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

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Five decades of stomach content data allowed insight into the development of consumption, diet composition, and resulting somatic growth of *Gadus morhua* (Atlantic cod) in the eastern Baltic Sea. We show a recent reversal in feeding level over body length. Present feeding levels of small cod indicate severe growth limitation and increased starvation-related mortality. For young cod, the low growth rate and the high mortality rate are manifested through a reduction in size-at-age. The low feeding levels are likely the result of a decrease in benthic prey abundance due to increased hypoxic areas, while decreasing abundances of pelagic species in the area of cod distribution have prevented a compensatory shift in diet. Our study emphasizes that environmental forcing and the decline in pelagic prey caused changes in consumption and growth rates of small cod. The food reduction is amplified by stunted growth leading to high densities of cod of smaller size competing for the scarce resources. The average growth rate is negative, and only individuals with feeding levels well above average will survive, though growing slowly. These results suggest that the relation between consumption rate, somatic growth and predatorprey population densities is strongly environmentally mediated.

Keywords: Baltic Sea, bioenergetics modelling, environmental change, *Gadus morhua*, growth, predation, stomach data.

Introduction

The somatic growth of consumers depends on the availability of suitable food items (Ursin, 1967; Fretwell, 1987). Food deprivation leads to stunted growth (Deelder, 1951; Amundsen and Klemetsen, 1988) and in the worst case to starvation (Dutil and Lambert, 2000). Reduced growth of predatory fishes may also hamper the ontogenetic transition to an energetically more profitable, piscivorous diet (Werner and Gilliam, 1984), because of insufficient mouth gape size (Werner, 1974) and other attack capabilities, such as fast-start swimming (Domenici and Blake, 1997). In this way, decreased somatic growth can affect the structuring role of a predator in the ecosystem (Brooks and Dodson, 1965; Hall *et al.*, 1976), as previously suitable prey species are released from predation.

Food restriction at population level can be ascribed to density dependence, assuming that an increase in predator density leads to a decrease in the amount of prey available per individual predator (Murdoch, 1994; Turchin, 2003), reduced prey availability controlled by environmental conditions or anthropogenic activities, such as fisheries (Uzars, 1994; Neuenfeldt and Beyer, 2006;

ICES, 2018), or a combination of the two processes. The effects of environmental changes can be immediate, as for example hypoxia events (Diaz and Rosenberg, 2008), or changes in predator-prey spatial overlap (Neuenfeldt and Beyer, 2006). On the other hand, the effects of density dependence are often delayed (Murray, 1994). This interplay between environmental changes and density dependence in shaping the dynamics of marine fish predators and prey populations is complex and difficult to unravel.

During the past four decades, the Baltic Sea ecosystem went through a major reorganization with 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 state is characterized by decreased cod and increased sprat abundances (Möllmann *et al.*, 2009; Casini, 2013). This shift has been attributed to a combination of overfishing of cod intertwined with unfavourable environmental conditions for cod reproduction and favourable conditions for sprat recruitment (Alheit *et al.*, 2005; Casini, 2013). 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 has 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.

In this study, 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 invertebrates (Hüssy *et al.*, 1997), while larger individuals consume a mixture of fish and benthic invertebrates (Uzars, 1994; Neuenfeldt and Beyer, 2006; Pachur and Horbowy, 2013). We, therefore, examine the ontogenetic development of diet composition and energy intake to identify life stages with critical feeding conditions. Subsequently, we track the temporal dynamics in feeding levels and growth during these sensitive life stages. Using empirical data and bioenergetics, we address the following questions: (i) Have size-specific feeding levels changed during the past five decades and which are the likely causes? (2) What are the expected long-term changes in cod growth considering the changes in feeding level? (3) When during life history is the bottleneck for cod growth and survival?

Material and methods
Stomach data
Approximately 120 000 stomachs of Atlantic cod in the eastern Baltic Sea have been sampled by trawling between 1963 and 2014

(Figure 1). Sampling covered the distributional area of the eastern Baltic cod population (Bagge, 1994) except in the period 1995–2004, where sampling was limited to the north-eastern part. Prey items in the stomachs were recorded at the highest possible taxonomic resolution with total mass and, where identifiable, number of individuals and lengths per prey taxon. At least individual predator length was also recorded (except 1975–1979), and in later years also predator weight (Huwer *et al.*, 2014; ICES, 2014a). The data are available at ICES (www.ices.dk).

Previous studies have shown that 15–40% of cod stomachs are empty (Uzars, 1994; Neuenfeldt and Beyer, 2003), which has an important impact on estimates of population-level mean consumption 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 the treatment of cod with signs of regurgitation 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
The average daily energy consumption rates *C* (kilojoules per day) were estimated using the cylinder gastric evacuation rate model (Andersen and Beyer, 2005a, b) by year and 1-cm predator length group for cod with the total length of between 20 and 80 cm, 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 temperatures throughout the year, only significant trends in average temperature regime for the cod in their preferred habitat might potentially bias our analyses. Such trends have not been shown for the Baltic Sea. We assumed constant energy densities E_i for benthic prey (3.5 kJ g^{-1}) and consumed fishes [*Clupea harengus* L. (herring) and sprat 5.5 kJ g^{-1} and cod 4.0 kJ g^{-1}; Pedersen and Hislop, 2001]. *E* denotes the average energy densities (kilojoules per gram) of the individually observed total stomach contents *S* (gram). Using the principle that consumption rate *C* (kilojoules per day) on average over population and time equals evacuation rate (Pennington, 1985), and knowing the total length *L* (cm) of cod and the basic evacuation rate parameter $\rho_0 = 2.43 \times 10^{-3}$, we used the parametrization of the cylinder model for cod presented in Andersen (2012):
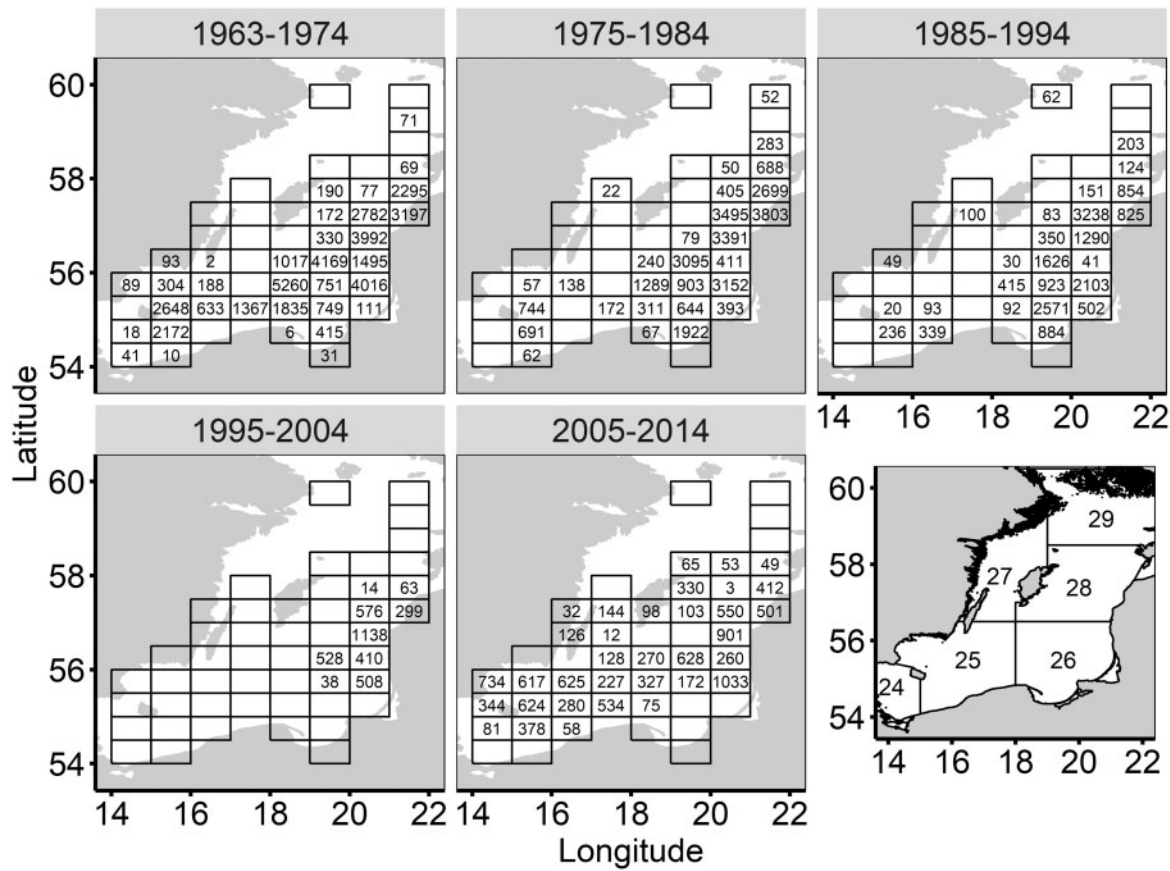
Figure 1. ICES sub-divisions (bottom right panel) and stomach sampling coverage: number of *Gadus morhua* stomachs by ICES statistical rectangle for each period specified on top of each panel.

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

The feeding level *f* is the actual energy intake *C* expressed relative to maximum sustained energy intake C_{max} ($f = C/C_{max}$). The maximum intake C_{max} was obtained from Jobling (1988):

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

where *T* is the temperature (°C). The stomach data rarely specified cod weight *W* (g); so here a relationship based on data from the Danish part of the Baltic International Trawl Survey (BITS) covering the cod distributional area (data on www.ices.dk) was used:

$$W = \quad 6.838 \; \times \; 10^{-3} \; L^{3.07}. \qquad (3)$$

The condition of cod in the eastern Baltic Sea has declined since 1990. We have not considered this when calculating C_{max}, and thus feeding level *f*, because the condition of the cod used by Jobling (1988) to establish (2) is unknown. The assimilative capacity of fish is related to the structural size (i.e. the body length) rather than the condition and hence the body mass (e.g. Andersen, 2001). The consequence is that our estimates of C_{max} using (2) become lower and, thus, that of *f* becomes higher, when condition declines because the body mass at specific length becomes lower. This further means that our estimates of the

temporal development of *f* are conservative—for example the decline in small cod is probably more pronounced than we find.

Bioenergetics growth model

We estimated the somatic growth rates P_B (kilojoules per day) from the observed feeding levels using a simplified energy balance equation (Andersen and Riis-Vestergaard, 2003):

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

where the net food conversion efficiency κ is described by a simple power function of food consumption rate $\kappa = 0.426$ $(fC_{max})^{0.109}$, and $R_S = 5.52 \; (0.001W)^{0.75} e^{0.08T}$ (Andersen and Riis-Vestergaard, 2003) and R_A are standard metabolic rate and costs of swimming activity (kilojoules per day). R_A is determined by the activity multiplier 1.25 (Hansson *et al.*, 1996) as $R_S + R_A$ $= 1.25R_S$. Due to the focus on juvenile cod, gonadal maturation was assumed to be negligible in the bioenergetics growth model and set to 0. Body mass (g) was determined iteratively as $W_{t+\Delta t} = W_t + P_{B,t} \, (0.057L_t + 3.37)$. The energy to mass conversion factor $0.057L_t + 3.37$ (Pedersen and Hislop, 2001) was assumed to depend on length only. Time increments Δt were in daily steps, and the length was measured in centimetres and was calculated using (3).

Observational data on catch per unit of effort and hypoxic areas

Indices of cod density in the first quarter of the year (calculated as catch per unit of effort, in numbers per hour; herein referred to as density) from the BITS in ICES sub-divisions 25, 26, and 28 were retrieved from the ICES DATRAS database (http://www.ices.dk/marine-data/data-portals/Pages/DATRAS.aspx). The indices are based on bottom trawl hauls typically swept between 20- and 100-m depth, whereas hauls shallower than 20 m and deeper than 100 m are very rare (ICES, 2014b).

Time series of total areas (kilometer square) of hypoxic bottoms [here taken as areas between 20- and 100-m depth (Casini et al., 2016) with an oxygen concentration of $<1\,\mathrm{ml\,l^{-1}}$, i.e. $\sim 1.4\,\mathrm{mg\,l^{-1}}$] by sub-division (25, 26, and 28) were obtained from the Swedish Meteorological and Hydrological Institute (www.smhi.se). We used $1\,\mathrm{ml\,l^{-1}}$ as threshold for hypoxia to indicate failure in benthic productivity (Karlson et al., 2002; Conley et al., 2009).

Results

The data show a pronounced change in the average mass of prey in stomachs containing that prey for all sizes of cod after the Baltic regime shift (Figure 2). The mass of the benthic isopod *Saduria entomon* in the stomachs in the period 1963–1988 was increasing constantly with increasing cod size, while in the period 1994–2014, after the regime shift, the mass of *S. entomon* is rather constant at a low level through cod ontogeny. The mass of the

nektobenthic crustacean *Mysis mixta* increased slightly in the diet of cod <35 cm but decreased in the diet of cod >35 cm after the regime shift, although the biomass of this prey in the stomachs has been small throughout the entire time series. Sprat mass has also declined in the stomachs of small cod, with the decline becoming more obvious with increasing cod size after the regime shift. The average mass of herring in the stomachs of larger cod remained unchanged between the two periods, while herring mass in the stomachs increased in the later period for cod between 25 and 35 cm. (Figure 2). In the most recent period, there is on average about twice as much cod in the stomach of cod >40 cm than before the regime shift. The mass of other prey, mainly benthic organisms and flatfish, in the cod stomachs increased for cod >50 cm after the regime shift.

The average daily consumption rate of 20–30-cm cod increased in the beginning of the time series, reached a maximum in 1990s, and rapidly decreased in the early 2000s (Figure 3). In contrast, consumption of 30–40-cm cod showed an increasing trend during the whole time series, except for a slight decline in early 1990s (Figure 3). This development is the same also for cod >40 cm (not shown here). In connection to the diet represented in Figure 2, the decrease in consumption rates of cod <30 cm is due to a reduction in benthos and to a limited extent also of sprat in the diet, partialy compensated by increased herring consumption. The minor increase in the consumption rates of 30–40-cm cod is driven by increased consumption on mysids and herring and a few observations of cannibalism.
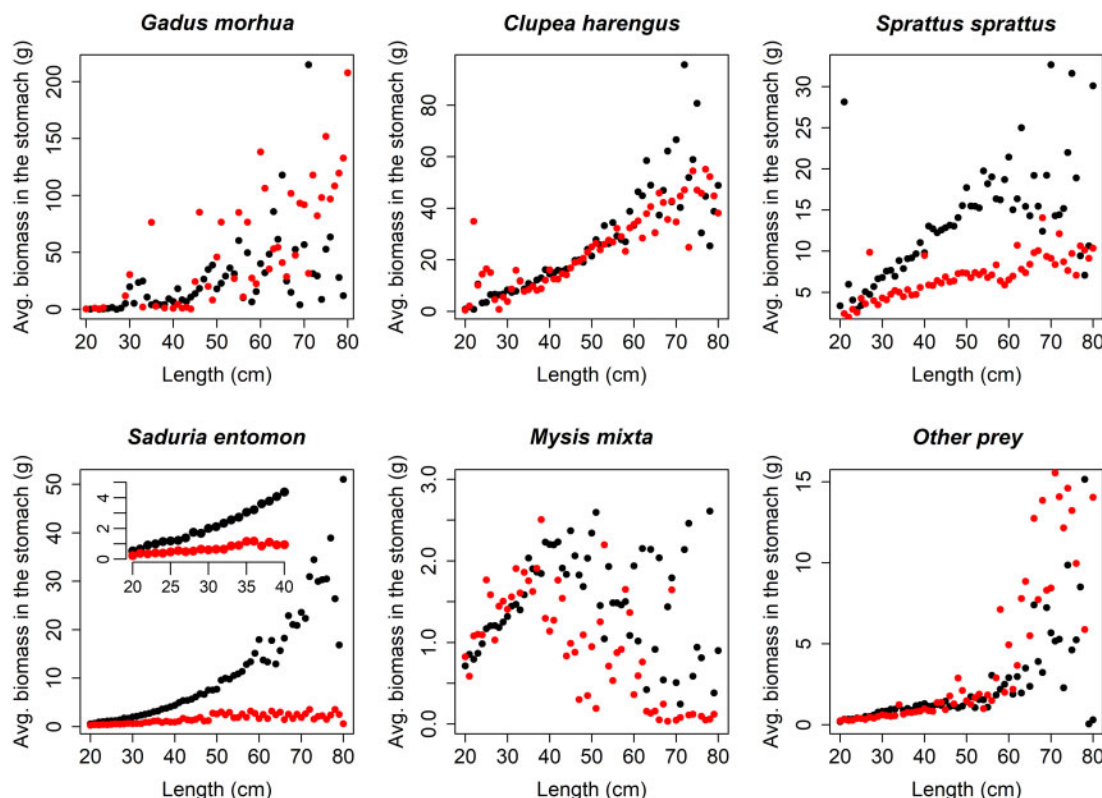

Figure 2. Diet composition in *Gadus morhua* stomachs by average mass, given that the specific prey is found in the stomach, before 1988 (dark closed dots) and after 1994 (light closed dots). The transition period between ecological regimes from 1988 to 1993 (Möllmann et al., 2009) is left out. The diet is given in average biomass observed in the stomachs of a given length (centimetres) during the two respective periods. For *Saduria entomon*, the biomass in the stomachs is given in an insert for cod with the total length of ≤40 cm.

The decreasing consumption rates of small cod in the latest years, and the average increasing rates for larger ones, become clearly visible in the development of feeding levels over cod length during the last five decades (Figure 4). Feeding levels of cod 20–30 cm were among the lowest on record in 2005–2014. Low average feeding levels of 20–30-cm cod, comparable with the recent low values, could also be observed in 1965–1974. The average feeding levels of larger cod were continuously increasing with
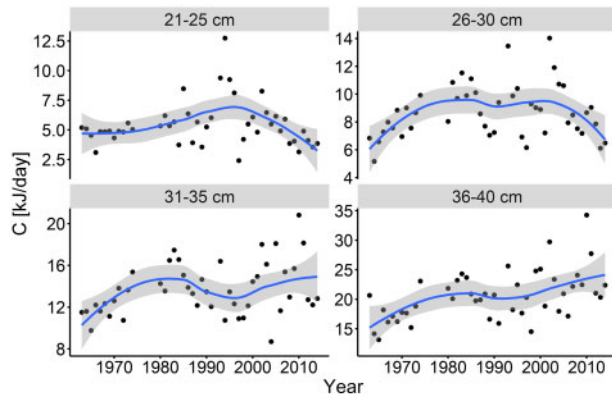
length during 2005–2014, which was unseen in the four decades before.

The growth curve of immature cod in the last decade, emerging from the bioenergetics model, differed clearly from the four decades before, with average growth becoming negative (Figure 5). This negative modelled average growth implies that, *in vivo*, a large fraction of cod <35 cm does not grow in length, gets thinner over time, and likely dies due to starvation.

The size distribution of cod is progressively truncated from 2009 onwards (Figure 6). There is more fish of the same, small size in the stock. The abundance of specimen >35–40 cm decreased drastically.

There are basin-specific differences in the development of hypoxic areas (Figure 7). Before the mid-1990s, hypoxic event was only temporary and, thus, the inter-annual extent of hypoxic areas varied extensively. Conversely, hypoxic area size in the Bornholm Basin reached a plateau in 1994 until 2001, when ~5000 km^2 of the bottom was hypoxic. Again between 2005 and 2010, hypoxia was constantly at high levels, corresponding to 6000 km^2, in the Bornholm Basin. These two periods of long-term chronic hypoxia in the most important distributional and reproductive area for cod (Figure 7) have been unprecedented during the time series.

Figure 3. Trends in daily food consumption rate of *Gadus morhua* in four length classes; locally estimated scatterplot smoothing based trend-lines are plotted together with shadowed confidence limits.
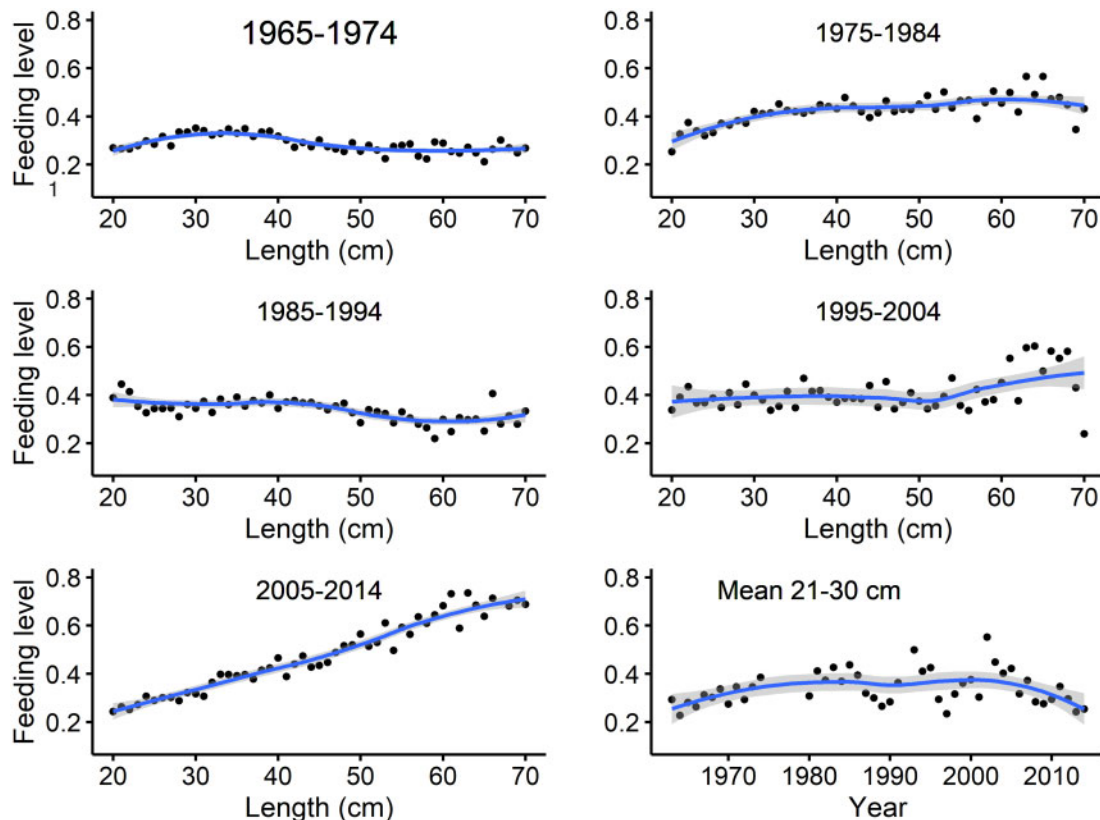
Discussion

Our analyses revealed that decreased growth and survival of small cod may be an extension of the juvenile, post-settlement

Figure 4. Feeding levels of *Gadus morhua* by length during the past five decades. Locally estimated scatterplot smoothing based trend-lines are plotted together with shadowed confidence limits. The lower right panel: feeding level over time for *G. morhua* with the total length of 21–30 cm.
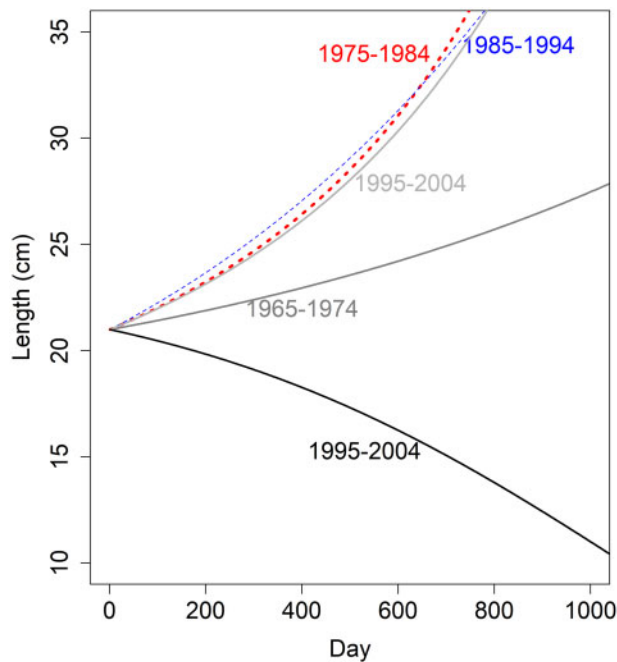
Figure 5. Simulated growth trajectories of *Gadus morhua* in the total length range 21–35 cm for the five decades covered by the stomach sampling programme.

Figure 6. Catches per unit of effort (CPUE) for eastern Baltic cod by 1-cm cod length group for three different periods since 2009.

Figure 7. Extent of hypoxic bottom areas in different basins of the Baltic Sea during the stomach sampling programme. Hypoxic condition is defined as <1 ml l^{-1} oxygen concentration and given in 10^3 km^2. The different basins are the Bornholm Basin (ICES sub-division 25), the Gdansk Deep (ICES sub-division 26), and the Gotland Basin (ICES sub-division 28).

bottleneck (Tupper and Boutilier, 1995; Hüssy *et al.*, 1997). Feeding levels of small cod have been critically low in recent years, at or even below minimum fish maintenance levels (Kitchell *et al.*, 1977; Andersen and Riis-Vestergaard, 2003). The low feeding levels most probably result from a decrease in benthic prey availability due to increased hypoxic areas. The resulting growth reduction in this life stage that we calculated based on a bioenergetics model is supported by the observed length distributions from the survey. The size structure of the cod population has changed towards smaller individuals. Our study emphasizes that, under the current ecosystem state, environmental forcing, as well as a decline in pelagic prey, causes changes in the consumption and growth rates of small cod in the Baltic Sea, resulting in an accumulation of small-sized cod in its population.

In our study, we modelled the expected changes in the cod growth from the changes in the stomach content data. The analyses suggest a reduction in growth that can explain the shift of the cod length distribution towards lower sizes over time. Moreover, the negative average modelled growth rate in the most recent period implies that many cod individuals die due to starvation. Only the fishes with feeding levels well above average will survive, though growing slowly. Size at sexual maturation (L_{50}) has declined from 45 to 50 cm for females and 37 to 41 cm for males in 1984–1988 (Cardinale and Modin, 1999) to ∼19 cm in 2015 (Köster *et al.*, 2017). Since we did not account for energy spent for maturation in our bioenergetics model, growth might have been slowed down even further, if energy was used for gonadal maturation. The surviving part of the population may be estimated by comparing the growth rates presented here, based on stomach data and bioenergetics modelling, to growth rates estimated independently, for example from tagging data. However, even in the absence of such analyses, the available survey data with practical absen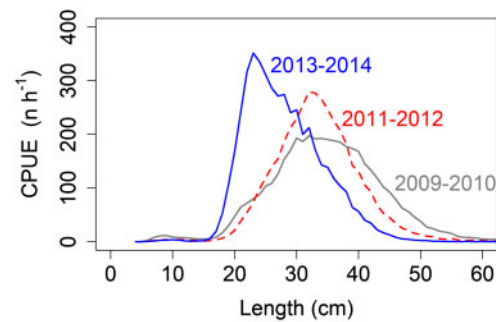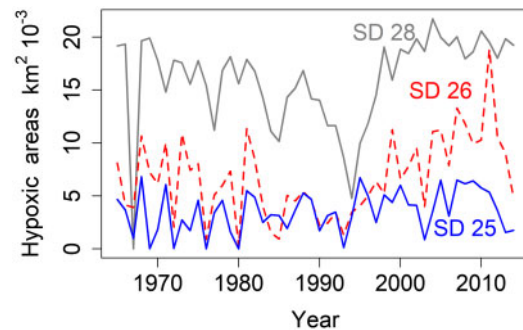ce of cod >40 cm in recent years, presented in this study, strongly support increased natural mortality and stunted growth. Although dead emaciated fish are found only very rarely in the environment, starvation nevertheless occurs frequently (Holdway and Beamish, 1984; Dutil and Lambert, 2000). The slower growth of the survivors renders small cod easier to be preyed upon by larger cod, because they remain longer in the size window that is vulnerable to predation. Starvation makes the cod probably more vulnerable to parasites, which is in line with recent observations of increasing liver worm *Contracaecum osculatum* infection in the eastern Baltic cod (Haarder *et al.*, 2014; Horbowy *et al.*, 2016; Sokolova *et al.*, 2018).

The growth reduction results in a change in cod size distribution with increased densities of smaller sizes. Since the relevant, benthic, and pelagic food items are scarce, as visible by their decline in the diet, implied by the extent of hypoxic areas and the observed decline in sprat biomass (Casini *et al.*, 2016), a feedback loop emerges, because the accumulation intensifies the competition for food in the benthivore life stage leading to further food limitation and growth reduction. Consequently, the growth is arrested and the population is trapped in an ontogenetic bottleneck. The bottleneck occurs below 30 cm and, thus, inhibits the ontogenetic trophic niche shift towards a diet dominated by pelagic fish. Furthermore, it stops the production of individuals that recruit into the commercial fisheries, currently at 35 cm (ICES, 2018). Thus, there are very few cod with above-average growth, and the survey size distributions (Figure 6) imply that

this fraction of large cod is decreasing over time. The stomach data indicate that the high average feeding levels of these large specimens are mainly caused by rare events of cannibalism, which nevertheless probably increase mortality for the small cod. Consequently, due to the decreasing abundance of large cod, the predatory impact of the cod population on larger prey, such as herring and flounder, decreases. In the area of cod distribution, Baltic sprat started to decline in the mid-1990s (Casini *et al.*, 2016). This decline coincides with the changes in the cod food intake after the regime shift. Coinciding with the sprat decline in the area of cod distribution, sprat consumption by cod also declined.

Recolonization time of benthic areas by invertebrates after an extended hypoxic period needs to be investigated to predict cod food availability after re-oxygenation of the deep water. Two prolonged stagnation periods in the main distributional area of the cod population have obviously decimated the benthic prey species. In this study, the cod stomachs themselves serve as indicators in the absence of reliable biomass data for benthic prey. Also, the abundance and spatial distribution of competitors for benthic prey, such as flounder (Orio *et al.*, 2019), have to be taken into account and could have worsened the feeding conditions for cod. Knowing the body size and condition that a predatory cod would need to successfully forage on the pelagic sprat would help to determine if reducing the commercial exploitation rate of sprat will potentially improve the food situation for the small, starving cod. These questions have to be answered spatially explicitly, probably on a scale smaller than the ICES sub-divisions, where biomass estimates of sprat match the prey field predatory cod experience.

Areas where feeding opportunities, growth, and condition of cod may be unaffected by hypoxia may exist in waters shallower than those covered by the BITS, of which >85% of the stations are located at depths >40 m and all on soft bottom. Stomach data from coastal areas would facilitate investigating the importance of shallow waters as source for replenishing the deteriorated population residing in deeper waters. However, juvenile cod has shifted its distribution towards deeper areas the last years (Orio *et al.*, 2019), suggesting that the shallow areas may currently not be that important after all.

Our study emphasizes that environmental forcing, giving rise to hypoxia, has probably triggered the observed changes in consumption and growth rates for cod in the Baltic Sea during the past decades by reducing the growth of pre-piscivorous specimens. Moreover, the resulting increased densities of small cod along with a decline in sprat densities have intensified the competition for food leading to further food limitation and growth reduction. Environmental changes decouple many population dynamic control mechanisms (Gårdmark *et al.*, 2015). Growth and mortality change independently of predator and prey densities and feedback loops that otherwise are considered key in the transition between alternative stable states (Möllmann *et al.*, 2009; Scheffer, 2009). Our results underline that the relation between population density and vital rates under environmental changes has to be understood mechanistically to fully comprehend the ecosystem changes currently observable in multiple places globally (Folke *et al.*, 2004) and to devise remedies where possible.

Data accessibility

All data supporting the results are already available online at www.ices.dk.

Author contributions

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