrease in consumption rates of cod < 30

220 is due to a reduction of benthos and to a limited extent also of sprat in the diet, partialy

221 compensated by increased herring consumption. The minor increase in the consumption rates of

222 30-40 cm cod is driven by increased consumption on mysids and herring, and a few observations of

223 cannibalism.

224

225 The decreasing consumption rates of small cod in the latest years, and the on average increasing

226 rates for larger ones, become clearly visible in the development of feeding levels over cod length

227 during the last five decades (Fig. 4). Feeding levels of cod 20-30 cm were among the lowest on record

228 in 2005-2014. Low average feeding levels of 20-30 cm cod, comparable with the recent low values,

229 could also be observed in 1965-1974. Average feeding levels of larger cod were continuously

230 increasing with length during 2005-2014, which was unseen in the 4 decades before.

231

232 The growth curve of immature cod in the last decade, emerging from the bioenergetics model,

233 differed clearly from the four decades before, with average growth becoming negative (Fig. 5). This

234 negative modelled average growth implies that, *in vivo,* a large fraction of cod < 35 cm does not

235 grow in length, gets thinner over time, and likely dies due to starvation.

236

237 The size distribution of cod is progressively truncated from 2009 onwards (Fig. 6). There is more

238 fish of the same, small size in the stock. The abundance of specimen >35-40 cm decreased

239 drastically.

240

241 There are basin-specific differences in the development of hypoxic areas (Fig. 7). Before the mid-

242 1990s, hypoxic event were only temporary, and thus the inter-annual extent of hypoxic areas varied

243 extensively. Conversely, hypoxic area size in the Bornholm Basin reached a plateau in 1994 until

244 2001, when about 5000 km^2 of the bottom were hypoxic. Again between 2005 and 2010 hypoxia

245 was constantly at high levels, corresponding to 6000 km^2, in the Bornholm Basin. These two periods

246 of long-term chronic hypoxia in the most important distributional and reproductive area for cod

247 (Fig. 7) have been unprecedented during the time-series.

248

249

250 **Discussion**:

251   Our analyses revealed that decreased growth and survival of small cod may be an extension of the

252   juvenile, post-settlement bottleneck (Hüssy *et al.*, 1997; Tupper and Boutilier, 1995). Feeding levels

253   of small cod have been critically low in recent years, at or even below minimum fish maintenance

254   levels (Kitchell *et al.*, 1977; Andersen and Riis-Vestergaard, 2003). The low feeding levels most

255   probably result from a decrease in benthic prey availability due to increased hypoxic areas. The

256   resulting growth reduction in this life stage that we calculated based on a bioenergetics model, is

257   supported by the observed length distributions from the survey. The size structure of the cod

258   population has changed towards smaller individuals. Our study emphasizes that, under the current

259   ecosystem state, environmental forcing as well as a decline of pelagic prey causes changes in

260   consumption and growth rates of small cod in the Baltic Sea, resulting in an accumulation of small-

261   sized cod in its population.

262

263   In our study, we modelled the expected changes in the cod growth from the changes in the stomach

264   content data. The analyses suggest a reduction in growth that can explain the shift of the cod length

265   distribution towards lower sizes over time. Moreover, the negative average modelled growth rate

266   in the most recent period implies that many cod individuals die due to starvation. Only the fishes

267   with feeding levels well above average will survive, though growing slowly. Size at sexual maturation

268   (L_{50}) has declined from 45-50 cm for females and 37-41 cm in males in 1984-1988 (Cardinale &

269   Modin 1999) to about 19 cm in 2015 (Köster *et al*., 2016). Since we did not account for energy spent

270   for maturation in our bioenergetics model, growth might have been slowed down even further, if

271   energy was used for gonadal maturation. The surviving part of the population may be estimated by

272   comparing the growth rates presented here, based on stomach data and bioenergetics modelling,

273   to growth rates estimated independently, for example from tagging data. However, even in the

274 absence of such analyses, the available survey data with practical absence of cod > 40 cm in recent

275 years, presented in this study, strongly support increased natural mortality and stunted growth.

276 Although dead emaciated fish are found only very rarely in the environment, starvation nevertheless

277 occurs frequently (Dutil and Lambert, 2000; Holdway and Beamish, 1984). The slower growth of the

278 survivors renders small cod easier to be preyed upon by larger cod, because they remain longer in

279 the size window that is vulnerable to predation. Starvation makes the cod probably more vulnerable

280 to parasites which is in line with recent observations of increasing liver worm *Contracaecum*

281 *osculatum* infection in the Eastern Baltic cod (Sokolova *et al.*, 2018; Haarder, 2014; Horbowy *et al.*,

282 2016).

283

284 The growth reduction results in a change in cod size distribution with increased densities of smaller

285 sizes. Since the relevant, benthic and pelagic food items are scarce, as visible by their decline in the

286 diet, implied by the extent of hypoxic areas and the observed decline in sprat biomass (Casini et al.

287 2016), a feedback-loop emerges, because the accumulation intensifies the competition for food in

288 the benthivore life stage leading to further food limitation and growth reduction. Consequently,

289 growth is arrested, and the population is trapped in an ontogenetic bottleneck. The bottleneck

290 occurs below 30 cm and thus inhibits the ontogenetic trophic niche shift towards a diet dominated

291 by pelagic fish. Further, it stops the production of individuals that recruit into the commercial

292 fisheries, currently at 35 cm (ICES, 2018). This way, there are very few cod with above-average

293 growth, and the survey size distributions (Fig. 6) imply that this fraction of large cod is decreasing

294 over time. The stomach data indicate that the high average feeding levels of these large specimens

295 are mainly caused by rare events of cannibalism, that nevertheless probably increase mortality for

296 the small cod. Consequently, due to the decreasing abundance of large cod, the predatory impact

297   of the cod population on larger prey such as herring and flounder decreases. In the area of cod

298   distribution, Baltic sprat started to decline in the mid-1990s (Casini *et al.*, 2016). This decline

299   coincides with the changes in the cod food intake after the regime shift. Coinciding with the sprat

300   decline in the area of cod distribution, sprat consumption by cod declined, too.

301

302   Recolonization time of benthic areas by invertebrates after an extended hypoxic period needs to be

303   investigated in order to predict cod food availability after re-oxygenation of the deep water. Two

304   prolonged stagnation periods in the main distributional area of the cod population have obviously

305   decimated the benthic prey species. Here, the cod stomachs themselves serves as indicators in the

306   absence of reliable biomass data for benthic prey. Also, the abundance and spatial distribution of

307   competitors for benthic prey, such as flounder (Orio *et al.*, 2019), have to be taken into account and

308   could have worsened the feeding conditions for cod. Knowing the body size and condition that a

309   predatory cod would need to successfully forage on the pelagic sprat would help to determine if

310   reducing the commercial exploitation rate of sprat will potentially improve the food situation for

311   the small, starving cod. These questions have to be answered spatially explicitly, probably on a scale

312   smaller than the ICES sub-divisions, where biomass estimates of sprat match the prey field

313   predatory cod experience.

314

315   Areas where feeding opportunities, growth and condition of cod may be unaffected by hypoxia may

316   exist in waters shallower than those covered by the Baltic International Trawl survey of which more

317   than 85% of the stations are located at depths >40 m and all on soft bottom. Stomach data from

318   coastal areas would facilitate investigating the importance of shallow waters as source for

319   replenishing the deteriorated population residing in deeper waters. However, juvenile cod has

320 shifted its distribution towards deeper areas the last years (Orio et al., 2019), suggesting that the

321 shallow areas may currently not be that important after all.

322

323 Our study emphasizes that environmental forcing, giving rise to hypoxia, has probably triggered the

324 observed changes in consumption and growth rates for cod in the Baltic Sea during the past decades

325 by reducing growth of pre-piscivorous specimens. Moreover, the resulting increased densities of

326 small cod along with a decline in sprat densities have intensified the competition for food leading

327 to further food limitation and growth reduction. Environmental changes decouple many population

328 dynamic control mechanisms (Gårdmark *et al.*, 2015). Growth and mortality change independently

329 of predator and prey densities and feedback loops, that otherwise are considered key in the

330 transition between alternative stable states (Moellmann *et al.*, 2009; Scheffer, 2009). Our results

331 underline that the relation between population density and vital rates under environmental changes

332 has to be understood mechanistically to fully comprehend the ecosystem changes currently

333 observable in multiple places globally (Folke *et al.*, 2004), and to devise remedies where possible.

334

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345 this study were collected during ordinary field monitoring under the EU Data Collection Framework,

346 for which no species research or animal ethics permissions are required.

347

348 **Data accessibility:**

349 All data supporting the results are already available online at www.ices.dk. A more compiled data

350 set will be made available in an appropriate public repository, should the manuscript be accepted.

351

352 **Author's contributions:**

353 STN was responsible for research design with assistance from MC, and drafted the main text and

354 figures. VB and AO pre-processed the data and improved the figures. STN, KHA and NGA developed

355 the modelling framework. STN, SN, UB, NK and MC pre-processed data. DU compiled the major part

356 of the stomachs data. All authors were involved in discussions and editing of the text.

357

358 **Competing interests:** The authors have no competing interests.

359

360

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Figure captions:

Fig. 1:

ICES sub-divisions (bottom right panel) and stomach sampling coverage: number of *Gadus morhua*

stomachs by ICES statistical rectangle for each period specified on top of each panel.

Fig. 2:

Diet composition in *Gadus morhua* stomachs by average mass, given that the specific prey is found

in the stomach, before 1988 (black) and after 1994 (red). The transition period between ecological

regimes from 1988 to 1993 (Moellmann *et al.* 2009) is left out. The diet is given in average biomass

observed in the stomachs of a given length (cm) during the two respective periods. For *Saduria*

entomon the biomass in the stomachs is given in an insert for cod ≤ 40 cm total length.

Fig. 3:

Trends in daily food consumption rate of *Gadus morhua* in four length classes; LOESS-based

smoothed trends are plotted in blue together with shadowed confidence limits.

Fig. 4:

Feeding levels of *Gadus morhua* by length during the past five decades. LOESS-based smoothed

trends are plotted in blue together with shadowed confidence limits. The lower right panel: feeding

level over time for *G. morhua* of 21 - 30 cm total length.

Fig. 5:

543 Simulated growth trajectories of *Gadus morhua* in the total length range 21-35 cm for the five

544 decades covered by the stomach sampling programme.

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546 Fig. 6:

547 Catches per unit of effort (CPUE) for Eastern Baltic cod by 1 cm cod length group for three different

548 periods since 2009.

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550 Fig. 7:

551 Extent of hypoxic bottom areas in different basins of the Baltic Sea during the stomach sampling

552 program. Hypoxic condition is defined as <1 ml l^{-1} oxygen concentration and given in 10^3 km^2. The

553 different basins are the Bornholm Basin (BB, ICES sub-division 25), the Gdansk Deep (GD, ICES sub-

554 division 26), and the Gotland Basin (GB, ICES sub-division 28).

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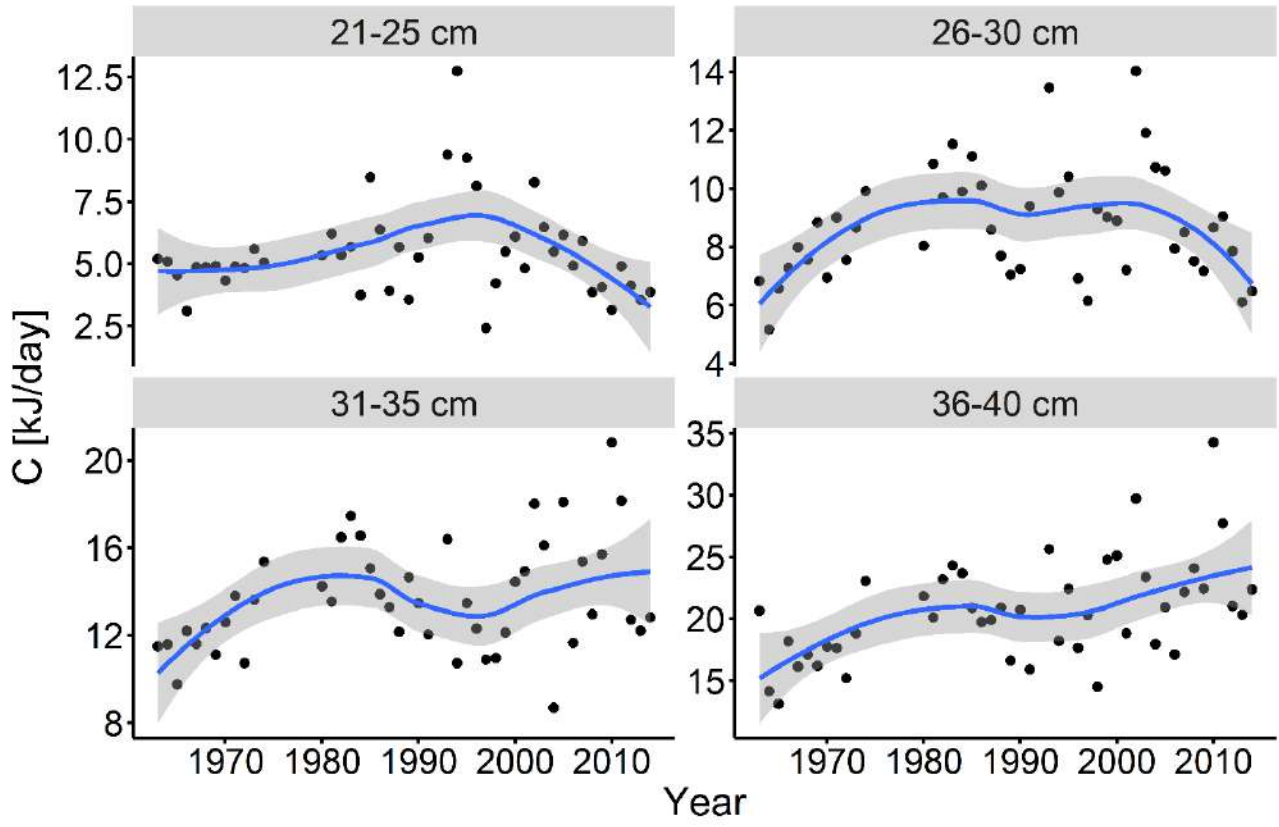559

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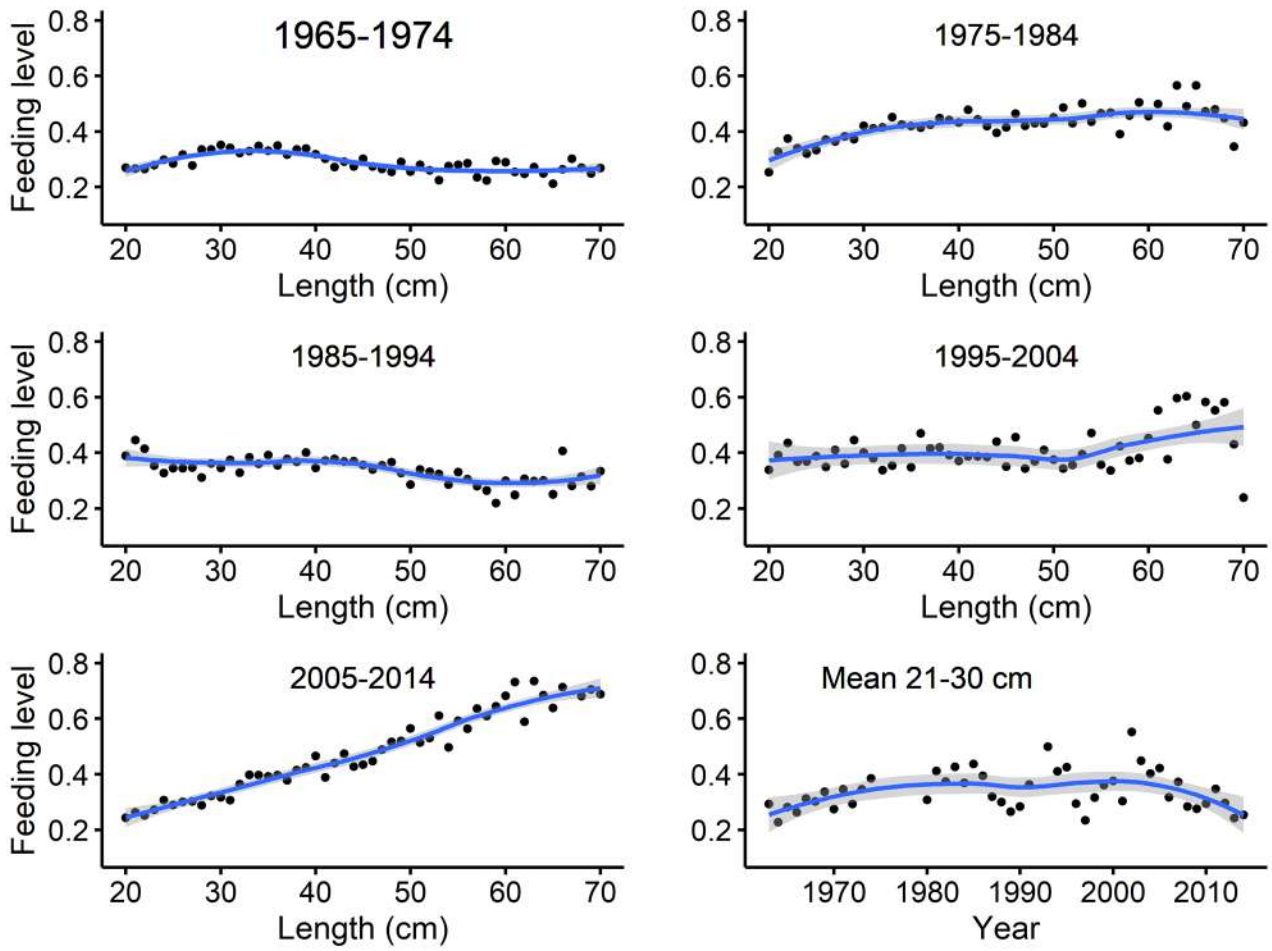
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571   Fig. 1

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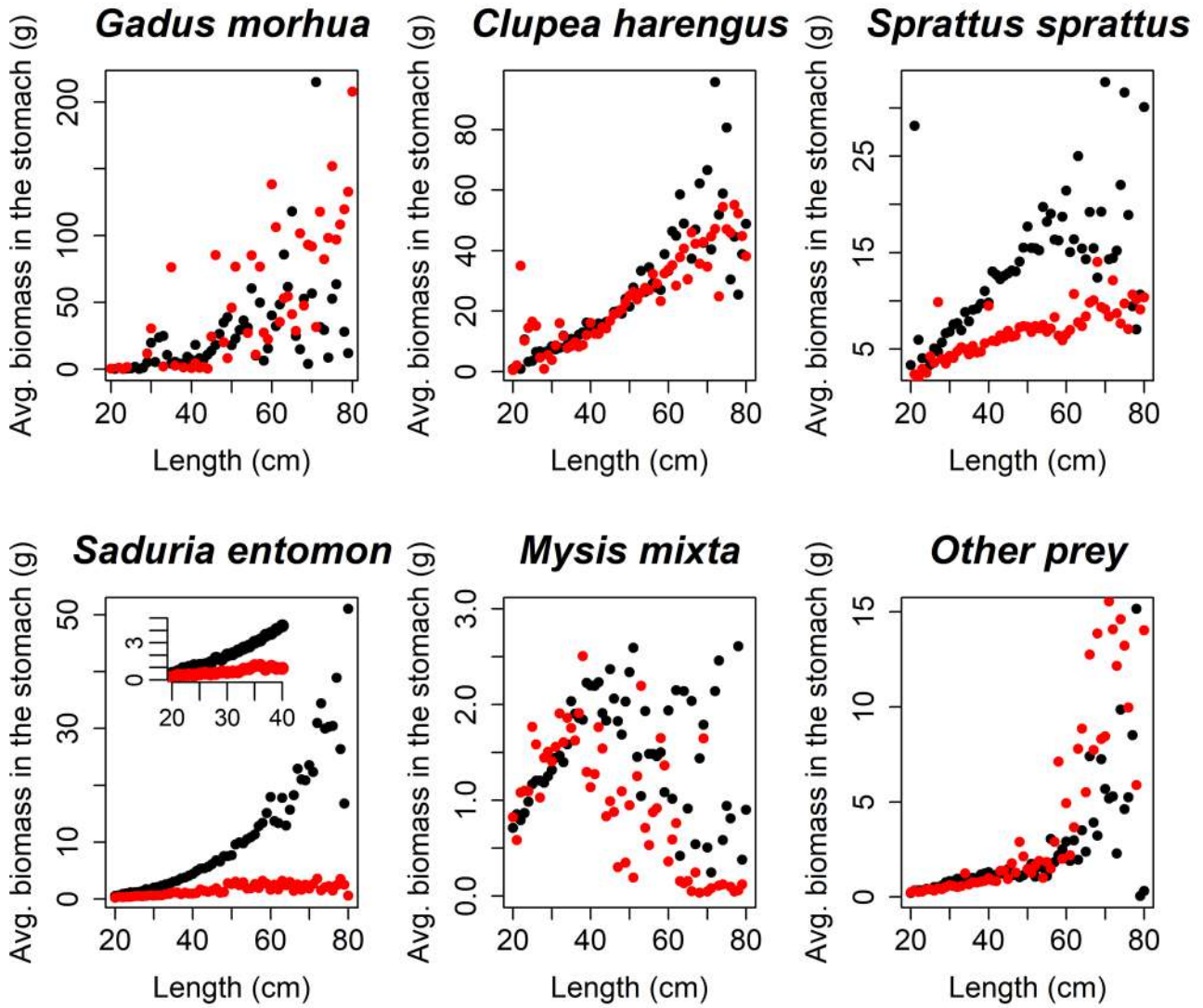
Fig. 2

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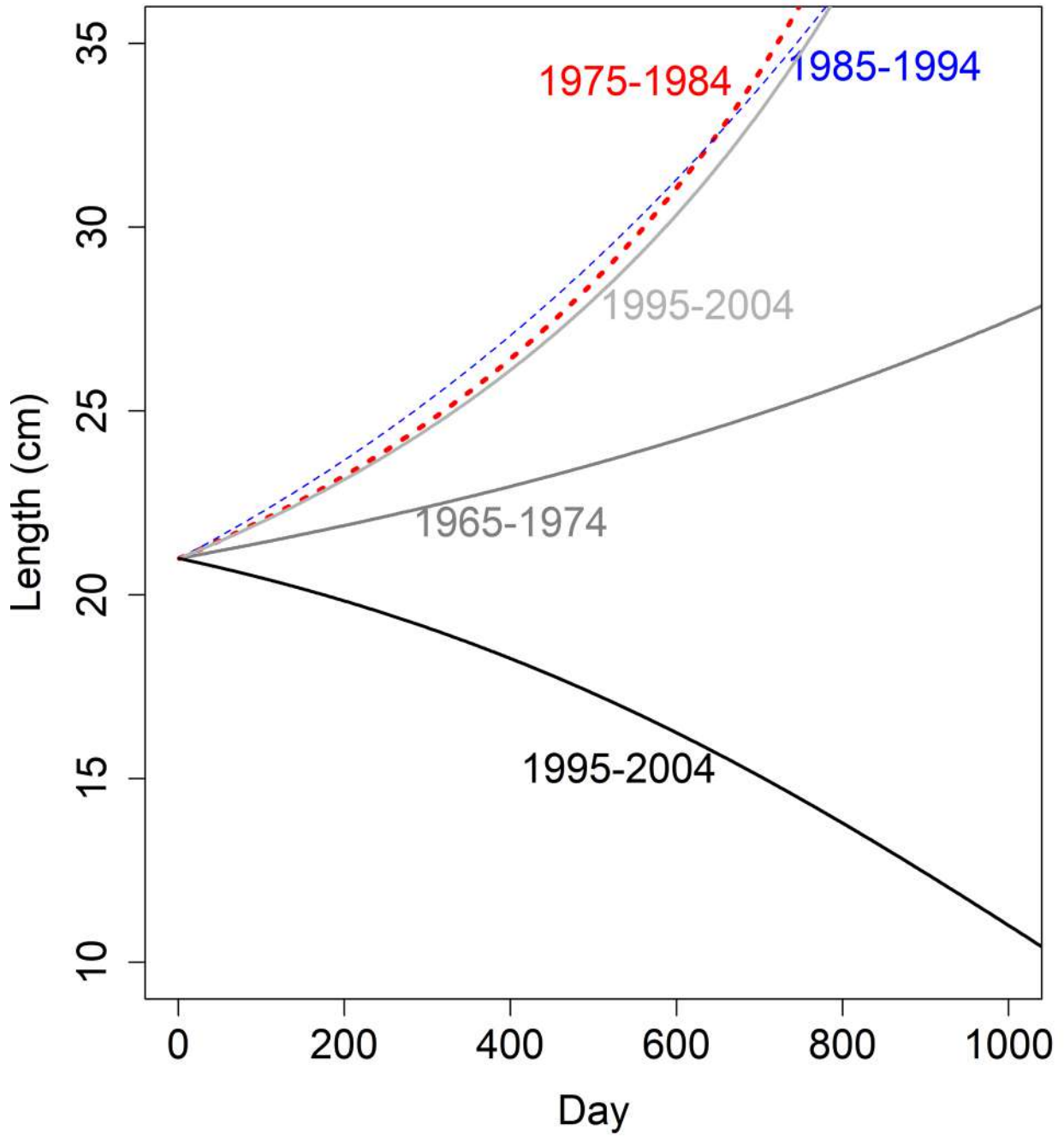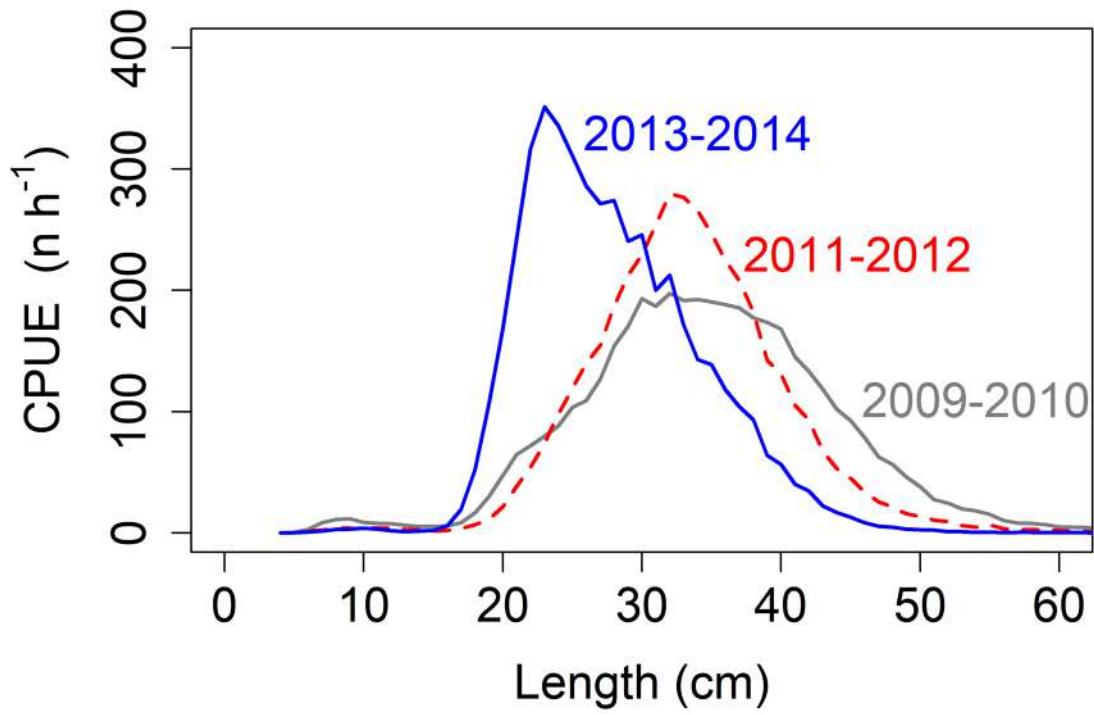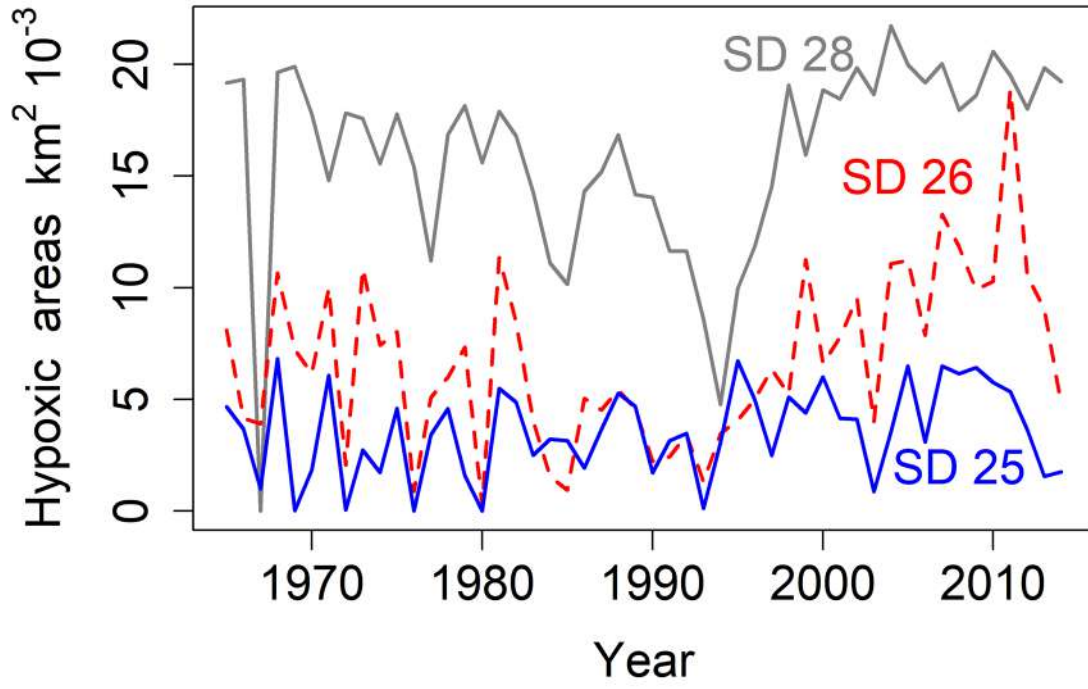
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