Western Baltic cod in distress: decline in energy reserves since 1977

Aurore Receveur [1], **Martina Bleil**[1], **Steffen Funk** [2], **Sven Stötera** [1], **Ulf Gräwe** [3], **Michael Naumann** [3], **Cyril Dutheil** [3] and **Uwe Krumme** [1,*]

[1]Thünen Institute of Baltic Sea Fisheries, Alter Hafen Süd 2, 18069 Rostock, Germany
[2]Institute of Marine Ecosystem and Fisheries Science, Centre for Earth System Research and Sustainability (CEN), University of Hamburg, Große Elbstraße 133, 22767 Hamburg, Germany
[3]Leibniz-Institute for Baltic Sea Research Warnemünde, Seestr. 15, 18119 Rostock, Germany

*Corresponding author: tel: +49 381 66099 148; e-mail: uwe.krumme@thuenen.de

The western Baltic Sea cod (WBC) stock is at historically low levels, mainly attributed to high fishing pressure and low recruitment. Stable stock assessment metrics suggested recovery potential, given appropriate fisheries management measures. However, changing environmental conditions violate stability assumptions, may negatively affect WBC, and challenge the resource management. The present study explored 42 years of changes in WBC biological parameters. WBC body condition gradually decreased over the last decades for juveniles and adults, with a rapid decrease in recent years when a single cohort dominated the overfished stock. The hepato-somatic index and the muscle weight decreased by 50% and 10% in the last 10 years, respectively, suggesting severely decreasing energy reserves and productivity. The changes in energy reserves were associated with changes in environmental conditions (increase in bottom water temperature, expansion of hypoxic areas during late summer/autumn), and changes in diet composition (less herring). A key bottleneck is the warming and longer-lasting summer period when WBC, trapped between warmed shallow waters and hypoxic deeper waters, have to mobilize energy reserves to account for reduced feeding opportunities and thermal stress. Our results suggest that stock recovery is unlikely to happen by fisheries management alone if environmental trajectories remain unchanged.

Keywords: Atlantic cod, Baltic Sea, climate change, condition factor, fish habitat, *Gadus morhua*, HSI, hypoxia, temperature stress.

Introduction

Atlantic cod (*Gadus morhua* L.) is an ecologically and economically important demersal fish species in the North Atlantic (Merino *et al.*, 2014; Trenkel *et al.*, 2014). However, stock assessments and field data show the poor status of many cod stocks on both sides of the Atlantic Ocean (e.g. North and South Gulf of St Lawrence, eastern Scotian Shelf, North Sea, Kattegat, and eastern Baltic cod; Myers *et al.*, 1996; Dutil *et al.*, 1999; Lilly, 2008a, b; Sguotti *et al.*, 2019), linked to high fishing pressure, changing environmental conditions, and unfavourable trophic cascades and feedback loops (e.g. Fu *et al.*, 2001; Bundy and Fanning, 2005; Frank *et al.*, 2016; Huebert *et al.*, 2018; Dinesen *et al.*, 2019). Rebuilding or recovery of collapsed cod stocks is often slow or absent (Lilly, 2008a; Sguotti *et al.*, 2019), suggesting that specific management measures are needed earlier to be effective (Zimmermann and Werner, 2019) as well as an incorporation of environmental conditions in the management (Winter *et al.*, 2020).

The metrics used in analytical stock assessments to determine the stock status are highly aggregated averages that integrate data collected mainly for stock assessment purposes and are linked to different levels of uncertainty. Moreover, analyses of the trajectories of these metrics (e.g. spawning stock biomass (SSB)) of declined cod stocks usually detect change points only in retrospect, and early warning signs are largely missing. Apparent changes in the physiological condition of individuals that compose the SSB, e.g. fish body condition, health status, or diet composition, may remain unnoticed because they are either not monitored or are not part of the routines applied in stock assessments. The historical prime examples of Canadian cod stock collapses show, in retrospect, that monitoring the temporal changes of the condition factor could help to earlier detect the decline of the different stocks (Lambert and Dutil, 1997a, b; Lapointe *et al.*, 2006).

The condition factor (i.e. the body–mass/length ratio of fish) is a critical diagnostic. It is easy to measure (only length and weight data are required) and can be used to estimate fish energy reserves (Lambert and Dutil, 1997b). When many fish are analyzed, the condition factor is indicative of the stock energy status. The level of the energy reserves in cod is closely linked to sensibility to environmental conditions and potential recovery after an external stressor (Dutil *et al.*, 2006). For example, low energy reserves limit the recovery after poor feeding conditions or parasitic infections (Yaragina and Marshall, 2000; Ryberg *et al.*, 2020). Furthermore, the condition factor directly influences the health of a fish stock through the reproductive potential (Rakitin *et al.*, 2011) by affecting the timing of maturation before spawning and length-at-first maturity (Marteinsdottir and Begg, 2002; Morgan, 2004), the quality and quantity of eggs (Brosset *et al.*, 2016), and the proportion of skip-spawners (Rideout *et al.*, 2000; Rideout and Rose, 2006; Skjæraasen *et al.*, 2012). Among 10 North Atlantic cod stocks, the lower average condition factor has been associated with a lower growth rate and recruitment potential, thus reducing the stock productivity (ätz and Lloret, 2003).

The condition factor is influenced by both internal metabolic processes and extrinsic parameters that influence the individual or population level. The water temperature, a variable mainly controlling the speed of metabolic reactions in ectothermic animals, has been correlated to changes in the condition factor, especially among different stocks. For example, cod stocks are, on average, in better conditions in warmer waters in the North Atlantic (Rätz and Lloret, 2003). In contrast, laboratory studies indicated more complex relationships, revealing that temperature has size-dependent effects, i.e. an increasing thermal niche width with increasing cod length (Árnason *et al.*, 2009). Further, the ambient water temperature can strongly influence the individual energy budget of cod and consequently the body condition by driving, e.g. metabolic rates (Saunders, 1963), gastric emptying, and consumption (Temming and Herrmann, 2003). In addition, temperatures above the thermal tolerance range of cod may limit the access to warmed feeding areas (Freitas *et al.*, 2015, 2016), potentially resulting in periodic starvation (Funk *et al.*, 2020, 2021). Generally, the limited spatial scale inhabited by many cod and restrictions in the locally available prey biomass can severely alter cod energy uptake (Funk, 2020), and thus the condition factor (Werner *et al.*, 2019).

Recently, the eastern Baltic cod (EBC) stock became another prime example of undetected changes before it was perceived to be in severe distress (Eero *et al.*, 2015). In 2014, the routine stock assessment was suspended virtually with no previous warning sign from the scientific community or fishing industry. A posteriori, the main issues identified were linked to biological parameters: (1) highly uncertain age determination (ICES, 2014a; Hüssy *et al.*, 2016), (2) maturation at a smaller size (Cardinale and Modin, 1999; Orio *et al.*, 2019), (3) decreased growth (Hüssy *et al.*, 2018; McQueen *et al.*, 2020; Mion *et al.*, 2021), (4) decline of relative abundance of larger individuals in the population (Eero *et al.*, 2015), and (5) a decrease of body condition (Eero *et al.*, 2012; Casini *et al.*, 2016, 2020). These complex biological changes have been linked to (1) a change in cod diet, with an increase of clupeids and a decrease of invertebrates (Casini *et al.*, 2016) and a weaker spatial overlap between cod and sprat and herring distribution (Neuenfeldt *et al.*, 2020); (2) an increase of liver infestation by larval stages of the nematode *Contracaecum osculatum* (Sokolova *et al.*, 2018; Ryberg *et al.*, 2020); (3) poor oxygen condition in deeper waters, with negative influence on growth (Chabot and Dutil, 1999; Limburg and Casini, 2019), on larval survival, benthic prey abundance (Carstensen *et al.*, 2014; Casini *et al.*, 2020), and (4) thiamine deficiency (Engelhardt *et al.*, 2020).

The neighboring western Baltic Sea cod (WBC) stock is considered overfished (F >> F_{MSY} since 2009), and the last stronger year class from 2016 is contributing the major part of the descending SSB in recent years (SSB below B_{lim}; ICES, 2020b). All year classes since 2017 were weak. However, the stock is generally still perceived as a stock with recovery potential. Before 2021, stock assessment data showed that there were still larger specimens (> 80 cm) in the stock, and the mean weight-at-age was considered stable (ICES, 2020a). However, similar to the Canadian cod stocks and the EBC, there are strong retrospective patterns in the analytical assessment, and failure of the WBC stock assessment in 2021 required an inter-benchmark (ICES, 2021). Except for high fishing pressure and a period of low recruitment, no warning signals had emerged in previous years (ICES, 2020b).

In this study, we present an analysis with 44 years of biological parameters, collected during scientific surveys and from commercial catches, ranging back to 1977, to assess the health and condition status of WBC. We shed light on the temporal changes in WBC condition factor and hepato-somatic index (HSI). Eventually, we investigated potential external drivers of the changes in biological parameters, using available data on temporal changes in WBC diet composition, feeding level, and the influence of oxygen, salinity, and water temperature.

Material and methods

Study area
The Baltic Sea is a heavily exploited, semi-enclosed, and postglacial microtidal brackish-water sea that has experienced substantial changes in anthropogenic pressures and environmental conditions over time (Reusch *et al.*, 2018). A total of two Baltic cod stocks are currently managed separately. The WBC stock occupies the western Baltic Sea, i.e. the Belt Sea (ICES subdivisions (SD) 22; Figure 1), the Sound (SD23), and the Arkona Sea (SD24). This study only used biological data of cod from samples collected in SD22 and SD24. The hydrographic conditions of SD22 and SD24 strongly depend on inflows of water from the Kattegat, bringing saline and oxygenated water (Matthäus and Franck, 1992; Matthäus *et al.*, 2008).

The Arkona Sea (SD24) is the westernmost area of the Baltic proper with water depths of 45 m and transitions to the shallower area of the Belt Sea (Figure 1). The brackish surface water (approximately 8 psu) is separated from the saline bottom water (approximately 15–20 psu) by a permanent halocline at 30–40 m (Lass and Mohrholz, 2003; Reissmann *et al.*, 2009). SD24 is the area of mixing WBC and EBC (Hemmer-Hansen *et al.*, 2019; Schade *et al.*, 2019; Weist *et al.*, 2019).

The shallow Belt Sea (SD22, 98% of the area is shallower than 30 m; ICES, 2014b; Figure 1) has salinities ranging between 10 and 25 psu near the bottom. The hydrography of the area is characterized by wind-induced current patterns, related primarily to changes in the two-layer exchange flow of more saline bottom water from the Kattegat and surface outflow from the central Baltic Seathrough the Danish Straits.

Sampling of cod
Biological data of cod were obtained from various German scientific trawl surveys supplemented by data obtained from the catch sampling programme of the German Baltic commercial fisheries (Supplementary Table S1; Figure 1). We decided to separately analyze cod data from SD22 and SD24 to account for different degrees of Baltic cod stock mixing and differences in environmental settings (e.g. bathymetry and oceanography). To back our conclusions on WBC dynamics, only results from SD22 samples are presented in the main manuscript, and results of SD24 cod are given in the Supplementary Material.

In SD22, a total of 77 769 cod were sampled in 42 years ranging from1977 to 2020 (no data from 1980 to 1981). Given seasonal changes in the catchability of cod by trawlers, the temporal coverage of samples varied among quarters (January–March (quarter 1–Q1): $N = 42$ 913; April–June (quarter 2–Q2): $N = 12$ 804; July–September (quarter 3–Q3): $N = 6$ 233; and October–December (quarter 4–Q4): $N = 15$ 819). Given 35, 26, 13, and 37 years of data for Q1,
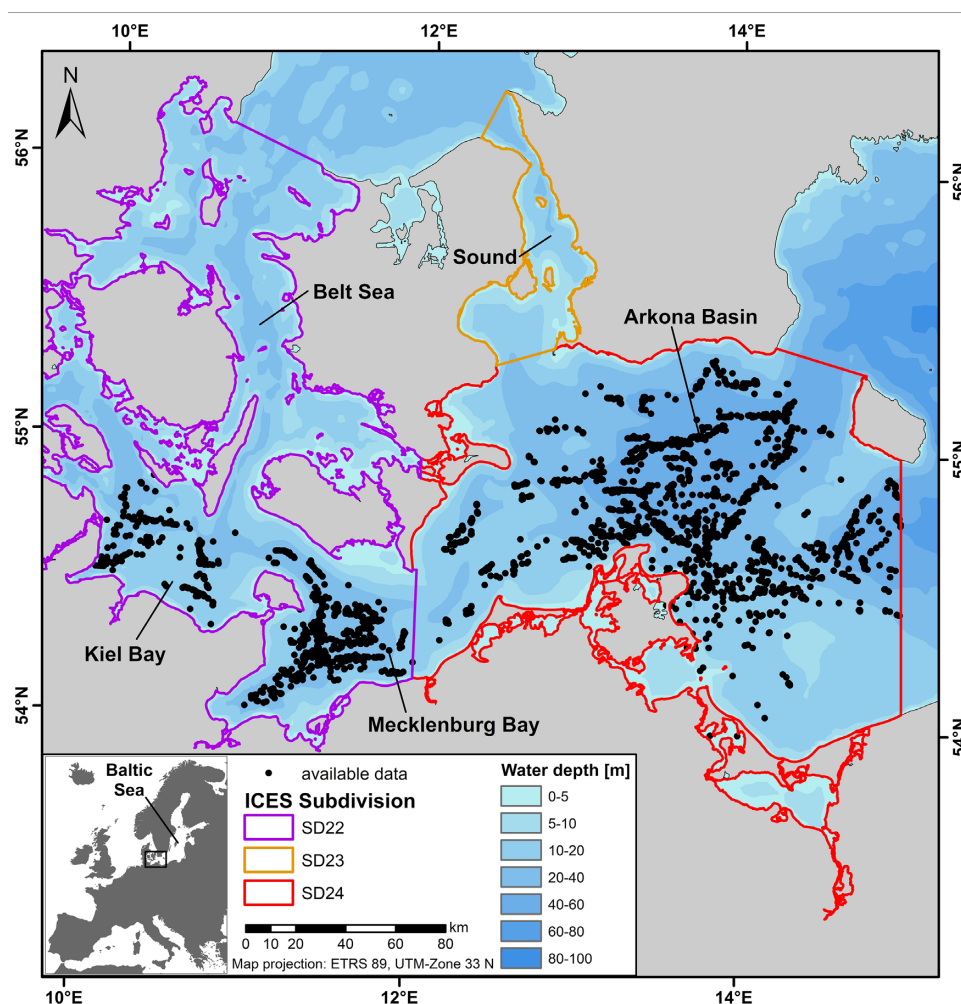
Figure 1. Map of available samples collected from 1997 to 2020 (black dots). Blue colours show the bathymetry. Purple, yellow, and red lines surround ICES subdivisions 22, 23, and 24, respectively. Important regions are indicated.

Q2, Q3, and Q4, respectively, we decided to only use data from Q1 and Q4. Furthermore, the available time series from Q2 and Q3 had started significantly later (Supplementary Figure S1).

Several size class intervals were tested but to ensure robust results and well-balanced sample sizes across domains (e.g. years and quarters), only two length classes were used: below 35 cm (juveniles) and above 35 cm (adults). This threshold corresponds to the minimum conservation reference size of cod in the western Baltic Sea (i.e. cod < 35 cm cannot be sold for human consumption but have to be landed; European Commission, 2014), approximates the ontogenetic transition between juveniles and adults (Krumme et al., 2020) and an ontogenetic feeding shift (Funk et al., 2021).

Biological measurements

The total length *(L*; cm) and full wet mass (*M*; g) were recorded for each individual (Supplementary Figure S1). The sex was determined by visual examination of the gonads for almost all individuals.

Since 1977 (only during Q4 between 1977 and 1987), the stomach fullness was visually determined based on six categories: "'empty' = 0, '¼ full' = 0.25, '½ full' = 0.5, '¾ full'

= 0.75, 'full' = 1, and 'regurgitated'" (the latter category was excluded from the analysis; Supplementary Figure S1).

Condition factor

As cod display an allometric growth pattern (McQueen et al., 2019, 2020; Árnason et al., 2009), the relative body condition index K_n (Le Cren, 1951; Froese, 2006) was calculated as: $K_n = M/M_t$ where M is the measured full wet weight (g) and

$$M_t = a * L^b, \tag{1}$$

the predicted wet mass (g) of an individual of length L (cm). The analysis relies on full wet weight data because these covered 41 years of data and 58 732 individuals compared to only 30 years of data and 35 570 individuals with gutted weight information. The results of the analysis on gutted weight data showed the same trends as the full weight data (Spearman correlation of 0.85; Supplementary Figure S2). The parameters a and b were calculated separately for SD22 ($a = 0.00\,729$ and $b = 3.0784$) and SD24 ($a = 0.00\,679$ and $b = 3.0958$) to account for differences in stock mixing dynamics and related differences in growth (McQueen et al., 2020; Mion et al., 2021) and spawning phenology between EBC and WBC (Bleil et al., 2009).

To facilitate comparison with other studies from the Baltic Sea and since the *b* parameters from the weight–length relationships of cod from SD22 and SD24 were close to 3, the Fulton index K_F was calculated using: $K_F = M * 100/L^3$ with M the full wet mass (g) and L the length (cm) of each individual. The two condition factor indices showed strongly similar results (Supplementary Figure S3), and therefore, only the Fulton index (K_F) is presented in the results.

Both higher K_n and K_F estimates indicate fish in better body condition. To facilitate comparisons with studies on EBC body condition, which used full wet weights (Eero *et al.*, 2015; Casini *et al.*, 2016; ICES, 2020a), we additionally computed the proportion of Fulton index values below 0.8.

Since K_F was calculated using the full weight of the fish, it can provide evidence of changes in total weight in relation to fish length. However, it does not explain whether these changes can be related to a decrease in liver mass, gonads, or somatic muscle tissue. To check especially for the latter, we calculated length–gutted-weight [Equation (1)] relationships for each sex (males: $N = 20\ 202$; $a = -4.82$, $b = 3.010$; females: $N = 15\ 368$; $a = -4.81$, $b = 3.004$). Furthermore, we calculated residuals (i.e. predicted gutted weight—observed gutted weight) for the respective length–gutted-weight relationship and present the residual distribution over time.

HSI

Given that the liver is the major organ of energy storage in cod (Kjesbu *et al.*, 1991; Hemre *et al.*, 1993; Karlsen *et al.*, 1995; Pardoe *et al.*, 2008), the HSI was computed with $HSI = 100 * M_l/M_t$ with M_l the wet mass of the fresh liver (g); and M_t the predicted wet mass [Equation (1)]. HSI was used as a metric to assess temporal changes in the energy status of the fish.

Assessment of diet composition

To explore the role of food intake on changes in the condition factor of cod, we assessed the temporal changes in cod diet composition and quantity. To study the change in diet quantity, a mean stomach fullness value (by considering the five categories: "'empty' = 0, '¼ full' = 0.25, '½ full' = 0.5, '¾ full' = 0.75, and 'full' = 1") was calculated by quarter, year, and length class. To ensure robustness, more than 10 individuals had to be present in each group combination.

Given the lack of a continuous cod stomach sampling, historic (Schulz, 1987; Weber and Damm, 1991) and contemporary cod diets (Funk *et al.*, 2021) were compared. From Funk *et al.* (2021), we extracted specimens as similar as possible to the two historic studies, i.e. choosing cod stomach samples originating from waters with depths $\geq$ 20 m, and caught with trawl gear ($N = 764$). All prey species identified by Funk *et al.* (2021) were allocated into six prey groups and two cod length classes for comparison with Weber and Damm (1991) data, and into five prey groups and three cod length classes for comparison with Schulz (1987).

In all cases, the masses of each prey item were summed by the prey group predator and divided by the corresponding total stomach content weight of the predator to obtain relative stomach content weights for each group and predator.

Measurements of environmental parameters

We extracted variables from the General Estuarine Transport Model to explore relationships between condition factor and environmental parameters. This hydrodynamic model has a spatial resolution of 600 m, and 50 terrain-following vertical adaptive layers, with a minimum layer thickness of 0.3 m. A detailed description of the setup, boundary conditions, surface forcing, nesting procedure, and validation of the model are given in Klingbeil *et al.* (2014) and Gräwe *et al.* (2015). In particular, Gräwe *et al.* (2015) demonstrated the robustness of this model to reproduce oceanographic changes.

To account for the demersal life style of cod, three parameters were extracted from a simulation covering the time period 1979–2020: the bottom salinity, the bottom water temperature, and the bottom water age. The bottom water age or ventilation is defined as the time elapsed since last contact with the surface (Delhez *et al.*, 1999). The bottom water age is used as a proxy for the oxygen concentration, i.e. the older the water, the lower the oxygen content. To simplify the interpretation of water age, we transformed the water age values into an oxygen proxy so that the proxy ranges and varies similar to oxygen concentrations. We computed monthly mean values per SD for all three variables for the whole period between 1977 and 2020.

Development of the 2016 cohort

To assess the development of the 2016 cohort, the data from all age-read cod from German scientific trawl surveys and commercial catch sampling in SD22 were used. Fish age was determined by using sliced otoliths, processed according to standard procedures. Ring patterns were interpreted using age-validated otoliths from recaptured tetracycline-marked WBC (McQueen *et al.*, 2019; Krumme *et al.*, 2020). An age-length-key was calculated using the frequency of fish in each length interval and age combination, and was used to assign individual ages to all length-measured cod using the method of Ogle (2016). A theoretical mean-length-at-age was calculated for the 2016 cohort in each year using the von Bertalanffy growth function (VBGF) and growth parameters of WBC by McQueen *et al.* (2019). Method details and parameter estimates are given in Textbox S1 in the Supplementary material.

Finally, we calculated the mean-length-at-age when age data were available and we assessed whether the K_F truly changed in the mass/length ratio. The mean-length-at-age was stable across time, especially for ages 2, 3, and 4; and not correlated to the K_F values (excepted for Age 1 in Q1; Supplementary Figure S4). Therefore, the K_F appears as the most appropriate criterion to study the temporal changes of cod body condition.

Statistical analysis

We tested for changes in condition factor over time. For this purpose, we calculated the mean condition factor per year and length class, which were used as a response variable in a linear regression model. The explanatory variables were "year" (quantitative) and "quarter" as a factor. The quarter was included to take seasonal variability in cod condition factor into account, given the seasonal spawning cycle and differences in habitat use and related food availabilities and intake (Funk *et al.*, 2021). Homogeneity of variance of condition factor values and of linear model residuals across quarters had been checked with two Bartlett tests (*p*-value > 0.05 for the
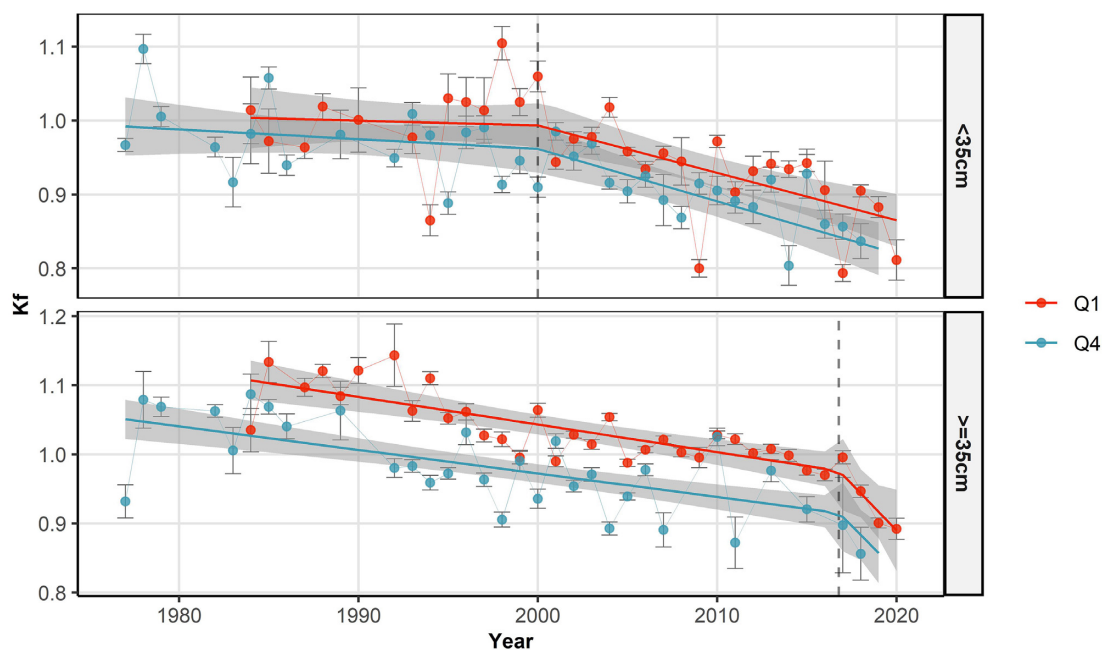
Figure 2. Mean Fulton's condition factor by year (*x*-axis), length class (rows), and quarter (colours) in SD22. The fitted linear regressions are shown, together with the predicted confidence interval (grey ribbon). Vertical dashed lines indicate the identified slope breaks.

two tests). Linear regression residuals had been checked and validated. Subsequently, we applied a breakpoint analysis in the slope to test for abrupt changes in the linear regressions (Muggeo, 2008).

The linear model and breakpoint detection method were chosen to detect and describe temporal trends and change in trends in body condition.

The relationship between condition factor and HSI was investigated with Spearman correlations.

To assess the influence of the different parameters on the condition factor of cod, we used the classification and regression tree (CART) approach of Breiman *et al.* (1984). Decision trees were built by partitioning the dataset into increasingly homogeneous subgroups based on fish body condition values. Each split was defined by a simple rule based on a single explanatory variable, and mean values of cod's K_F characterized each final group. The monthly mean values of body condition acted as a response variable and bottom salinity, water temperature, oxygen proxy, and mean stomach fullness value as quantitative explicative variables.

All analyses were done using the statistical computing program R, Version 4.0.2. The libraries *segmented* (Muggeo, 2008) and *rpart* (Therneau and Atkinson, 2019) were used to identify linear regression breakpoints and calculate the regression tree.

Results

Temporal changes in condition factor

K_F was higher during Q1 and Q4 compared to Q2 and Q3 in SD22 for all pooled years for adult ($\geq$ 35 cm) cod (Supplementary Figure S5). During Q1 and Q2, K_F was higher for the males than for the females. For juvenile (< 35 cm) cod, K_F across the quarters was relatively stable in both SDs, and similar for males and females.

From 1980 to 1999, K_F of juvenile cod remained relatively constant with a mean value of 0.99 (and a *SD* of 0.13; Figure 2) with no significant trend (Table 1) and high interannual variability in both quarters (i.e. Q1 and Q4). From 2000 onwards, K_F values displayed a steady decrease in Q1 and Q4.

For adult cod, clear differences in K_F were observed over the whole period, with K_F being consistently higher in Q1 than in Q4 (Figure 2). The condition factor showed a decreasing trend (*p*-value < 0.001) over time in both quarters since the beginning of the time series. The decline in K_F was significant for the entire period. The decline accelerated from 2016 onwards leading to especially low K_F values displayed in the first quarters of 2018, 2019, and 2020 (Table 1) with a negative slope (−0.026 for Q1 and Q4) seven times higher than in the previous period (around −0.0038 before 2016). The mean condition factor of adult Q1 cod fell from about 1.1 in the late 1980s to about 0.9 in 2020, i.e. a gradual reduction of approximately 18% in 30 years (Figure 2).

A similar trend was observed in the data from SD24 for juvenile cod, with a stagnation period and a decrease in K_F observed from 1999 onwards (Supplementary Figure S6). For adult cod in SD24, decline in K_F was also substantial, but started earlier than in SD22 (around 1989; Supplementary Figure S6).

The proportion of individuals in critical body conditions (i.e. K_F < 0.8; Eero *et al.*, 2015) increased over time in both juvenile and adult cod and in both SDs (Supplementary Figure S7). Since 2005, an increase in the proportion of individuals in poor body condition occurred for juvenile cod in SD22 and SD24 and for adult cod in SD24. For adult cod in SD22, the proportion of individuals with K_F < 0.8 showed a strong increase from 2017 onwards during Q1.

Length–gutted-weight relationship residuals (Supplementary Figure S8) also displayed a change over time indicating a

Table 1. Parameters (with intercept and slope's estimate, standard error, and *p*-value intercepts) and the R^2 from the two linear models for condition factor of juvenile (< 35 cm) and adult (≥ 35 cm) cod in SD22. A representation of these relationships is given in Figure 2.

| Length class	Parameter	Estimate	Std. Error	*p*-value	R^2 (%)
< 35 cm	Intercept Q1	2.26	3.16	3.09^{e-06}	
	Intercept Q4	3.59	2.11	2.12^{e-03}	
	Slope Q1 [1979–2000]	− 0.00063	0.0016	0.520	52.1
	Slope Q1 [2000–2020]	− 0.00642	0.0018	1.84^{e-03}	
	Slope Q4 [1979–2000]	− 0.0013	0.0011	0.38	
	Slope Q4 [2000–2020]	− 0.0071	0.0010	0.7^{e-05}	
≥ 35 cm	Intercept Q1	9.09	1.43	2.95^{e-08}	
	Intercept Q4	7.95	1.71	5.91^{e-07}	
	Slope Q1 [1979–2016.8]	− 0.0040	0.00071	$< 1^{e-16}$	66.5
	Slope Q1 [2016.8–2020]	− 0.027	0.00946	$< 1^{e-16}$	
	Slope Q4 [1979–2016.8]	− 0.0035	0.00085	$< 1^{e-16}$	
	Slope Q4 [2016.8–2020]	− 0.026	0.00034	$< 1^{e-16}$	
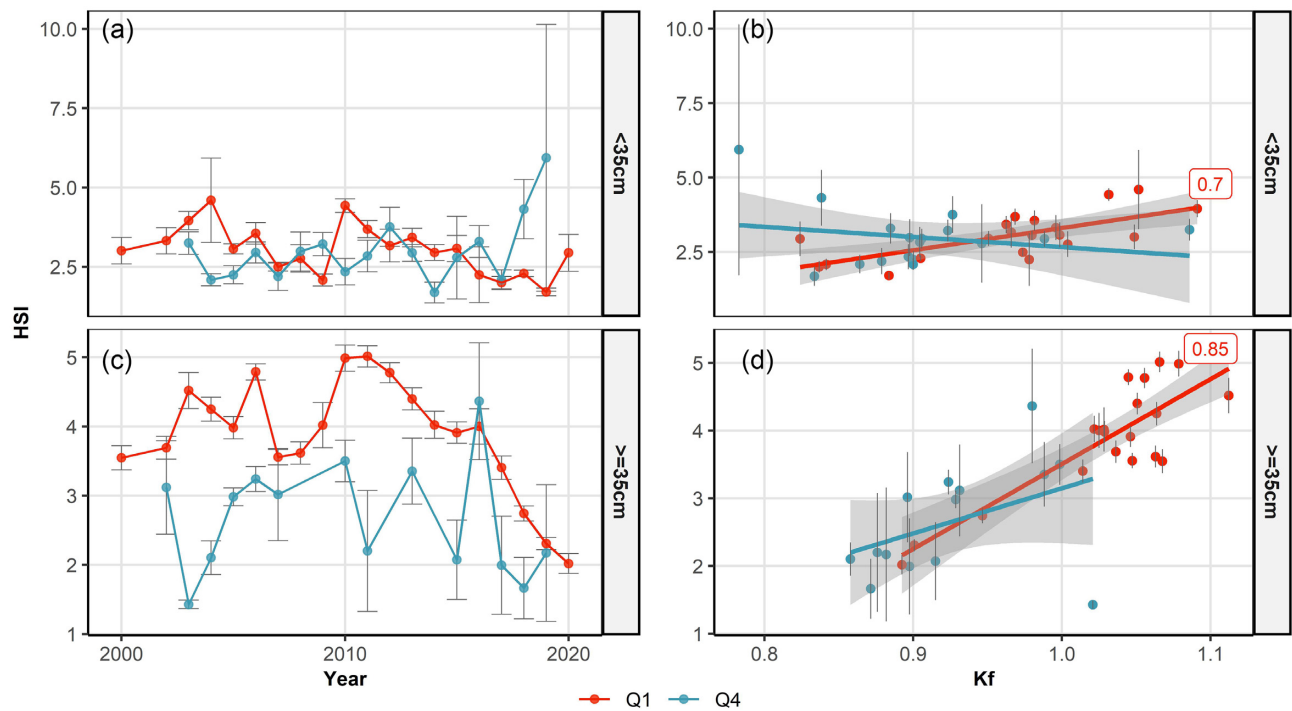
Figure 3. Hepatosomatic index (HSI) by quarter (colours) over time (in years, *x*-axis) for juvenile (a) and for adult (c) and vs. the Fulton index (*x*-axis) for juvenile (b) and for adult (d) in SD22; linear regressions with confidence interval; the coloured number indicates the significant Spearman correlation (*p*-value < 0.05).

clear change in somatic weight, i.e. muscle tissue. Both sexes displayed a similar trend in residual distribution over time, with only minor deviations. While positive medians of residual values occurred at the beginning of the time series between 1990 and 1993, negative medians occurred especially at the end of the time series from 2015 to 2020. From 2018 onwards, the negative trend steadily decreased, displaying the three lowest medians in the whole time series in a row.

Changes in HSI

HSI values of juvenile cod did not display any apparent change over time in both quarters (Figure 3a, top). The 2019 value during Q4 was higher than the previous values, but with a large standard deviation (grey bar). Juvenile HSI values were positively correlated to K_F values in Q1 (Figure 3b, top).

HSI values for adult cod were, for almost all years, higher in Q1 than in Q4 (Figure 3a, bottom). In Q1, HSI values of adult cod showed relatively high and stable levels (3.5–5) between 2000 and 2010, followed by a steady decline (from 5 to 2) with particularly low HSI values for the three most recent years. In the last 10 years, HSI of adult cod decreased by approximately 50% (Figure 3a) in Q1. This decrease was significantly correlated ($R = 0.77$) to the observed decrease in K_F (Figure 3b). In Q4, no temporal pattern in HSI of adult cod in SD22 was identified, and HSI values were not correlated to K_F.

For SD24, a similar trend was found for adult cod in Q1, lowest HSI values in recent years, and a significant correlation between K_F and HSI during Q1 (Supplementary Figure S9).

Development of the 2016 cohort

The annual length–frequency distributions of the 2016 cohort showed that the first faster-growing cod were already fished on as age-1 in 2017. It dominated the landings from 2018 (age-2) onwards. The observed average length-at-age of adult cod (age-2 and older) was about 32% lower than expected by the VBGF calculation (Supplementary Table S2; Figure 4).

Drivers of change

The CART model classified the condition factor into six classes, ranging from mean K_F values of 1.06 (highest) to 0.9 (lowest; Figure 5a). The class with the highest K_F was predominantly present in Q1 and at the beginning of the time series (i.e. from 1987 to 1995), while in recent years (i.e. from 2012 onwards), Q1 was mostly dominated by the class 4 ($K_F = 0.97$; Figure 5b). The class 3 ($K_F = 1.01$) primarily characterized Q4 until 2002 and the sixth class ($K_F = 0.9$) from 2013 onwards. Generally, the different classes changed revealed a gradual decrease in mean condition factor between the 1990s and 2020s of about 10% in both quarters (Figure 5c).

The regression tree based on four drivers (bottom water temperature, oxygen proxy, salinity, and mean stomach fullness) revealed a strong effect of bottom water temperature on cod K_F variability (Figure 5a). The two lowest condition factor classes were associated with highest bottom water temperatures (i.e. temperatures > 10.45°C), leading to a clear separation from the other classes. On the opposite, bottom salinity did not affect the cod body condition. Bottom oxygen proxy and stomach fullness was identified as a secondary driver of K_F variability. In Q1, the historic period 1987–2000 (class 1) was separated from the recent period (2012–2019, class 4) primarily by changes in oxygen proxy (historical period related to oxygen proxy values higher than 7.85 and recent period associated with lower oxygen proxy values). In the fourth quarter from 2000 onwards, a middle class in terms of condition factor (class 5; $K_F = 0.96$ as mean value) was split from the sixth class (i.e. the lowest $K_F = 0.9$) by a threshold on stomach fullness, with a lower condition factor displayed by individuals with lower stomach fullness.

For SD24, we also found temporal splitting of condition factor values (Supplementary Figure S10), with a mean decrease of about 15% and 8% across 30 years in Q1 and Q4, respectively. In contrast to SD22, in SD24 the stomach fullness index was revealed as the most critical parameter of cod body condition. Until 2005, the high mean condition factor values were explained by a high stomach fullness index for both quarters. From 2005 onwards, lower stomach fullness indices were linked to lower mean K_F (i.e. classes 4, 5, and 6). The bottom water temperature split the condition factor among quarters, but not consistently across the whole time series.

Diet comparison

The comparison of diet compositions of cod in SD22 from the 1980s (Weber and Damm, 1991) and the recent sampling (Funk et al., 2021) revealed a remarkable decrease in the proportions of Clupeids in the stomachs (Figure 6), especially for the length classes of adult cod (i.e. 40–49 cm and 50–69 cm) and in both quarters (i.e. Q1 and Q4). At the same time, the proportion of "other fish" increased in the four cases (two quarters * two length classes). The proportion of invertebrates showed a distinct increase over time for Q1, but a decrease for Q4.

The overall decrease of the proportion of fish prey (especially Clupeids) was confirmed by the comparison of the contemporary stomach data (Funk et al., 2021) to the data of Schulz (1987) (Supplementary Figure S11).

The increase of invertebrate prey in the cod diet during Q1 between the two periods can be primarily associated with a large increase in crustacea (mostly the common shore crab *Carcinus maenas*) and an increase of molluscs (mostly *Arctica islandica*) for cod in all length classes.

Discussion

Our analyses showed that the body condition of adult WBC is gradually declining since the 1980s in SD22, with a massive drop in the most recent years. This decline was due to a loss of both muscle tissue and liver weight. These changes suggest that fish of the WBC stock, across years and cohorts, are constantly losing energy reserves, thus adversely affecting stock productivity and resilience.

This negative trend in stock status was not detected in the weight-at-age data or any other of the metrics used in the ICES stock assessment (ICES, 2020a) and the fisheries management acted on a stock perceived as having full recovery potential. The weight loss of individual only raised concerns in the most recent 2021 stock assessment (ICES, 2021) when the weight-at-age drop characterizing the trajectory of the only stronger cohort from 2016 became apparent and resulted in a bycatch quota for 2022.

We argue that the gradual decline in energy reserves is due to an environmentally driven decrease in temporal and spatial availability of suitable habitat in terms of metabolic needs and food supply. The sharp decline in recent years when the overfished stock was dominated by the 2016 cohort, shows the fate of a single year-class going through the Rosa Lee phenomenon (Lee, 1912; Kraak et al., 2019) and a period of heat anomalies, with poor prospects given predicted environmental conditions (Dutheil et al., 2021; Meier et al., 2021).

Gradual decrease in energy reserves

The WBC stock is adapted to the life in the shallow, brackish waters of the western Baltic Sea. The fish display a characteristic seasonal, depth-related pattern in habitat use (Funk et al., 2020): from late December until March during low sea surface temperatures (SST) and a mixed water column, areas deeper than 15 m are favoured for spawning. Post-spawning cod use the warming shallower waters to feed (April–June). From July until August, at strong thermal stratification, high SST restrict cod access to the productive shallow water habitats while downslope movements are restricted by widespread hypoxia in the deeper waters. Thus, during summer WBC are trapped between warmed shallow waters and hypoxia in deeper waters, similar to the pattern found in a south Norwegian fjord (Freitas et al., 2015, 2016). This period is linked to poor feeding opportunities and reduced food intake (Funk et al., 2020), a metabolic deficit (Funk, 2020), and translucent zone formation in the otoliths (Krumme et al., 2020). In autumn, decreasing SST render shallow-water habitats usable again for cod and peak growth occurs (McQueen et al., 2019) before cod descend again for the next spawning cycle.
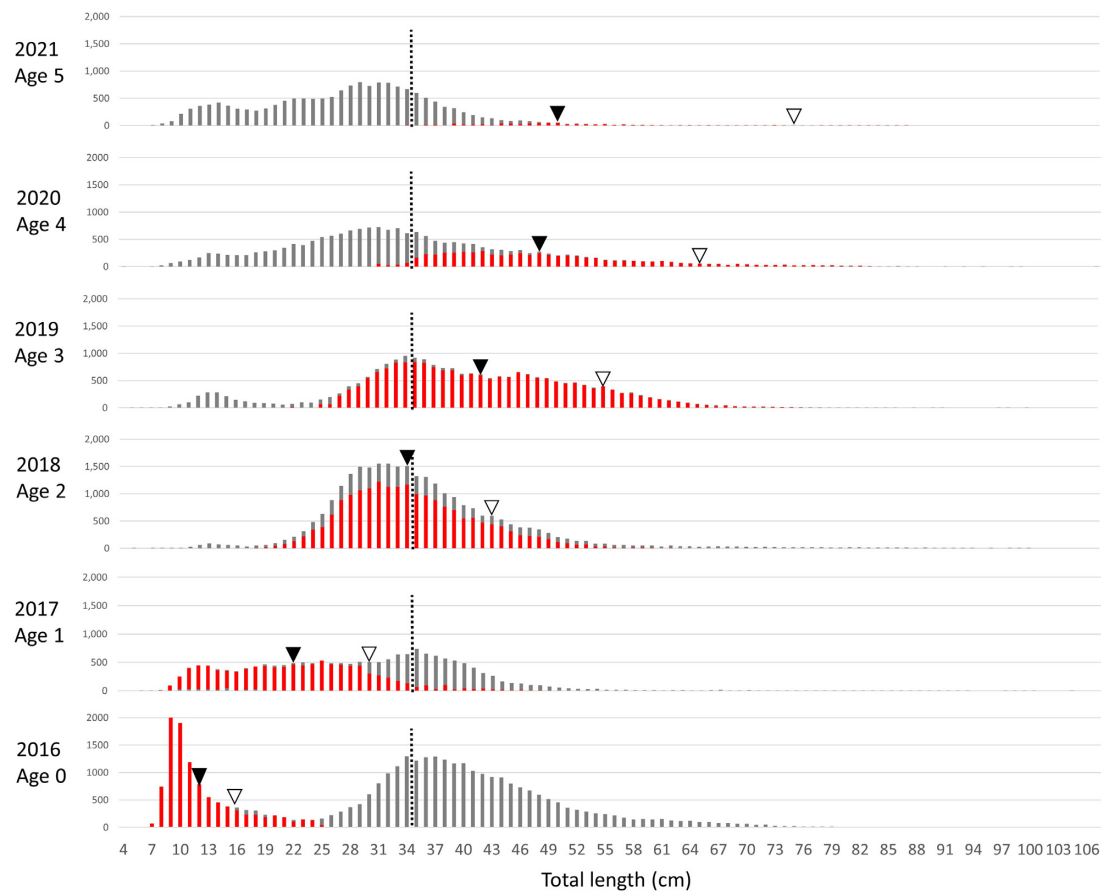
Figure 4. Length distribution of WBC between 2016 and 2021 following the 2016 cohort (red). Black triangle: observed average length-at-age, white triangle: expected length-at-age according to VBGF. Vertical dotted line: minimum conservation reference size of 35 cm. 2021 data are preliminary and only include Q1 survey data. Data source: German survey and commercial catch sampling data from SD22.

Temperature

The primary adverse effects of high SST in summer are loss of the possibility to use productive shallow-water habitats and metabolic stress. Laboratory experiments suggest that Atlantic cod experience optimum temperatures between 6 and 13°C, depending on the size of the fish, with optimal temperature decreasing with individual size (Björnsson and Steinarsson, 2002). Árnason *et al.* (2009) demonstrated a weak negative effect between 16 and 20°C and no effect between 4 and 16°C. Freitas *et al.* (2015, 2016) identified 15°C as the threshold in summer when cod avoided using the productive shallow-water habitats. Free-ranging WBC of the Arkona and Bornholm Sea did not fully avoid higher temperatures and experienced maximum temperatures of 18.1°C during summer (S. Haase, pers. comm.). However, Funk *et al.* (2021) showed that reduced food intake in WBC occurred during summer. This reduced food intake in warm condition is in line with experimental results showing that Atlantic cod display reduced gastric evacuation rates (at ambient temperatures > 15°C) or even stop food intake when temperatures exceed threshold temperatures (i.e. 19°C; Tyler, 1970). Thus, high ambient temperatures result in an accelerated decrease in the overall energy intake of cod. Moreover, high ambient temperatures should result in increased metabolic losses, and thus in an overall increased metabolic turnover, which negatively affects the energy reserves in WBC. However, under-water observations of relatively inactive, aggregated cod during peak

summer (S. Funk and U. Krumme, pers. comm.) suggest an aestivation behaviour, likely to minimize metabolic turnover. Overall, prolonged summers are likely to result in longer aestivation periods with reduced food intake and use of energy reserves in WBC.

The observed overall increase of yearly mean sea bottom temperature in our regression tree analysis is mainly due to the overall prolongation of summer periods, which in recent years start earlier (i.e. in mid-June) and last longer than in the past (e.g. in 2016 warm SST lasted until late September). The prolongation is linked to an earlier start of temperature rise in spring (due to warmer winters) and heat waves in summer. A worsening of the bottom oxygen situation in coastal waters during recent years is also reported by the local state authorities of Schleswig Holstein, Germany (LLUR, 2020) and Denmark (DCE, 2020). The oxygen-depleted area at the Belt Sea and the Mecklenburg Bay in October 2020, along with 2016 was the largest registered for the season since 2008 (DCE, 2020). In waters deeper than 15 m, LLUR (2020) measured at 22 out of 30 stations dissolved oxygen values lower than 2.8 ml l^{-1} (73%), slightly less than in September 2019 (93% of the stations with < 2.8 ml l^{-1} dissolved oxygen).

A climate warming-induced earlier start and delayed end of aestivation in summer equals contracted periods of shallow-water habitat use of WBC in spring and autumn. WBC cannot compensate for the temporal loss of feeding opportunities in shallow waters by using deeper, cooler waters because (i) in
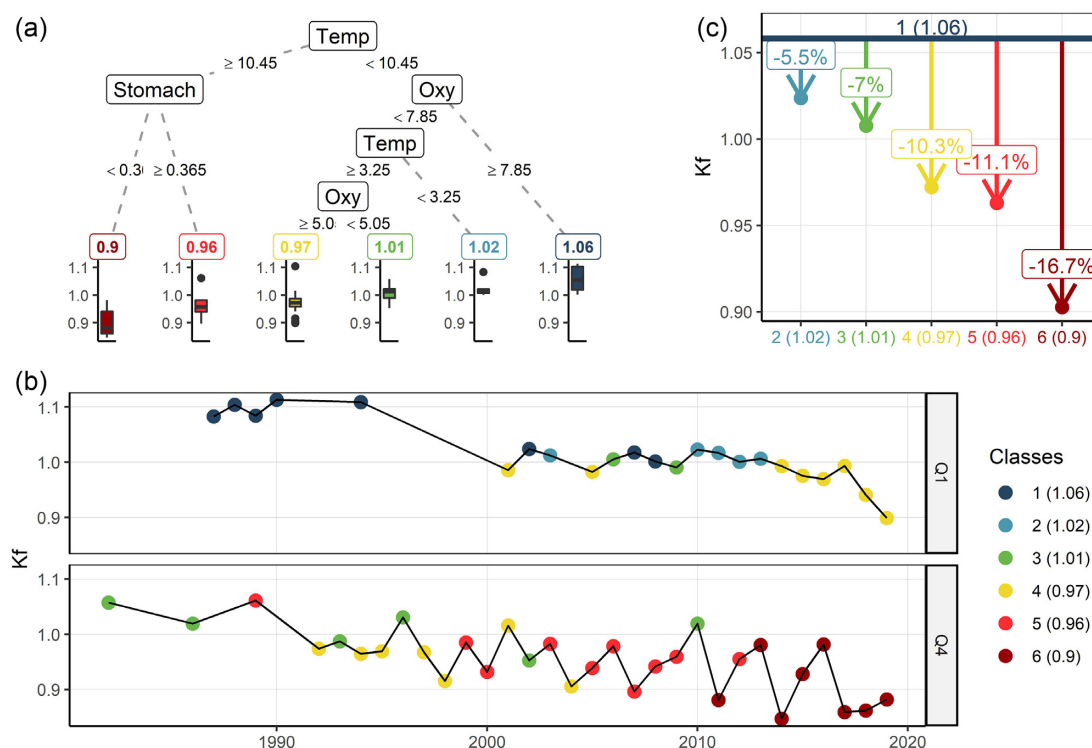
Figure 5. CART assessing the importance of the bottom salinity, bottom temperature (Temp), oxygen proxy (Oxy), and mean stomach fullness value (Stomach) on monthly mean Fulton's condition factor values for (35–110 cm) cod in SD22. Terminal nodes show the classes with the associated mean Fulton's condition factor values and the boxplot of all mean Fulton's condition values by class (a). Time series of monthly mean Fulton's condition factor values by quarter coloured by the class extracted from the tree (b). Mean Fulton's condition values of 2–6 classes are represented on the *x*-axis and the decrease in % for each of these class in comparison to the first class, which is characterized by the highest mean Fulton's condition value (c).

winter the fish are engaged in spawning and low water temperatures coincide with slow gastric evacuation rates (even if food were in sufficient supply) and (ii) in summer, hypoxia restricts habitat use and feeding opportunities.

Hypoxia

In the Baltic, hypoxia is exacerbated by excess of anthropogenic nutrient input. Presently, in the western Baltic Sea hypoxia only prevails during summer and early autumn. In the Arkona and Bornholm basin wild-ranging WBC, unlike EBC, never entered hypoxic waters (S. Haase, pers. comm.). Hence, direct adverse effects of pulsed or chronic hypoxia (Chabot and Claireaux, 2008) on WBC metabolism are unlikely. Hypoxic areas may rather act by (i) restricting habitat access to deeper areas, which would offer e.g. cooler and more saline environmental conditions or food, (ii) reducing abundance, biomass, and diversity of sessile and mobile animals during and after the hypoxic period, and (iii) potentially causing local fish kills of unknown magnitude when hypoxic waters are drawn to shore by local upwelling events in late summer and autumn. Therefore, the relationship between a decrease in condition factor and a decrease in oxygen proxy most likely is caused by the use of sub-optimal, unfavourable habitats and reduced feeding opportunities over weeks or months during longer-lasting and warmer summers, which are linked to the use of energy reserves. Overall, gradually shortened feeding periods and prolonged starvation periods are therefore likely reasons for the gradual decline in cod nutritional condition over the years.

Diet composition

The environmental changes have also gradually changed the availability of prey species of WBC. Hence, contemporary WBC do not rely on different food sources compared to historical studies, but the proportions of different prey species, and thus the metabolic quality of the diet composition, may have changed drastically.

The western Baltic spring spawning herring stock showed a distinct decline in stock biomass since the 1990s and is presently in a poor state (ICES, 2021). A key driver may be the warming winters result in reduced reproductive success (Polte *et al.*, 2021). While herring was the major prey organism of WBC in the 1980s (Schulz, 1987; Weber and Damm, 1991), it contributed little to the stomach content of WBC in SD22 in recent dietary studies (Funk *et al.*, 2021). Currently, dominating prey species are demersal fish and benthic invertebrates, especially the common shore crab *Carcinus maenas*. This new diet composition suggests a temporal diet shift related to a compensatory feeding behaviour of WBC in this area.

Such dietary changes can have a negative impact on the total energy intake of WBC. Especially hard-shelled crustaceans, such as *C. maenas*, generally display slower gastric evacuation rates than fish prey and also have a lower energy density compared to high-fat clupeids (Temming and Herrmann, 2003; Andersen *et al.*, 2017; Funk *et al.*, 2021). As a consequence, contemporary cod must consume larger quantities of crabs to achieve the same energy level as with clupeids. Beyond the two-sided habitat exclusion during summer, a shift from energy-rich to energy-poor prey items is
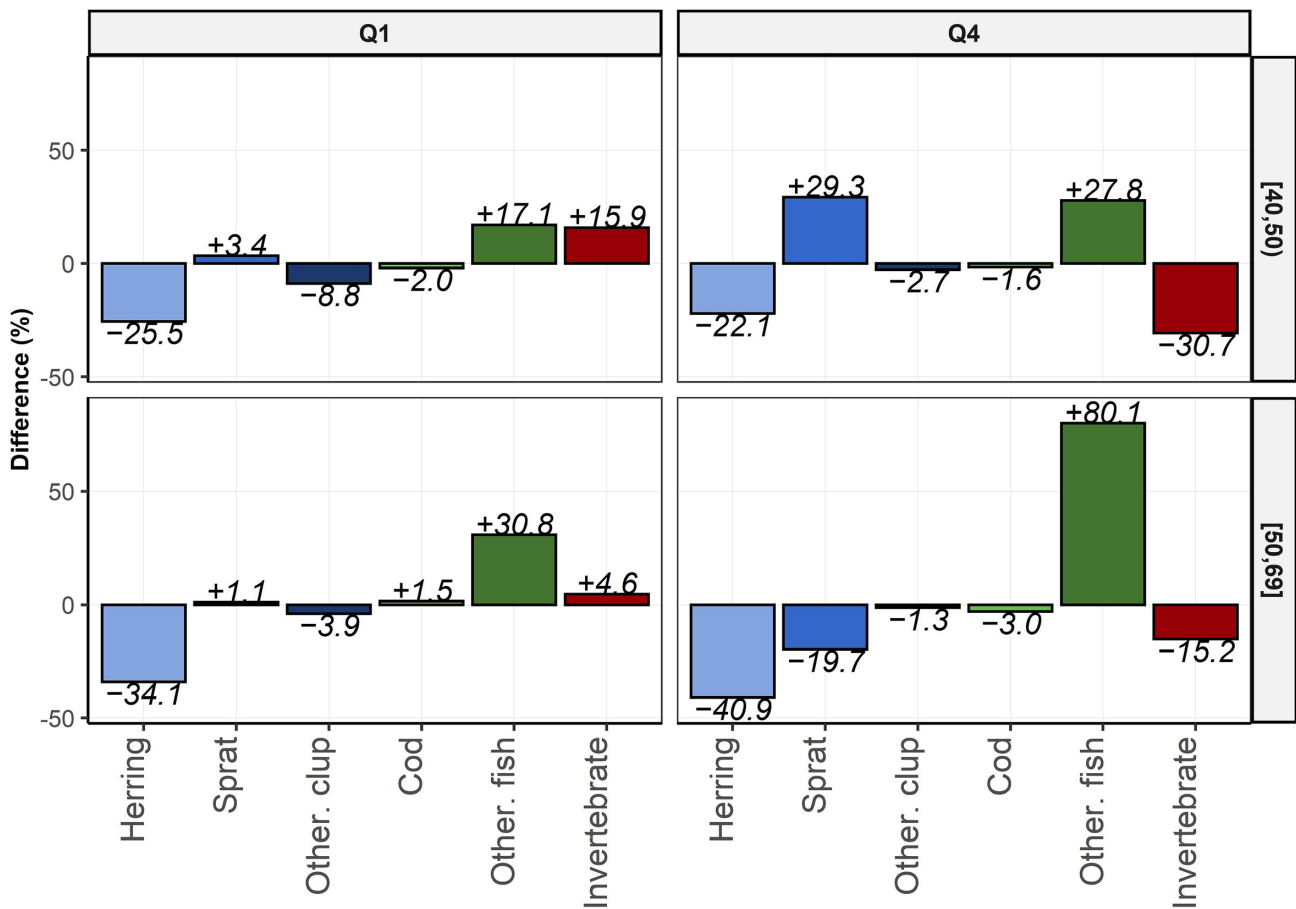
Figure 6. Temporal change in diet composition of cod from SD22 (in %) between the present (2016–2017; Funk *et al.*, 2021) and the past reference period (1981–1989; Weber and Damm, 1991) of the prey groups proportion by cod size (rows) and quarter (columns).

likely to contribute to an overall deterioration of cod body condition.

However, there are alternative explanations for the decrease of herring in the diet of cod in SD22. Potential sampling biases were discussed in Funk *et al.* (2021), e.g. historic samples were restricted to areas deeper than 20 m; cod could have shifted feeding grounds; several hypoxia events in Weber and Damm (1991) could have produced an underestimate of the role of invertebrates in the historic cod diet.

Moreover, density-dependent mechanisms in cod foraging behaviour may have occurred, too. Studies of cod off New-foundland showed that cod at higher densities tend to school and aggregate at lower structured areas, while cod tend to reside in small groups on structured habitats at low densities (Laurel *et al.*, 2004). Similarly, the decrease in WBC stock size may have been accompanied by a shift in foraging behaviour from historically larger schools feeding on highly fatty clupeids to a smaller population characterized by specimens mainly using shallow-water habitats, where they mainly feed on benthic invertebrates and less-energy dense forage fish, rather than fatty clupeids.

Given the uncertainty on a food shift in WBC and historic changes in the energy budget of WBC, stable isotope analysis of otolith archives (Grønkjær *et al.*, 2013) may be a promising approach to obtain more information on the present and past feeding ecology of WBC and help to identify changes in diet composition and overall energy intake.

Role of liver weight and muscle loss in body condition decline

When fish body condition decreases, weight loss can be due to reduced liver weight, muscle weight, gonad weight, or stomach fullness. Here, we found that the decline of body condition and HSI did not follow the same trajectory: body condition and HSI started to decrease around 1995 and around 2010, respectively. The high correlation between K_F and HSI must be driven by changes in recent years when a decrease in K_F and HSI co-occurred.

To build up energy reserves, (1) cod store energy-rich lipids in the liver (Kjesbu *et al.*, 1991; Kjesbu, 1994), which can be remobilized during starvation to compensate for energy deficits caused by metabolic losses (Lambert and Dutil, 2000); and (2) proteins in their muscle mass (Hemre *et al.*, 1993). We found evidence that liver weight declined (mostly for the 2010–2020 period) and muscle proteins (since 1980s). It suggests that the WBC stock has significantly lost energy reserves leading to a true decrease in somatic weight. It should be noted that our biological HSI time series only covered two decades starting in 2000. The 150 years HSI time series of Barent Sea cod (Kjesbu *et al.*, 2014) identified periods of stable HSI values that covered two to six decades, so that the significance of our time series is certainly restricted. It is, however, notable that the lowest HSI of Barent Sea cod also occurred in the recent time period (2004–2012; Kjesbu *et al.*, 2014).

The liver lipids, and therefore, the HSI, can be considered directly related to the lipid intake from food supply

(Yaragina and Marshall, 2000; Pardoe *et al.*, 2008). Thus, the observed decrease in HSI from the 2010s might be closely linked to the potential decrease of herring, a high-fat prey fish species (Røjbek *et al.*, 2014; Keinänen *et al.*, 2017) of WBC.

Moreover, in controlled feeding experiments, muscle metabolic capacities decreased progressively while the body condition of cod deteriorated (Lemieux *et al.*, 2004). Reduced muscle metabolic capacities were linked to lower swimming capacities and slower recovery following burst swimming (Martínez, 2003; Martínez *et al.*, 2004; Lapointe *et al.*, 2006). These results suggest that poor body condition may lead to reduced capacity to catch mobile prey, and thus worsen the status of cod in poor body condition.

It is notable that, unlike to EBC, the decrease in body condition and HSI in WBC cannot be linked to infection by the liver worm *C. osculatum* because cod in SD22 are characterized by very low infection levels, i.e. the lowest values in the whole Baltic Sea (Sokolova *et al.*, 2018; Ryberg *et al.*, 2020). However, one possible reason for reduced body condition that WBC and EBC may have in common is thiamine deficiency, which was reported for EBC (Engelhardt *et al.*, 2020), but not for WBC or other cod stocks. To conclude, the two declines in body condition detected for WBC and EBC stocks seem to involve remarkably different metabolic processes.

Potential effects on reproductive success

Generally, the development of reproductive products in Atlantic cod is highly dependent on the overall energy status (Kjesbu *et al.*, 1991; Lambert and Dutil, 2000). Laboratory experiments revealed a substantial decrease in cod fecundity for females in poor body condition (Lambert and Dutil, 2000), which has already been confirmed by *in situ* measurements for cod around Iceland (Marteinsdottir and Begg, 2002) and in the Northwest Atlantic (Alonso-Fernández *et al.*, 2009). Thus, energy deficits and related low energy storage during maturation and spawning can negatively affect the reproductive success of the stock by influencing egg quantity. Moreover, it can be assumed that changes in cod fecundity can amplify the postulated negative effect of environmental changes on cod larvae (Stiasny *et al.*, 2018; Voss *et al.*, 2019, Wasmund *et al.*, 2019). Finally, cod in poor condition have been shown to skip the reproduction more often (Rideout *et al.*, 2000; Rideout and Rose, 2006; Skjæraasen *et al.*, 2012). Hence, an overall decrease in WBC reproductive success may be partly linked to the constant decrease in body condition of adult cod.

Accelerated decline with the 2016 cohort

The cod stock virtually collapsed in 2015 with the lowest SSB of the time series at that time. Surprisingly, the 2016-year class was strong and constituted the major part of the SSB since 2018 because all year classes from 2017 and onwards were very weak. The difference between the observed and expected mean length of juvenile cod (age-0 year and age-1 year) of the 2016 cohort suggests that density-dependence affected this strong cohort before it entered the fishery. Given the extremely unbalanced age structure of the overfished stock, the fishing mortality massively reduced cod densities from 2018 onwards so that cod of age-2 year and older were released from density-dependence.

The accelerated decline in body condition and HSI in WBC in recent years is, therefore, closely linked to the development of the 2016-year class, which is a representative for "Lee's

Phenomenon" (Lee, 1912) where the faster-growing individuals in a cohort enter the fishery earlier, and the slower-growing individuals become over-represented in older age groups. And slower-growing individuals are more likely to display lower than average body condition.

In addition, the 2016 cohort experienced a series of warming records in the western Baltic Sea: in 2016 the summer was extraordinarily long, lasting until end September. In 2018 and 2019/2020, the warmest summer (Naumann *et al.*, 2019) and winter occurred, respectively. The latest years represent a series of winters much warmer than the long-term average (Naumann *et al.*, 2021). In 2021, the June was the second hottest on record, and three of the six summers of 2016–2020 were in the "top ten" of warmest summers in the regional time series at Warnemünde (dating back to 1948; Naumann *et al.*, 2021). Thus, the habitat restriction during the summer (i.e. cod trapped between warmed nearshore waters and hypoxic waters in the deep) was probably severe in terms of space (extremely small band of suitable habitat) and time (long-lasting), likely with strong negative effects on energy reserves of the 2016 cohort. This habitat restriction is backed by anecdotal evidence from gill net fishers in SD22 and SD24 who reported extraordinarily small livers in cod caught over the summer period in recent years (when the fish reside in deeper waters) and a constant increase in liver sizes when the fish resumed using the shallow-water areas in late summer/early autumn. Our results demonstrated that the overall proportion of WBC individuals in SD22 in body conditions below 0.8 exceeded 20% in 2020 for adult cod, and this proportion of thinner cod was even higher during Q4 than Q1 and higher for juvenile than for adult cod. This decrease is a recent drop to levels similar to EBC (Eero *et al.*, 2015).

Conclusions

The decrease in body condition was gradual, and therefore, difficult to detect. It may have been noticed only now because the accelerated decline with the 2016 cohort produced a remarkable drop that counteracted a shifting baseline syndrome (Pauly, 1995; Soga and Gaston, 2018). In the routine stock assessment, weight-at-age should be the indicative metric for weight gains or losses in the population. However, there are uncertainties linked to the weight-at-age metric (e.g. uncertainties in age-reading Hüssy *et al.*, 2016; Krumme *et al.*, 2020; variation among national weight sampling and raising procedures; large weight range for single year age classes; official transformation factors for the relationship gutted weight vs. fresh weight). In the end, the variance of the international weight-at-age estimate used in stock assessment may be too high to realistically depict inter-annual and longer-term changes. If the environmental stability assumption inherent in single stock assessment models, no longer holds and a stock responds to these changes by a decrease in individual quality of the fish, standard stock assessment metrics and a biomass reference point may be no longer useful as the only metrics.

As environmental changes strongly influence the stock properties, there is a crucial need to monitor the environmental changes, as well as the impact of these changes on the physiology and ecology of the individual fish composing the stock. The time series of key biological parameters (e.g. the body condition factor) add another important dimension relevant for sustainable resource use and could for example be

stronger and routinely incorporated in the stock assessment process and advice.

Supplementary material

Supplementary material is available at the *ICESJMS* online version of the manuscript.

Data availability statement

Biological data of cod (length, weight, and liver weight), stomach content data, and environmental data are available upon reasonable request at the Thünen-Institute of Baltic Sea Fisheries (uwe.krumme@thuenen.de), the University of Hamburg (steffen.funk@uni-hamburg.de), and the IOW (ulf.graewe@io-warnemuende.de), respectively.

Competing interest statements

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

References

Alonso-Fernández, A., Vallejo, A. C., Saborido-Rey, F., Murua, H., and Trippel, E. A. 2009. Fecundity estimation of Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) of Georges Bank: application of the autodiametric method. Fisheries Research, 99: 47–54.

Andersen, N. G., Lundgren, B., Neuenfeldt, S., and Beyer, J. E. 2017. Diel vertical interactions between Atlantic cod *Gadus morhua* and sprat *Sprattus sprattus* in a stratified water column. Marine Ecology Progress Series, 583: 195–209.

Árnason, T., Björnsson, B., and Steinarsson, A. 2009. Allometric growth and condition factor of Atlantic cod (*Gadus morhua*) fed to satiation: effects of temperature and body weight. Journal of Applied Ichthyology, 25: 401–406.

Björnsson, B., and Steinarsson, A. 2002. The food-unlimited growth rate of Atlantic cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciences, 59: 494–502. NRC Research Press.

Bleil, M., Oeberst, R., and Urrutia, P. 2009. Seasonal maturity development of Baltic cod in different spawning areas: importance of the Arkona Sea for the summer spawning stock. Journal of Applied Ichthyology, 25: 10–17.

Breiman, L., Friedman, J., Stone, C. J., and Olshen, R. A. 1984. Classification and Regression Trees. Taylor & Francis. 372pp.

Brosset, P., Lloret, J., Muñoz, M., Fauvel, C., Van Beveren, E., Marques, V., Fromentin, J.-M. *et al.* 2016. Body reserves mediate trade-offs between life-history traits: new insights from small pelagic fish reproduction. Royal Society Open Science, 3: 160202. Royal Society.

Bundy, A., and Fanning, L. P. 2005. Can Atlantic cod (*Gadus morhua*) recover? Exploring trophic explanations for the non-recovery of the cod stock on the eastern Scotian Shelf, Canada. Canadian Journal of Fisheries and Aquatic Sciences, 62: 1474–1489. NRC Research Press Ottawa, Canada. https://cdnsciencepub.com/doi/abs/10.1139/f05-086 (last accessed 16 December 2020).

Cardinale, M., and Modin, J. 1999. Changes in size-at-maturity of Baltic cod (*Gadus morhua*) during a period of large variations in stock size and environmental conditions. Fisheries Research, 41: 285–295.

Carstensen, J., Andersen, J. H., Gustafsson, B. G., and Conley, D. J. 2014. Deoxygenation of the Baltic Sea during the last century. Proceedings of the National Academy of Sciences, 111: 5628–5633. National Academy of Sciences.

Casini, M., Hansson, M., Orio, A., and Limburg, K. 2020. Changes in population depth distribution and oxygen stratification explain the current low condition of the Eastern Baltic Sea cod (*Gadus morhua*). Biogeosciences Discussions, 18: 1–28. Copernicus GmbH.

Casini, M., Käll, F., Hansson, M., Plikshs, M., Baranova, T., Karlsson, O., Lundström, K. *et al.* 2016. Hypoxic areas, density-dependence and food limitation drive the body condition of a heavily exploited marine fish predator. Royal Society Open Science, 3: 160416. Royal Society.

Chabot, D., and Claireaux, G. 2008. Environmental hypoxia as a metabolic constraint on fish: the case of Atlantic cod, *Gadus morhua*. Marine Pollution Bulletin, 57: 287–294.

Chabot, D., and Dutil, J.-D. 1999. Reduced growth of Atlantic cod in non-lethal hypoxic conditions. Journal of Fish Biology, 55: 472–491.

Jens Würgler, Hansen, and David, Rytter. 2020. Iltsvind i danske farvande – september- oktober 2020. Aarhus University, DCE – Nationalt Center for Miljø og Energi, 22 s. Rådgivningsnotat nr. 2020|72. https://dce.au.dk/fileadmin/dce.au.dk/Udgivelser/Notatet_2020/N2020_72.pdf (last accessed 18 Feburary 2022).

Delhez, E. J. M., Campin, J.-M., Hirst, A. C., and Deleersnijder, E. 1999. Toward a general theory of the age in ocean modelling. Ocean Modelling, 1: 17–27.

Dinesen, G. E., Neuenfeldt, S., Kokkalis, A., Lehmann, A., Egekvist, J., Kristensen, K., Munk, P. *et al.* 2019. Cod and climate: a systems approach for sustainable fisheries management of Atlantic cod (*Gadus morhua*) in coastal Danish waters. Journal of Coastal Conservation, 23: 943–958.

Dutheil, C., Meier, H. E. M., Gröger, M., and Börgel, F. 2021. Understanding past and future sea surface temperature trends in the Baltic Sea. Climate Dynamics, https://doi.org/10.1007/s00382-021-06084-1.

Dutil, J.-D., Castonguay, M., Gilbert, D., and Gascon, D. 1999. Growth, condition, and environmental relationships in Atlantic cod (*Gadus morhua*) in the northern Gulf of St. Lawrence and implications for management strategies in the Northwest Atlantic. Canadian Journal of Fisheries and Aquatic Sciences, 56: 1818–1831. NRC Research Press Ottawa, Canada. https://cdnsciencepub.com/doi/abs/10.1139/f99-140 (last accessed 7 January 2021).

Dutil, J.-D., Godbout, G., Blier, P. U., and Groman, D. 2006. The effect of energetic condition on growth dynamics and health of Atlantic cod (*Gadus morhua*). Journal of Applied Ichthyology, 22: 138–144.

Eero, M., Hjelm, J., Behrens, J., Buchmann, K., Cardinale, M., Casini, M., Gasyukov, P. *et al.* 2015. Eastern Baltic cod in distress: biological changes and challenges for stock assessment. ICES Journal of Marine Science, 72: 2180–2186. Oxford Academic.

Eero, M., Vinther, M., Haslob, H., Huwer, B., Casini, M., Storr-Paulsen, M., and Köster, F. W. 2012. Spatial management of marine resources can enhance the recovery of predators and avoid local depletion of forage fish. Conservation Letters, 5: 486–492.

Engelhardt, J., Frisell, O., Gustavsson, H., Hansson, T., Sjöberg, R., Collier, T. K., and Balk, L. 2020. Severe thiamine deficiency in eastern Baltic cod (*Gadus morhua*). Plos ONE, 15: e0227201. Public Library of Science.

European Commission. 2014. Regulation of the Europian Parliament and Council establishing a multiannual plan for the stocks of cod, herring and sprat in the Baltic Sea and the fisheries exploiting those stocks. 2014/0285 (COD).

Frank, K. T., Petrie, B., Leggett, W. C., and Boyce, D. G. 2016. Large scale, synchronous variability of marine fish populations driven by commercial exploitation. Proceedings of the National Academy of Sciences, 113: 8248–8253. National Academy of Sciences.

Freitas, C., Olsen, E. M., Knutsen, H., Albretsen, J., and Moland, E. 2016. Temperature-associated habitat selection in a cold-water marine fish. Journal of Animal Ecology, 85: 628–637.

Freitas, C., Olsen, E. M., Moland, E., Ciannelli, L., and Knutsen, H. 2015. Behavioral responses of Atlantic cod to sea temperature changes. Ecology and Evolution, 5: 2070–2083.

Froese, R. 2006. Cube law, condition factor and weight–length relationships: history, meta-analysis and recommendations. Journal of Applied Ichthyology, 22: 241–253.

Fu, C., Mohn, R., and Fanning, L. P. 2001. Why the Atlantic cod (*Gadus morhua*) stock off eastern Nova Scotia has not recovered. Canadian Journal of Fisheries and Aquatic Sciences, 58: 1613–1623. NRC Research Press Ottawa, Canada. https://cdnsciencepub.com/doi/abs/10.1139/f01-095 (last accessed 16 December 2020).

Funk, S. 2020, February. Spatio-Temporal Distribution, Food Intake and Growth of cod (Gadus morhua L.) in the Western Baltic Sea. University of Hamburg, Hamburg.

Funk, S., Frelat, R., Möllmann, C., Temming, A., and Krumme, U. 2021. The forgotten feeding ground: patterns in seasonal and depth-specific food intake of adult cod *Gadus morhua* in the Western Baltic Sea. Journal of Fish Biology, 98: 707–722.

Funk, S., Krumme, U., Temming, A., and Möllmann, C. 2020. Gillnet fishers' knowledge reveals seasonality in depth and habitat use of cod (*Gadus morhua*) in the Western Baltic Sea. ICES Journal of Marine Science, 77: 1816–1829. Oxford Academic.

Gräwe, U., Naumann, M., Mohrholz, V., and Burchard, H. 2015. Anatomizing one of the largest saltwater inflows into the Baltic Sea in December 2014. Journal of Geophysical Research: Oceans, 120: 7676–7697.

Grønkjær, P., Pedersen, J. B., Ankjærø, T. T., Kjeldsen, H., Heinemeier, J., Steingrund, P., Nielsen, J. M. *et al.* 2013. Stable N and C isotopes in the organic matrix of fish otoliths: validation of a new approach for studying spatial and temporal changes in the trophic structure of aquatic ecosystems. Canadian Journal of Fisheries and Aquatic Sciences, 70: 143–146.

Hemmer-Hansen, J., Hüssy, K., Baktoft, H., Huwer, B., Bekkevold, D., Haslob, H., Herrmann, J.-P. *et al.* 2019. Genetic analyses reveal complex dynamics within a marine fish management area. Evolutionary Applications, 12: 830–844.

Hemre, G. I., Karlsen, O., Lehmann, G., Holm, J. C., and Lie, O. 1993. Utilization of protein, fat and glycogen in cod (*Gadus morhua*) during starvation. Fiskeridirektoratets Skrifter Serie Ernaering, 6: 1–9.

Huebert, K. B., Pätsch, J., Hufnagl, M., Kreus, M., and Peck, M. A. 2018. Modeled larval fish prey fields and growth rates help predict recruitment success of cod and anchovy in the North Sea. Marine Ecology Progress Series, 600: 111–126.

Hüssy, K., Eero, M., and Radtke, K. 2018. Faster or slower: has growth of eastern Baltic cod changed?. Marine Biology Research, 14: 598–609. Taylor & Francis.

Hüssy, K., Mosegaard, H., Albertsen, C. M., Nielsen, E. E., Hemmer-Hansen, J., and Eero, M. 2016. Evaluation of otolith shape as a tool for stock discrimination in marine fishes using Baltic Sea cod as a case study. Fisheries Research, 174: 210–218.

ICES. 2014a. Report of the Baltic fisheries assessment working group (WGBFAS). *In* ICES Scientific Reports, pp. 919. ICES, ICES HQ, Copenhagen. Reports/Forms/DispForm.aspx?ID = 36625. (last accessed 1 December 2020).

ICES. 2014b. Manual for the Baltic International Trawl Surveys (BITS). Series of ICES Survey Protocols SISP 7-BITS. Baltic International Fish Survey Working Group.

ICES. 2020a. Baltic fisheries assessment working group (WGBFAS). ICES Scientific Reports, 2:45: 643 pp. ICES.

ICES. 2020b. Cod (*Gadus morhua*) in subdivisions 22–24, western Baltic stock (western Baltic Sea). *In* Report of the ICES Advisory Committee, 2020., ICES Advice 2020. ICES, Copenhagen. http://www.ices.dk/sites/pub/Publication Reports/Forms/DispForm.aspx?ID = 36600 (last accessed 1 December 2020).

ICES. 2021. Baltic fisheries assessment working group (WGBFAS). ICES Scientific Reports, 3: 717pp. ICES.

Karlsen, Ø., Holm, J. C., and Kjesbu, O. S. 1995. Effects of periodic starvation on reproductive investment in first-time spawning Atlantic cod (*Gadus morhua* L.). Aquaculture, 133: 159–170.

Keinänen, M., Käkelä, R., Ritvanen, T., Myllylä, T., Pönni, J., and Vuorinen, P. J. 2017. Fatty acid composition of sprat (*Sprattus sprattus*) and herring (*Clupea harengus*) in the Baltic Sea as potential prey for salmon (*Salmo salar*). Helgoland Marine Research, 71: 4.

Kjesbu, O. S. 1994. Time of start of spawning in Atlantic cod (*Gadus morhua*) females in relation to vitellogenic oocyte diameter, temperature, fish length and condition. Journal of Fish Biology, 45: 719–735.

Kjesbu, O. S., Klungsøyr, J., Kryvi, H., Witthames, P. R., and Walker, M. G. 1991. Fecundity, atresia, and egg size of captive atlantic cod (*Gadus morhua*) in relation to proximate body composition. Canadian Journal of Fisheries and Aquatic Sciences, 48: 2333–2343.

Kjesbu, O. S., Opdal, A. F., Korsbrekke, K., Devine, J. A., and Skjæraasen, J. E. 2014. Making use of Johan Hjort's "unknown" legacy: reconstruction of a 150-year coastal time-series on northeast arctic cod (*Gadus morhua*) liver data reveals long-term trends in energy allocation patterns. ICES Journal of Marine Science, 71: 2053–2063.

Klingbeil, K., Mohammadi-Aragh, M., Gräwe, U., and Burchard, H. 2014. Quantification of spurious dissipation and mixing – discrete variance decay in a finite-volume framework. Ocean Modelling, 81: 49–64.

Kraak, S. B. M., Haase, S., Minto, C., and Santos, J. 2019. The Rosa Lee phenomenon and its consequences for fisheries advice on changes in fishing mortality or gear selectivity. ICES Journal of Marine Science, 76: 2179–2192.

Krumme, U., Stötera, S., McQueen, K., and Pahlke, E. 2020. Age validation of age 0–3 wild cod *Gadus morhua* in the western Baltic Sea through mark-recapture and tetracycline marking of otoliths. Marine Ecology Progress Series, 645: 141–158.

Lambert, Y., and Dutil, J. 2000. Energetic consequences of reproduction in Atlantic cod (*Gadus morhua*) in relation to spawning level of somatic energy reserves. Canadian Journal of Fisheries and Aquatic Sciences, 57: 815–825. NRC Research Press.

Lambert, Y., and Dutil, J.-D. 1997a. Condition and energy reserves of Atlantic cod (*Gadus morhua*) during the collapse of the northern Gulf of St. Lawrence stock. Canadian Journal of Fisheries and Aquatic Sciences, 54: 2388–2400. NRC Research Press Ottawa, Canada. (last accessed 16 December 2020).

Lambert, Y., and Dutil, J.-D. 1997b. Can simple condition indices be used to monitor and quantify seasonal changes in the energy reserves of cod (*Gadus morhua*)? Canadian Journal of Fisheries and Aquatic Sciences, 54: 104–112. NRC Research Press.

Lapointe, D., Guderley, H., and Dutil, J. 2006. Changes in the condition factor have an impact on metabolic rate and swimming performance relationships in Atlantic cod (*Gadus morhua* L.). Physiological and Biochemical Zoology, 79: 109–119. The University of Chicago Press.

Lass, H. U., and Mohrholz, V. 2003. On dynamics and mixing of inflowing saltwater in the Arkona Sea: SALTWATER PLUMES IN THE ARKONA SEA. Journal of Geophysical Research: Oceans, 108, doi:10.1029/2002JC001465.

Laurel, B., Gregory, R., Brown, J., Hancock, J., and Schneider, D. 2004. Behavioural consequences of density-dependent habitat use in

juvenile cod *Gadus morhua* and *G. ogac*: the role of movement and aggregation. Marine Ecology Progress Series, 272: 257–270.

Le Cren, E. D. 1951. The length-weight relationship and seasonal cycle in gonad weight and condition in the perch (*Perca fluviatilis*). Journal of Animal Ecology, 20: 201–219. Wiley, British Ecological Society.

Lee, R. M. 1912. An investigation into the methods of growth determination in fishes by means of scales. ICES Journal of Marine Science, s1: 3–34.

Lemieux, H., Dutil, J.-D., Guderley, H., and Larocque, R. 2004. Growth, starvation and enzyme activity in white muscle of Atlantic cod: at what point do muscle metabolic capacities change?. Marine and Freshwater Behaviour and Physiology, 37: 287–294.

Lilly, G. 2008a. The decline, recovery, and collapse of Atlantic cod (*Gadus morhua*) off Labrador and Eastern Newfoundland. *In* Resiliency of Gadid Stocks to Fishing and Climate Change, K-SG-08-01, pp. 67–88. Alaska Sea Grant College Program, Fairbanks, AK. (last accessed 24 March 2021).

Lilly, G. 2008b. Decline and recovery of Atlantic cod (*Gadus morhua*) Stocks throughout the North Atlantic. *In* Resiliency of Gadid Stocks to Fishing and Climate Change, pp. 39–66. Alaska Sea Grant College Program, Fairbanks, AK. http://seagrant.uaf.edu/bookstore/pubs/AK-SG-08-01.html (last accessed 24 March 2021).

Limburg, K. E., and Casini, M. 2019. Otolith chemistry indicates recent worsened Baltic cod condition is linked to hypoxia exposure. Biology Letters, 15: 20190352. Royal Society.

LLUR. 2020. Sauerstoffmangel im bodennahen Wasser der westlichen Ostsee. 6pp. https://www.schleswig-holstein.de/DE/Fachinhalte/M/meeresschutz/Downloads/Bericht_LLUR_Sauerstoff_20 20.pdf (last accessed 26 November 2021).

McQueen, K., Casini, M., Dolk, B., Haase, S., Hemmer-Hansen, J., Hilvarsson, A., Hüssy, K. *et al.* 2020. Regional and stock-specific differences in contemporary growth of Baltic cod revealed through tag-recapture data. ICES Journal of Marine Science, 77: 2078–2088. https://academic.oup.com/icesjms/advance-article/doi/10.1093/icesjms/fsaa104/5880832 (last accessed 14 October 2020).

Marteinsdottir, G., and Begg, G. A. 2002. Essential relationships incorporating the influence of age, size and condition on variables required for estimation of reproductive potential in Atlantic cod *Gadus morhua*. Marine Ecology Progress Series, 235: 235–256.

Martínez, M. 2003. Condition, prolonged swimming performance and muscle metabolic capacities of cod *Gadus morhua*. Journal of Experimental Biology, 206: 503–511.

Martínez, M., Bédard, M., Dutil, J.-D., and Guderley, H. 2004. Does condition of Atlantic cod (*Gadus morhua*) have a greater impact upon swimming performance at Ucrit or sprint speeds?. Journal of Experimental Biology, 207: 2979–2990. The Company of Biologists Ltd.

Matthäus, W., and Franck, H. 1992. Characteristics of major Baltic inflows—a statistical analysis. Continental Shelf Research, 12: 1375–1400.

Matthäus, W., Nehring, D., Feistel, R., Nausch, G., Mohrholz, V., and Lass, H.-U. 2008. The inflow of highly saline water into the Baltic Sea. *In* State and Evolution of the Baltic Sea, 1952–2005, pp. 265–309. John Wiley & Sons, Ltd, Hoboken, NJ. https://onlinelibrary.wiley.com/doi/abs/10.1002/9780470283134.ch10 (last accessed 4 December 2020).

McQueen, K., Eveson, J. P., Dolk, B., Lorenz, T., Mohr, T., Schade, F. M., and Krumme, U. 2019. Growth of cod (*Gadus morhua*) in the western Baltic Sea: estimating improved growth parameters from tag–recapture data. Canadian Journal of Fisheries and Aquatic Sciences, 76: 1326–1337, NRC Research Press. https://cdnsciencepub.com/doi/abs/10.1139/cjfas-2018-0081 (last accessed 20 October 2020).

Meier, M., Dieterich, C., and Gröger, M. 2021. Natural variability is a large source of uncertainty in future projections of hypoxia in the Baltic Sea. Communications Earth and Environment, 2: 1–13.

Merino, G., Barange, M., Fernandes, J. A., Mullon, C., Cheung, W., Trenkel, V., and Lam, V. 2014. Estimating the economic loss of recent North Atlantic fisheries management. Progress in Oceanography, 129: 314–323.

Mion, M., Haase, S., Hemmer-Hansen, J., Hilvarsson, A., Hüssy, K., Krüger-Johnsen, M., Krumme, U. *et al.* 2021. Multidecadal changes in fish growth rates estimated from tagging data: a case study from the eastern Baltic cod (*Gadus morhua*, Gadidae). Fish and Fisheries, 22: 413–427.

Morgan, M. J. 2004. The relationship between fish condition and the probability of being mature in American plaice (*Hippoglossoides platessoides*). ICES Journal of Marine Science, 61: 64–70. Oxford Academic.

Muggeo, V. M. R. 2008. segmented: an R package to fit regression models with broken-line relationships. R NEWS. 8/1. 20–25 pp.

Myers, R. A., Hutchings, J. A., and Barrowman, N. J. 1996. Hypotheses for the decline of cod in the North Atlantic. Marine Ecology Progress Series, 138: 293–308.

Naumann, M., Gräwe, U., Mohrholz, V., Kuss, J., Kanwischer, M., Osterholz, H., Feistel, H. *et al.* 2021. Hydrographic-Hydrochemical Assessment of the Baltic Sea 2020. Meereswissenschaftliche Berichte, Warnemünde.119pp.

Naumann, M., Gräwe, U., Mohrholz, V., Kuss, J., Siegel, H., Waniek, J. J., and Schulz-Bull, D. E. 2019. Hydrographic-Hydrochemical Assessment of the Baltic Sea 2018. Meereswissenschaftliche Berichte, Warnemünde. 110pp.

Neuenfeldt, S., Bartolino, V., Orio, A., Andersen, K. H., Andersen, N. G., Niiranen, S., Bergström, U. *et al.* 2020. Feeding and growth of Atlantic cod (*Gadus morhua* L.) in the eastern Baltic Sea under environmental change. ICES Journal of Marine Science, 77: 624–632. Oxford Academic.

Ogle, D. H. 2016. Introductory Fisheries Analyses With R. The R series. CRC Press, Taylor & Francis Group, Boca Raton, FL. 317pp.

Orio, A., Karpushevskaia, A., Nielsen, A., Sundelöf, A., Berg, C. W., Albertsen, C. M., Stralka, C. *et al.* 2019. Benchmark workshop on Baltic Cod Stocks (WKBALTCOD2). ICES Scientific Report. International Council for the Exploration of the Sea (ICES), Copenhagen. 9pp.

Pardoe, H., Thórdarson, G., and Marteinsdóttir, G. 2008. Spatial and temporal trends in condition of Atlantic cod *Gadus morhua* on the Icelandic shelf. Marine Ecology Progress Series, 362: 261–277.

Pauly, D. 1995. Anecdotes and the shifting baseline syndrome of fisheries. Trends in Ecology and Evolution, 10: 430.

Polte, P., Groehsler, T., Kotterba, P., von Nordheim, L., Moll, D., Santos, J., Rodriguez-Tress, P. *et al.* 2021. Reduced reproductive success of Western Baltic herring (*Clupea harengus*) as a response to warming winters. Frontiers in Marine Science, 8: 231694409. Frontiers. (last accessed 5 January 2021).

Rakitin, A., Ferguson, M. M., and Trippel, E. A. 2011. Sperm competition and fertilization success in Atlantic cod (*Gadus morhua*): effect of sire size and condition factor on gamete quality. Canadian Journal of Fisheries and Aquatic Sciences, 56: 2315–2323. NRC Research Press, Ottawa, Canada. https://cdnsciencepub.com/doi/abs/10.1139/f99-164 (last accessed 16 December 2020).

Rätz, H.-J., and Lloret, J. 2003. Variation in fish condition between Atlantic cod (*Gadus morhua*) stocks, the effect on their productivity and management implications. Fisheries Research, 60: 369–380.

Reissmann, J. H., Burchard, H., Feistel, R., Hagen, E., Lass, H. U., Mohrholz, V., Nausch, G. *et al.* 2009. Vertical mixing in the Baltic Sea and consequences for eutrophication – A review. Progress in Oceanography, 82: 47–80.

Reusch, T. B. H., Dierking, J., Andersson, H. C., Bonsdorff, E., Carstensen, J., Casini, M., Czajkowski, M. *et al.* 2018. The Baltic Sea as a time machine for the future coastal ocean. Science Advances, 4: eaar8195. American Association for the Advancement of Science.

Rideout, R. M., Burton, M. P. M., and Rose, G. A. 2000. Observations on mass atresia and skipped spawning in northern Atlantic cod, from Smith Sound, Newfoundland. Journal of Fish Biology, 57: 1429–1440.

Rideout, R. M., and Rose, G. A. 2006. Suppression of reproduction in Atlantic cod *Gadus morhua*. Marine Ecology Progress Series, 320: 267–277.

Røjbek, M. C., Tomkiewicz, J., Jacobsen, C., and Støttrup, J. G. 2014. Forage fish quality: seasonal lipid dynamics of herring (*Clupea harengus* L.) and sprat (*Sprattus sprattus* L.) in the Baltic Sea. ICES Journal of Marine Science, 71: 56–71.

Ryberg, M. P., Skov, P. V., Vendramin, N., Buchmann, K., Nielsen, A., and Behrens, J. W. 2020. Physiological condition of eastern Baltic cod, *Gadus morhua*, infected with the parasitic nematode *Contracaecum osculatum*. Conservation Physiology, 8: 1–14. Oxford Academic. https://academic.oup.com/conphys/article/8/1/coaa093/5909674 (last accessed 1 December 2020).

Saunders, R. L. 1963. Respiration of the Atlantic Cod. Journal of the Fisheries Research Board of Canada, 20: 373–386. NRC Research Press.

Schade, F. M., Weist, P., and Krumme, U. 2019. Evaluation of four stock discrimination methods to assign individuals from mixed-stock fisheries using genetically validated baseline samples. Marine Ecology Progress Series, 627: 125–139.

Schulz, N. 1987. First results of cod stomach investigations in the western Baltic (ICES-subdivision 22 and 24) since 1978. Baltic Fish Committee, 1987/J:25. ICES C.M.

Sguotti, C., Otto, S. A., Frelat, R., Langbehn, T. J., Ryberg, M. P., Lindegren, M., Durant, J. M. *et al*. 2019. Catastrophic dynamics limit Atlantic cod recovery. Proceedings of the Royal Society B: Biological Sciences, 286: 20182877. Royal Society.

Skjæraasen, J. E., Nash, R. D. M., Korsbrekke, K., Fonn, M., Nilsen, T., Kennedy, J., Nedreaas, K. H. *et al*. 2012. Frequent skipped spawning in the world's largest cod population. Proceedings of the National Academy of Sciences, 109: 8995–8999. National Academy of Sciences.

Soga, M., and Gaston, K. J. 2018. Shifting baseline syndrome: causes, consequences, and implications. Frontiers in Ecology and the Environment, 16: 222–230.

Sokolova, M., Buchmann, K., Huwer, B., Kania, P. W., Krumme, U., Galatius, A., Hemmer-Hansen, J. *et al*. 2018. Spatial patterns in infection of cod *Gadus morhua* with the seal-associated liver worm *Contracaecum osculatum* from the Skagerrak to the central Baltic Sea. Marine Ecology Progress Series, 606: 105–118.

Stiasny, M. H., Mittermayer, F. H., Göttler, G., Bridges, C. R., Falk-Petersen, I.-B., Puvanendran, V., Mortensen, A. *et al*. 2018. Effects of parental acclimation and energy limitation in response to high CO_2 exposure in Atlantic cod. Scientific Reports, 8: 8348. Nature Publishing Group.

Temming, A., and Herrmann, J.-P. 2003. Gastric evacuation in cod: prey-specific evacuation rates for use in North Sea, Baltic Sea and Barents Sea multi-species models. Fisheries Research, 63: 21–41.

Therneau, T., and Atkinson, B. 2019. rpart: recursive partitioning and regression trees. https://CRAN.R-project.org/package=rpart (last accessed 25 June 2021).

Trenkel, V. M., Huse, G., MacKenzie, B. R., Alvarez, P., Arrizabalaga, H., Castonguay, M., Goñi, N. *et al*. 2014. Comparative ecology of widely distributed pelagic fish species in the North Atlantic: implications for modelling climate and fisheries impacts. Progress in Oceanography, 129: 219–243.

Tyler, A. V. 1970. Rates of gastric emptying in young cod. Journal of the Fisheries Research Board of Canada, 27: 1177–1189. NRC Research Press.

Voss, R., Quaas, M. F., Stiasny, M. H., Hänsel, M., Stecher Justiniano Pinto, G. A., Lehmann, A., Reusch, T. B. H. *et al*. 2019. Ecological-economic sustainability of the Baltic cod fisheries under ocean warming and acidification. Journal of Environmental Management, 238: 110–118.

Wasmund, N., Nausch, G., Gerth, M., Busch, S., Burmeister, C., Hansen, R., and Sadkowiak, B. 2019. Extension of the growing season of phytoplankton in the western Baltic Sea in response to climate change. Marine Ecology Progress Series, 622: 1–16.

Weber, W., and Damm, U. 1991. Investigation on cod stomachs in the Western Baltic 1981–1989. Baltic Fish Committee, ICES C.M.1991/J:23. International Council for theExploration of the Sea (ICES), Copenhagen.

Weist, P., Schade, F. M., Damerau, M., Barth, J. M. I., Dierking, J., André, C., Petereit, C. *et al*. 2019. Assessing SNP-markers to study population mixing and ecological adaptation in Baltic cod. Plos ONE, 14: e0218127. Public Library of Science.

Werner, K.-M., Taylor, M. H., Diekmann, R., Lloret, J., Möllmann, C., Primicerio, R., and Fock, H. O. 2019. Evidence for limited adaptive responsiveness to large-scale spatial variation of habitat quality. Marine Ecology Progress Series, 629: 179–191.

Winter, A.-M., Richter, A., and Eikeset, A. M. 2020. Implications of Allee effects for fisheries management in a changing climate: evidence from Atlantic cod. Ecological Applications, 30: e01994.

Yaragina, N. A., and Marshall, C. T. 2000. Trophic influences on interannual and seasonal variation in the liver condition index of Northeast Arctic cod (*Gadus morhua*). ICES Journal of Marine Science, 57: 42–55. Oxford Academic.

Zimmermann, F., and Werner, K. M. 2019. Improved management is the main driver behind recovery of Northeast Atlantic fish stocks. Frontiers in Ecology and the Environment, 17: 93–99.

Handling Editor: Henn Ojaveer