



Future perspectives for cod in the eastern Baltic Sea – stock development, fisheries and management challenges in a changing ecosystem

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Margit Eero (ed.)

DTU Aqua Report no. 425-2023



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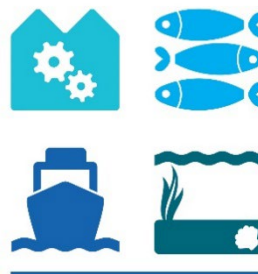
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Preface

This report presents the results from the project “Fremtidsperspektiver for torsk i den østlige Østersø – bestandsudvikling samt fiskeri- og forvaltningsmuligheder i et økosystem under forandring (FREMTOR)” with journal no. 33113-B-20-157, which received financial support from the European Maritime and Fisheries Fund (EMFF) and the Danish Fisheries Agency.

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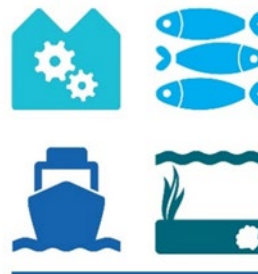
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Summary

The present report describes results of the project "Future perspectives for cod in the Eastern Baltic Sea—stock development, fisheries and management challenges in a changing ecosystem (FREMTOR)", funded by European Maritime and Fisheries Fund and the Danish Fisheries Agency. The project provides new knowledge on some key aspects of the status of the stock and associated drivers, as well as synthesizes existing information, altogether providing state-of-the art basis for evaluating future perspectives for this stock. Improved understanding of the factors responsible for the low productivity of the stock is crucially important for being able to assess its recovery potential. Furthermore, realistic targets for stock recovery in the current state of the ecosystem need to take account of changes in biological parameters, including growth and recruitment as well as other indicators of stock health, such as body condition and parasite load.

In this project, time series of various biological parameters of the Eastern Baltic cod (incl. condition, size at maturity, parasite load, length structure) were extended back to the 1940s, i.e. the beginning of intensive exploitation of this stock. These data show that the cod stock is presently in unprecedented poor state. Cod body condition and infection load of *C. osculatum* were in similar adverse states in the 1940s–1950s, however, the relatively more favorable states of other biological parameters back then indicate that the stock was overall in a better shape than is presently the case. The long-term data reveal concurrent trends in seal abundance and *C. osculatum* infection, the latter being inversely related to cod body condition, which provides correlation based evidence regarding potential associations between these variables. Spatial contrasts in the present state of cod are apparent in cod from the Åland Sea being in a substantially better condition and larger in size compared to the average specimen in the main distribution area of the stock. This is despite the much higher number of nematodes and intensity of infection of cod in Åland Sea with *C. osculatum*. This points at the importance of initial condition at infection time, potentially in combination with different dynamics of infection between cod from the two areas.

The prospects of the eastern Baltic cod stock depend largely on its reproductive potential and resulting recruitment, as well as growth. Growth patterns of the Eastern Baltic cod were investigated using advanced techniques based on otolith microchemistry that provided new insights on the effects of temperature and hypoxia. Concerning recruitment, we investigated the effects of parental quality on reproductive success and implications for cod recruitment. The most remarkable result is that the small-sized females were found to have an extraordinary high potential fecundity. Experimental results suggest that the small-sized spawners in poor condition are still capable of producing viable offspring. However, the high investment in reproduction likely occurs at the expense of growth, probably also leading to increased mortality, rendering the Baltic cod stock in a depressed state.

Fisheries management presently only has a limited impact of overall mortality of the cod stock, as natural mortality substantially exceeds the mortality due to fishing. A factor that could be influenced by fisheries management is the availability of fish prey (especially sprat) in the distribution area of cod, as the overlap between these species is rather limited in autumn. We found that overall fishing impact on sprat biomass in the distribution area of cod in autumn is relatively limited, however with occasionally relatively higher catches of the smallest sprat, which may be of essential importance for the small-sized cod.

The present exceptionally poor state of the stock on all metrics suggests that more drivers and mechanisms are having simultaneous adverse effects than has been the case in the past. This complicates

our understanding of the recovery potential of the stock. The possible benefits to the cod stock resulting from management interventions influencing the ecosystem conditions is presently not possible to quantify. This is due to the complexity of the processes involved, as different parameters of stock health are interacting with one another, and are influenced by several external drivers, affecting recruitment, growth and/or mortality and ultimately stock biomass. Continued regular monitoring of a wider range of stock health indicators is recommended, and future stock assessment and management should consider multiple indicators of stock health, not only biomass, in defining overall stock status and appropriate management measures.

Background and outline

The Eastern Baltic cod stock is currently in a remarkably poor state. The stock biomass has declined to the lowest level on record (ICES 2022), and additionally pronounced deterioration in various biological parameters has taken place over the last decade. On average, cod are small, suffer from low body condition and a high load of parasitic nematodes in the liver; they mature at a small size and the distribution range of the stock has contracted to a relatively small area (Haarder et al. 2014; Eero et al. 2015; Casini et al. 2016a). Growth of the fish has declined (Mion et al. 2021), natural mortality has increased (ICES 2022) and there is no surplus production in the stock to support fisheries (Eero et al. 2020). Consequently, to protect the stock and aid its recovery, targeted cod fisheries have been banned since 2019.

Much of the process-oriented research on Eastern Baltic cod in the last few decades has focused on the hydrographic drivers of recruitment. The deterioration of cod body condition, length structure and liver worm load has only relatively recently attracted increasing attention to these aspects of population health, in scientific literature. Several research projects carried out in recent years have addressed aspects related to the current poor state of the stock. There include number of earlier EMFF projects, for example "Eastern Baltic cod- knew knowledge on growth and mortality is a way to improved management advice" (33113-B-16-047) and "Improved knowledge base of management of cod stocks in the Baltic Sea and Kattegat" (33113-B-17-092). These projects had much focus on growth of the Eastern Baltic cod and re-establishment of analytical stock assessment that had broken down in 2014. The BalticSea2020 funded project "Tagging Baltic Cod" (TABACOD) provided new information on growth of the cod based on tagging data (Hüssy et al. 2020). Furthermore, several EMFF projects have focused on investigating the effects of liver worm infection on cod (e.g., 33113-B-16-071; 33113-B-17-110, 33113-B-20-161). Concerning the drivers and mechanisms involved in the currently poor state of the stock, there is so far no consensus, but intense ongoing debate (Casini et al 2016a; Brander 2020; Neuenfeldt et al. 2020; Svedäng et al. 2022; Brander 2022). A recent review of the state-of- the art knowledge is provided in Birgersson et al. (2022).

In the present project, our aim is to provide new knowledge on some key aspects of the state of the Eastern Baltic cod that contribute to elucidating future perspectives for development of this stock. We assemble and analyse historical information to extend the time series of a range of life history and demographic parameters of the Eastern Baltic cod (Section 1). The longer time series of Eastern Baltic cod stock health indicators are valuable in adding new perspectives to the perception of the present state of the stock and shed light on realistic recovery expectations. We also look at spatial variations and contrasts in the data, both within the main cod distribution area in the Baltic Proper and contrasting the state of cod in its main distribution area with the apparently better state of cod in Åland Sea (Section 2). The prospects of the Eastern Baltic cod stock, and whether it can support sustainable fisheries depend on developments in its productivity, i.e. recruitment and growth. At present poor parental condition, cod fecundity and survival of offspring can be of increased importance for the recruitment success. We contribute data analyses and experimental investigations to provide new knowledge on these aspects (Section 3). Furthermore, we provide new insights regarding growth of the fish, by combining tagging data with newly developed advanced technics using otolith microchemistry that provide information on the chemical composition of the water as well as age and growth of the fish. Combined, these data provide information on cod movements in relation to hypoxia, and enable linking this with information on growth (Section 4). One of the factors hypothesised to affect negatively the health state of cod is limited availability of sprat as prey. This issue is of interest also for fisheries management that could at least partly influence the sprat abundance. In this project, we address

this topic by updating information on the amount of sprat available in the area relative to cod, analysing energy demands for cod compared to the energy provided by sprat and conducting stomach data analyses to elucidate changes in cod diet and feeding levels (Section 5). We also look into changes in sprat fishing patterns, to elucidate potential connections to sprat availability for cod. Finally, we synthesise the new and existing knowledge on factors influencing the state of the Eastern Baltic cod, both external drivers as well as interactions between different health aspects of the stock which may reinforce the poor states of one another (Section 6). We address associated challenges for ecosystem based management, and future perspectives for the stock under the present state-of-the-art knowledge.

1. New insights into cod stock status from historical data

By Margit Eero, Keith Brander, Maris Plikshs[†], Tatjana Baranova, Uwe Krumme, Krzysztof Radtke and Jane W. Behrens

Introduction

International standardized monitoring data for the Eastern Baltic cod stock is available from 1991 onwards. Longer term information is available for biomass and fishing mortality from stock assessment (ICES 2022). Also, for some other biological parameters, such as body condition (Casini et al. 2016a) and growth (Mion et al. 2021), the time series have been extended back from the 1990s. However, a more comprehensive overview bringing together information on multiple health aspects of the stock (including size at maturity, size structure etc) is only available since the early 1990s. Thus, the much healthier states observed in the early 1990s have come to be regarded as the historic reference for a number of biological parameters, presented in fisheries management advice (ICES 2022). Given the present state of the stock, it is questionable to what level recovery is possible, and realistic targets in the current state of the ecosystem need to take account of changes in biological parameters affecting stock productivity. Historical perspectives have in many cases provided valuable insights regarding baselines and targets for management and conservation of marine life (Lotze and Worm 2009; Jackson et al. 2011). Hence, in this section, we make available eight decades of observations on a wide range of Eastern Baltic cod biological parameters, which is exceptional even compared with the other well-studied North Atlantic cod stocks. The extended time series of EBC stock health indicators are considered valuable in adding new perspectives to the perception of the present state of the stock and shed light on realistic recovery expectations. The results of this study are published in Eero et al. (2023).

Materials and Methods

In this study, we reconstructed the historical developments in Eastern Baltic cod body condition, length at first maturity, infection load of parasitic liver worm, length structure and sex ratio in the population and spatial distribution of the stock, focusing on the time period from the 1990s back to the 1940s. For the indicators associated with length structure and spatial distribution of the stock, as well as liver worm load, historical information was derived from published literature and various ICES reports and materials provided to the ICES Working Groups assessing the status of the cod stock back in time. Time series of average body condition of cod, length at maturity and sex ratio were based on individual fish measurement data (length, body and liver weight, sex, maturity stage). The data for the 1940s–1990s were obtained from the archives of the research institutes in Germany (Thünen Institute of Baltic Sea Fisheries), Latvia (Institute of Food Safety, Animal Health and Environment), Poland (National Marine Fisheries Research Institute) and Denmark (Institute for Aquatic Resources, Technical University of Denmark). The data originated both from sampling of commercial cod catches and from research cruises and covered ICES Subdivisions 25–28. Further details are described in Eero et al. (2023).

Spatial distribution

We used the proportion of the commercial cod landings taken in ICES SDs 27–32 as a proxy for the relative cod distribution in these areas. Spatially disaggregated data on cod landings were extracted from ICES WGBFAS and its predecessor's reports, supplemented by national statistics and literature information for the earliest decades in the time series.

Body condition

Analyses of body condition used data on total length (L) and total body weight (W) of individual cod. The cod included in the analyses were between 20 and 100 cm in length. Le Cren's condition index was applied. As a first step, data from all years were pooled to estimate the parameters *a* and *b* of the length–weight relationship: $W = a * L^b$

Subsequently, for each individual fish *i*, Le Cren's condition index *K* was calculated as the ratio between its weight (in g) and the predicted weight of the fish at a given length (in cm) from the length–weight relationship:

$$K_i = \frac{W_i}{a * L_i^b}$$

To investigate possible effects of SD, quarter and data source on our average condition estimates, we first visually inspected the temporal trends in average body condition separately for each data source (commercial or survey), ICES SD and quarter. Additionally, we conducted generalized additive model (GAM) analyses of cod body condition with smoothing spline for year and including quarter, ICES SD and data source as categorical variables.

Length at maturity

Length at maturity (L50) was defined as the length at which half of the fish have become mature. The historical individual fish data used for L50 calculations for the years before the 1990s originated from the 1st and 2nd quarters of the year. From 1991 onwards, data from the 1st quarter BITS were used, as in ICES stock assessments. We also applied the same calculation procedures for L50, as in the ICES assessments for this stock.

Sex ratio

Females generally dominate among older cod, as observed in several stocks. For Eastern Baltic cod, time series of sex ratios in the population were constructed based on sex information of individual cod in samples, combined for all seasons for which data were available. As an average over the time series, females started to dominate in length classes > 40 cm, and their proportion in the stock increased with length. Since we were interested in potential multi-decadal changes in the degree of female dominance among larger cod, we constructed time series of sex ratios for > 40 cm and > 50 cm cod.

Parasitic nematodes in cod livers

We focus on *Contracaecum osculatum* in this study because of the marked increase in infection loads of this parasitic nematode in EBC livers since the 2010s (Haarder et al. 2014, Nadolna and Polska 2014, Sokolova et al. 2018). Monitoring of liver worms in cod has hitherto not been part of standard surveys in the Baltic Sea and information is only available from site-specific scientific investigations reported in literature (Table 1.1). This allowed for comparison of *C. osculatum* loads in cod in recent years with the 1940s–1950s and the 1970s–1980s. Only data from fish above 30 cm in length were included in the analysis, because *C. osculatum* is nearly absent in smaller cod.

Table 1.1. Data sources for parasitic liver worm (*Contracaecum osculatatum*) infection loads in Eastern Baltic cod. The table shows also the years and areas of sampling, including approximate ICES Subdivision (SD), and numbers (n) and length range of investigated cod.

Year of sampling	Sampling areas	SD	n	Cod length (cm)	Source
1946	Liepaja	26, 28	25	35-73	Shulman, 1948
1949	Gotland trench, Liepaja	26, 28	742	30-100	Petrushevsky & Shulman, 1955
1950,1955	Klaipeda	26	1000	45-60	Gecevicjute 1955
1974–1975	Pomeranian Bay and adjacent waters	24, 25	1215	33-90	Grabda, 1976
1982–1983	Bornholm Basin	25	92	30-100	Haarder et al. 2014
1987–1990	Polish, Danish, Swedish waters	25, 26	2816	>31	Myjak et al. 1994
2012	Bornholm Basin	25	185	30-80	Haarder et al. 2014
2013–2015	Bornholm Basin	25	100	31-50	Zuo et al. 2016
2016–2017	Bornholm Basin, south of Gotland	25	321	35-50	Sokolova et al. 2018
2017, 2019	Bornholm Basin	25	304	30-53	Ryberg et al. 2020
2017–2020	Bornholm Basin	25	370	30-58	Ryberg et al. 2022

Length structure

Data on length structure of cod commercial catches in the years 1938–1991 were partly derived from literature reports (doi:10.11583/DTU.21981698). In addition, we used the national data that countries historically had provided to the ICES stock assessment working groups in paper form (O. Bagge and E. Ojaveer; pers. comm). The information was mostly country-specific, in some cases further broken down to sub-areas or quarters, resulting in more than one length composition dataset per year. We treated each dataset separately when calculating length-based indicators, and subsequently averaged the indicator values for a given year. From 2000 onwards, we only used the combined annual length structure of the total commercial catch of the Eastern Baltic cod (including discards) from ICES (2022).

Length at 95th percentile of a length distribution (L95) was used as an indicator characterizing the proportion of large individuals in the stock. L95 was calculated including fish > 40 cm in length, to reduce the possible effects of both recruitment variability and gear selectivity on the estimates. We compared our L95 estimates based on commercial catch data with the ones calculated from BITS from 1991 onwards, supplemented with survey information for some years in the 1950s and 1960s. The L95 estimates based on data from commercial catch and research cruises were similar, providing assurance that major changes observed in L95 over time reflect changes in population length structure.

Results

Spatial distribution

Spatial distribution of commercial landings suggests that the bulk of the Eastern Baltic cod stock has been concentrated in the southern Baltic Sea (SDs 25–26) throughout the entire time series, going back to the 1940s. The fraction of the landings taken in the northeastern Baltic Sea (SDs 27–32) was highest in the late 1970s–early 1980s, when it reached up to 25%. During the 1940s to 1970s, these northeastern areas contributed at most 10% of the landings, and less than 5% since the 2000s.

Body condition

Long-term trends in the average Le Cren's condition index K show a gradual increase from low values in the 1940s–1950s to relatively good condition in the early 1970s, followed by a drop in the late 1970s–early 1980s. Thereafter the average body condition quickly improved, reaching a peak in the late 1980s–early 1990s, from which it gradually declined to low level in the 2010s with a slight increase in latest years, especially in in Q1 (Fig. 1.1). GAM analyses showed that data source, SD and quarter (Q) all had significant effects on body condition. However, the overall pattern of peaks and troughs in average body condition (as shown in Fig 1.1) was apparent in all quarters, SDs, and in data from both commercial catches and research surveys. Notably, the body condition of average cod in Q1–Q2 in 1948–1955 (all SDs and data sources combined) was estimated to be significantly lower (Welch two sample t-test, $p < 0.001$, $t = 26.803$) than the average in recent years (2015–2021). The condition of cod was also relatively low for a short period in the late 1970s–early 1980s. The highest average body condition in the time series occurred in the late 1980s–early 1990s, significantly higher than during the peak in the early 1970s.

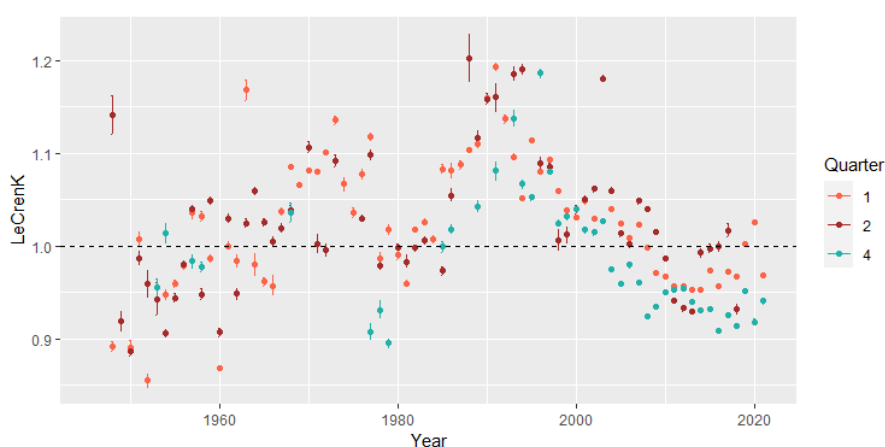


Figure 1.1. Time series of body condition (Le Cren's K) of Eastern Baltic cod. The bars indicate standard error of the mean. (Modified from Eero et al. 2023).

Length at maturity and sex ratio

L50 of the cod has declined from around 40 cm in the early 1990s to 20 cm in recent years, which is unprecedented in the time series extending back to the late 1940s (Fig. 1.2A). L50 estimates for the 1940s–1980s showed considerable inter-annual variability, but fluctuated mostly in the range of 30–40 cm. Recruitment produced per spawning stock biomass has varied remarkably over time, largely related to environmental impacts. However, the declining trend in R/SSB in later years may be additionally associated with small size at maturity as well as poor condition of the spawners.

In parallel with the decline in L50 since the 1990s, the proportion of males among larger individuals in the stock (> 40 cm in length) declined substantially (Fig 1.2B). Females have dominated in this part of the population throughout the time series, however the proportion of males was at least 40% or higher in most years until the 2000s, after which it dropped to around 30% in recent years.

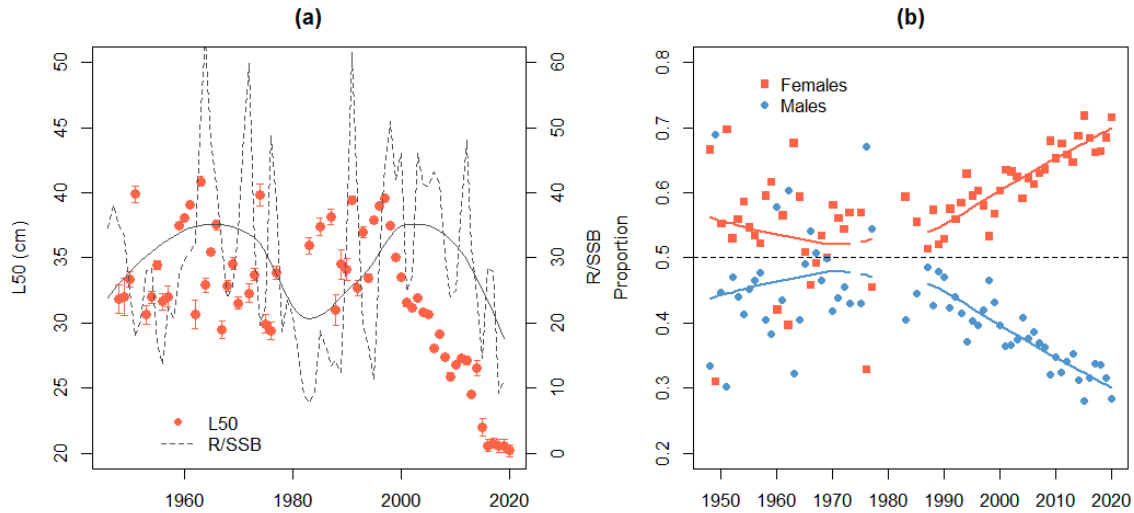


Figure 1.2. (a) Time series of length at maturity (L50, red dots) and recruitment per unit of spawning stock biomass (R/SSB, shown as a dotted line and smoothed trend). The bars indicate standard error of the L50 estimates. (b) Proportion of female and male cod in the stock is shown for fish > 40 cm in length. The lines illustrate smoothed trends over time. (Modified from Eero et al. 2023).

Parasitic nematodes in cod livers

C. osculatum loads in cod were highest in recent years (2016–2020), when most investigated cod were infected (prevalence of 88–100%), with an average infection intensity of 29–33 nematodes per liver (Fig 1.3). Both prevalence and intensity of infection were somewhat lower in 2012–2015, ranging between 55 and 81% and 16–20 worms per liver, respectively. Studies of *C. osculatum* infection from the 1940s estimated that 80–88% of cod were infected, with an average of 23 worms per liver, i.e. similar to recent years. A somewhat lower *C. osculatum* load was found in the 1950s, with prevalence of 44% and average infection intensity of 15. Lowest prevalence (2–22%) and intensity (4–14 worms per liver) were recorded in the 1970s and 1980s. Changes in both the prevalence and infection intensity followed roughly similar patterns over time, and coincided with trends in grey seal abundance in the Baltic Sea (Fig 1.3).

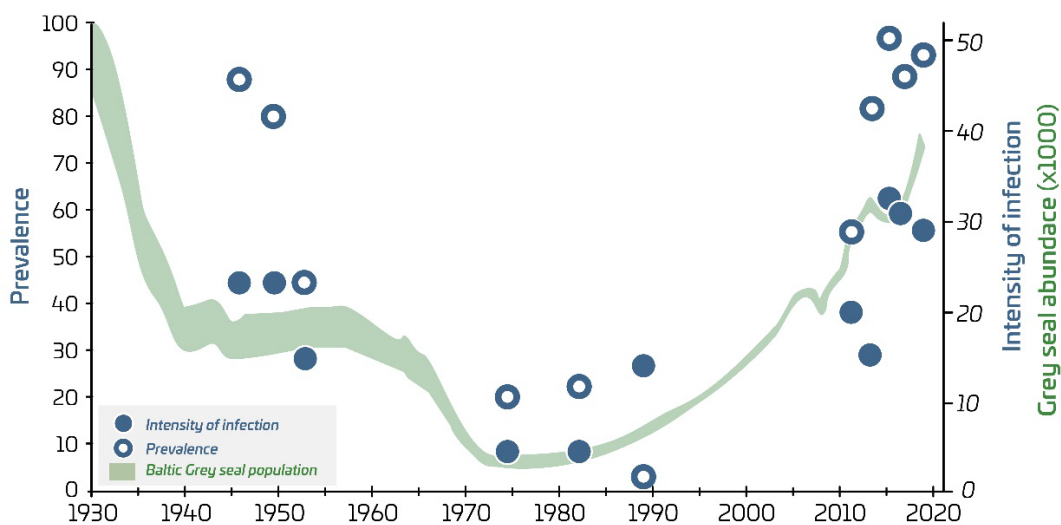


Figure 1.3. Liver worm (*C. osculatum*) infection loads (prevalence and intensity) in Eastern Baltic cod in comparison with trends in grey seal abundance in the Baltic Sea (Based on Eero et al. 2023).

Length structure

The L95 indicator for the cod stock has declined to around 50 cm in recent years, which is the lowest value in a time series that goes back to the late 1930s (Fig 1.4). In the late 1930s–early 1940s, L95 was around 70 cm and declined to around 60 cm by the early 1960s. Thereafter, L95 gradually increased, reaching 65 cm or slightly above in the 1980s. Since 2000s, L95 has sharply declined to the present record low level. Historically, before the 2000s, smoothed L95 appears at least to some extent inversely related to fishing mortality ($r^2 = 0.43$, $p < 0.001$). The high values of L95 in the beginning of the time series corresponded to a relatively low fishing mortality. Also, the second peak in L95 in the 1980s occurred simultaneously or slightly after a drop in fishing mortality. In contrast, the decline in L95 since the 2000s occurred in spite of the steep reduction in fishing mortality (Fig 1.4).

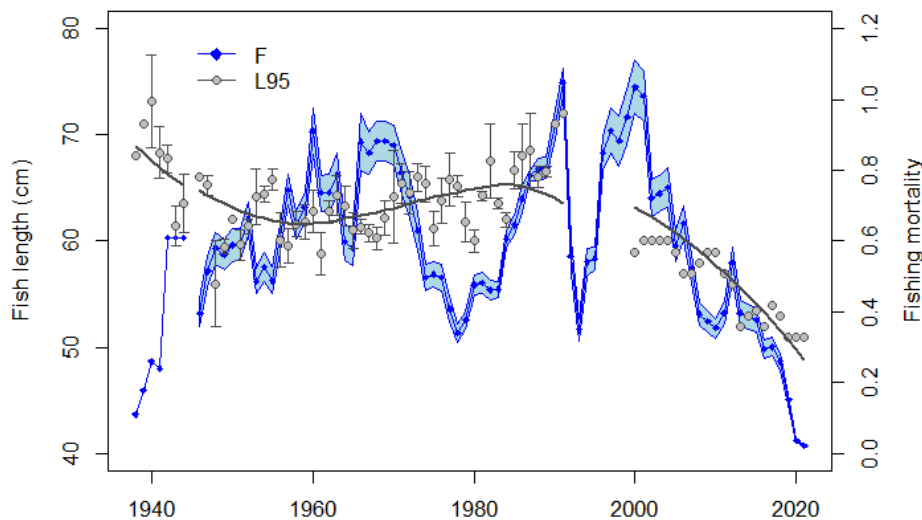


Figure 1.4. Time series of length structure (L95) of Eastern Baltic cod stock in comparison with trends in fishing mortality (F). The error bars show standard error of L95 for years where several length distribution datasets were available. The line illustrates smoothed trends in L95 over time. Fishing mortality (F) is average for ages 4–6, including 90% confidence intervals (ICES 2022; Eero et al 2008) (Based on Eero et al. 2023).

Conclusions

The historical data on a wide range of biological parameters indicate that the environmental-ecological conditions that prevailed in the Baltic Sea during the 1970s to early 1990s benefitted the Eastern Baltic cod stock in all aspects measured. In this period, the cod stock displayed a healthy demographic structure, wide distribution range and lower infection loads with *C. osculatum*. Furthermore, body condition of cod was good during the 1970s and early 1990s, though interrupted by a period of lower condition in the early 1980s. The indicator levels in recent years provide a sharp contrast, being the most adverse in the time series and confirming that the current poor state of the stock is unprecedented. It is noteworthy that cod body condition and infection load of *C. osculatum* were in similar adverse states in the 1940s–1950s, however, the relatively more favorable states of other biological parameters indicate that the stock was overall in a better shape than is presently the case.

2. Spatial variations in indicators of cod stock health

2.1 Spatial variability in body condition and size of cod in its main distribution area

By Margit Eero

Material and Methods

Spatial variability in cod body condition and size structure were investigated for the areas covered by BITS surveys, which include the currently main distribution area of the Eastern Baltic cod stock in ICES SDs 24-26 (ICES 2022). Individual fish measurement data from BITS were used to analyse spatial patterns in body condition of cod. Data for quarter 1 and quarter 4 were analysed separately. Le Cren's condition index was applied to minimize bias related to fish size (Le Cren 1951). As a first step, data from a given quarter from all years were pooled to estimate the parameters a and b of the length–weight relationship:

$$W = a * L^b \quad (1)$$

Subsequently, for each individual fish i , Le Cren's condition index K was calculated as the ratio between its weight (in g) and the predicted weight of the fish at a given length (in cm) from the length-weight relationship:

$$K_i = \frac{W_i}{a * L_i^b} \quad (2)$$

The resulting K values were then grouped to five categories (1-5) as follows:

- 1: ≤ 0.85
- 2: 0.85-0.95
- 3: 0.95-1.05
- 4: 1.05-1.15
- 5: > 1.15

We then calculated the proportion of fish in each condition category historically (1991-2000) and in recent period (2016-2022), in each ICES statistical rectangle. This was done separately for smaller cod (20-40cm) and larger cod (>40 cm).

We also investigated spatial patterns in the size of cod, using the indicator for large fish, i.e. length at 95th percentile of length distribution (L95). Similar to body condition, the L95 indicator was calculated for the historical period (1991-2000) and recent years (2016-2022). L95 was calculated for each ICES statistical rectangle covered by BITS survey, separately for Q1 and Q4.

Results

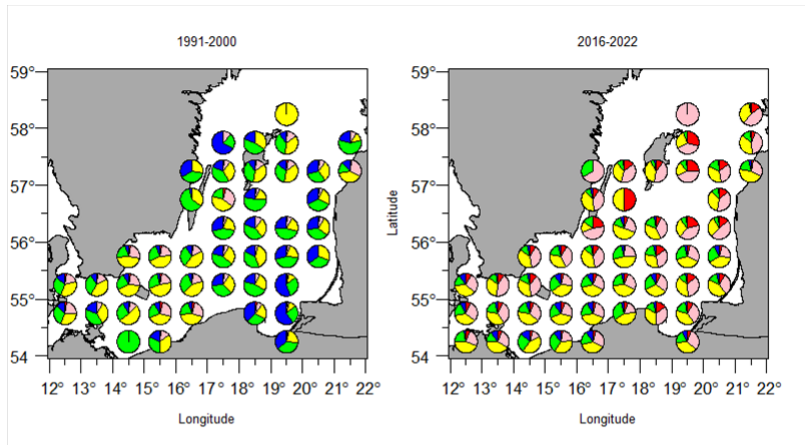
The deterioration of cod body condition in recent years (2016-2022) compared to 1991-2000 is apparent in the entire Baltic Proper. Variability in body condition between individual cod is high in nearly all areas, i.e. fish in all condition categories are present in nearly all ICES rectangles covered by BITS. In recent years, the proportion of cod in good condition has diminished nearly throughout the Baltic Proper, while the proportion of individuals in poorer condition has increased (Fig. 2.1.1, 2.1.2). However, there are some spatial patterns apparent.

For smaller cod (20-40 cm), the proportion of fish in best body condition was historically slightly lower in Bornholm Basin than further northeast (Fig. 2.1.1). Opposite, in recent years, in Q1, the small cod

in best condition mostly occurred in Bornholm Basin, with a higher proportion of fish in lowest condition in northeastern areas. In Q4, in recent years, small individuals in best condition were mostly found in near shore areas both in the southern and northeastern areas of the Baltic Proper. For larger cod (>40cm in length), the historical spatial pattern of body condition is relatively similar to that of the smaller fish. In recent years, in Q1, the proportion of larger cod in different condition groups is relatively similar throughout the Baltic Proper. In Q4, relatively higher proportion of fish in better condition were found in SD 24, in nearshore areas in the southern Baltic, and in some northeastern areas (Fig. 2.1.2).

The indicator for large fish (L95) based in BITS is generally relatively patchy, with relatively high and low values estimated for adjacent rectangles. However, the overall tendency of reduced L95 is apparent. Also, historically highest L95 values (60-70 cm) were estimated in some of the northernmost areas (SDs 27-29), both in Q1 and Q4 (Fig. 2.1.3). It should be noted that generally few fish are caught in BITS in these areas. Thus, the L95 estimates for these areas are less robust than for more southern areas where most of the cod stock is distributed. However, the relatively high L95 values estimated for some rectangles in SDs 27-29 indicate that the few fish that are caught in these areas are generally relatively large. This pattern has remained in recent period, where L95 has generally declined, but relatively high L95 values were still estimated for a few rectangles in SDs 27-29 (Fig. 2.1.3). These relatively high L95 estimates occur alongside with much lower values estimated for adjacent rectangles, indicating occurrence of local spots where these larger individuals have been found.

Q1



Q4

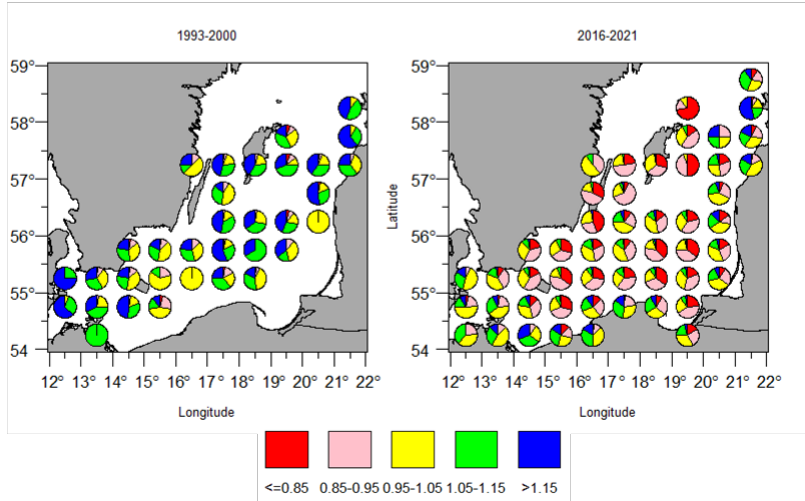
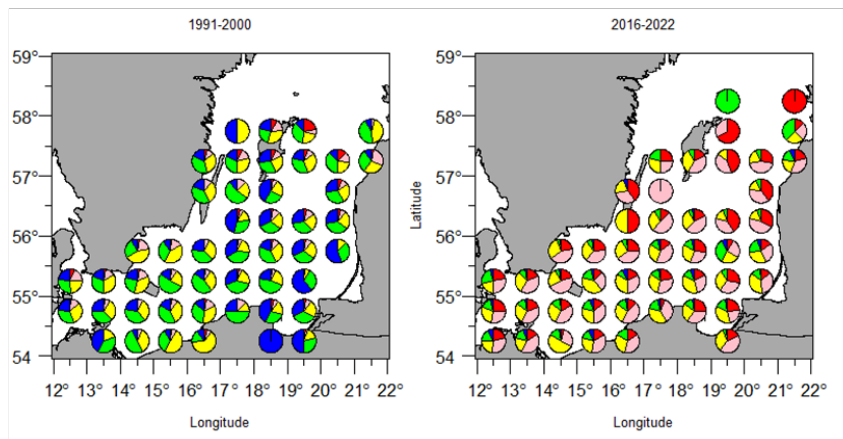


Figure. 2.1.1. Proportion of individual cod (20-40 cm in length) in different categories of body condition (Le Cren's K), with red representing the poorest and blue the best condition.

Q1



Q4

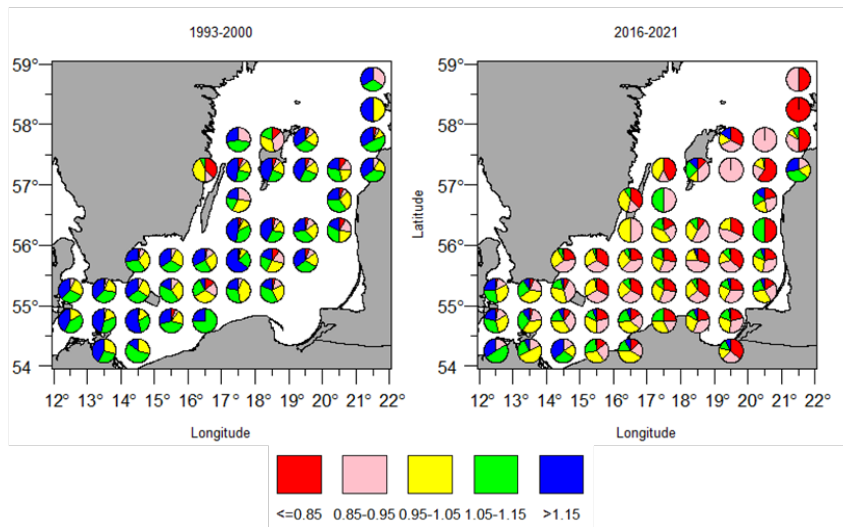


Figure 2.1.2. Proportion of individual cod (>40 cm in length) in different categories of body condition (Le Cren's K), with red representing the poorest and blue the best condition.

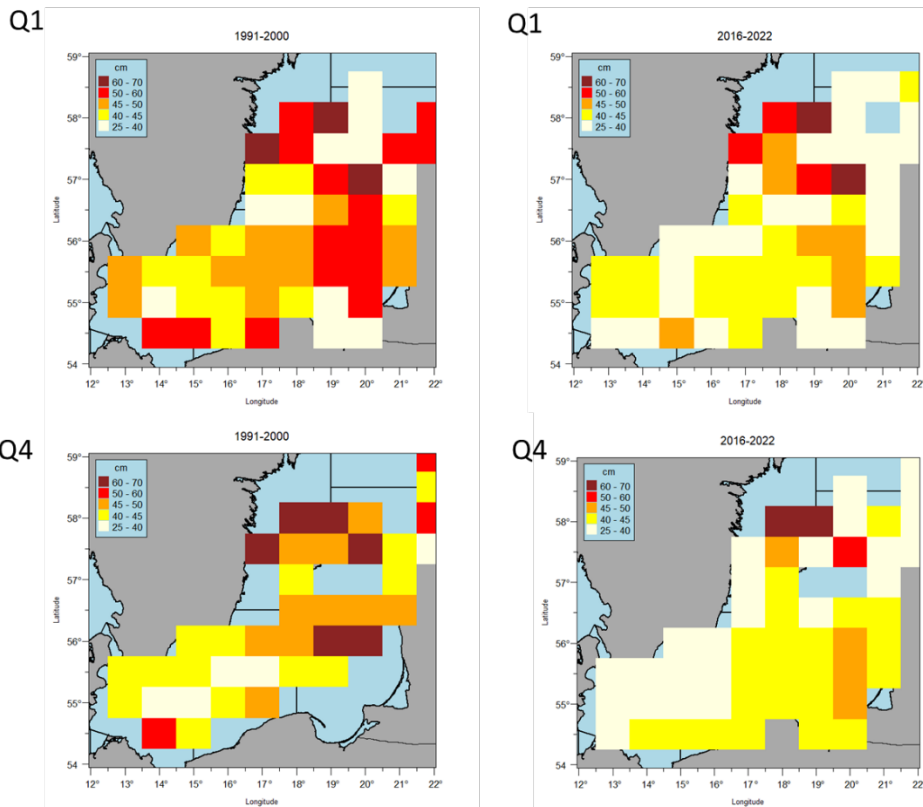


Figure 2.1.3. Average values of large fish indicator (L95, i.e. 95th percentile of length distribution, in cm) by ICES rectangle in 1991-2000 and 2016-2022.

Conclusions

Body condition of cod has generally deteriorated since the 1990s in all areas within the Baltic Proper, with a lower proportion of cod in good condition, and correspondingly higher proportion of fish in poor condition in most ICES rectangles. In recent years, fish in better condition are found in slightly higher proportions in nearshore areas in the Baltic Proper, both in the south and northeast. Indicator for large fish (L95) has generally a rather patchy distribution, but shows an overall tendency of a decline of larger cod. In the main distribution area of the stock, i.e. in SDs 25-26 the L95 values for recent years are consistently lower compared to the 1990s. The largest values of L95 were estimated for some rectangles in SDs 27-29, both historically and in recent years, indicating that the relatively few cod caught in these areas in BITS are relatively large.

2.2 Health status of cod in Åland Sea in contrast to its main distribution area

By Jane W. Behrens, Marie P. Ryberg, Margit Eero, Kurt Buchmann, Yvette Heimbrand, Sven-Gunnar Lunneryd, Charlotte Axén and Ulf Bergstrøm

Introduction

In this study, we compared cod living in the Bornholm Basin, within the main distribution area of the stock, and cod living in the Åland Sea (Fig. 2.2.1). In contrast to cod in the Bornholm Basin, the cod living in the Åland Sea have received relatively little attention and no monitoring, as cod in this region are relatively low in numbers and only support local, small-scale fishery. In the last decades, when the health status cod in the main distribution area of the stock has deteriorated in many

aspects (see Section 1), fishermen report that cod from the Åland Sea are large and in good nutritional condition.

Interestingly, cod from both areas are infected with the parasitic nematode *Contracaecum osculatum*, a parasite that infects the liver of cod (Ryberg et al., 2020; Sokolova et al., 2018; SVA, 2019). This parasite uses cod as a transport host to reach its final major host, which in the Baltic Sea is the grey seal. For cod in the Bornholm Basin, several studies have revealed a strong negative association between infection load and nutritional condition of the infected fish, and this parasite has been suggested to be one – amongst several – factor causing the poor status of cod from the Bornholm Sea (e.g., Horbowy et al., 2016; Sokolova et al., 2018; Ryberg et al., 2020; 2022; Behrens et al., 2023). Highly infected Bornholm cod also reveal compromised physiological performance and show signs of having a chronic liver disease (Ryberg et al., 2020). For cod from the Åland Sea, it is unclear if these fish that are seemingly healthy and well-fed are also affected negatively by this parasite.

In this study, we compare nutritional status and length distributions between cod from the Bornholm Basin and the Åland Sea, and further investigate the possible associations between high liver worm load and decreased nutritional condition, using information from the two areas with seemingly contrasting health status of cod.

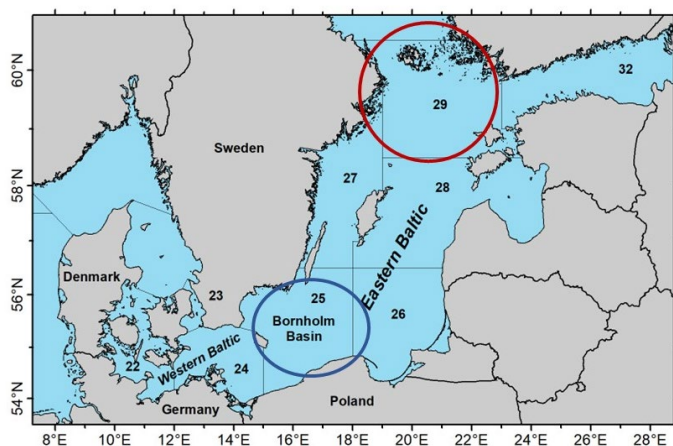


Figure 2.2.1. The Bornholm Basin (ICES Sub-division 25, blue circle) and the Åland Sea (ICES Sub-division 29, red circle) where cod were sampled for the analyses in the present study.

Materials and methods

Study areas and fish collection

Cod used in this study were caught by trawling in SD25 in June 2018 and March 2020 and with gillnets in SD29 in April, May and June 2019. All fish were processed fresh (without freezing or other conservation) directly on board. Total length (TL, mm), wet body weight (entire fish g) and liver weight (g) were recorded for each fish (Table 2.2.1) and individual livers were kept at -20°C for subsequent analysis of the total number of nematodes.

Table 2.2.1: Overview of numbers and parameter values for the cod used in the analyses of nutritional condition in relation to different infection densities. TL = total length, W = wet weight and LW = liver weight. The numbers in brackets represent ranges of variables. All numbers are mean ± SE.

Area	Number of fish	TL (cm)	W (g)	LW (g)
The Bornholm Basin	246	40.7 ± 0.36	699.9 ± 20.3	30.0 ± 1.2
		(20-58)	(54-2280)	(1-115)
The Åland Sea	98	61.9 ± 1.61	2947.2 ± 220.6	126.1 ± 12.9
		(32-104)	(300-10250)	(4-795)

Analysis of livers for nematodes and parasite identification

The majority of the livers (Bornholm Basin; n=246, Åland Sea; n=98) were analysed for parasites using the “compression method” while 50 livers were exposed to artificial digestion method according to the European Union Reference Laboratory for parasites. When using the “compression method,” livers were placed in a plastic bag (200 × 400 × 0.07 mm) and compressed between two glass plates (15 × 15 × 1 cm) to a thickness of 1 mm by gentle pressure (Buchmann, 2007). Livers were subsequently examined under a Leica stereomicroscope for examination of total number and species identification of nematodes (6.3–40× magnification, Leica Microsystems Germany). Livers exposed to the artificial digestion method were incubated in glass beakers (volume 1 L) containing pepsin, HCl and saline in an incubation chamber at 37 °C. The digest was then filtrated on a 300 m sieve and nematode larvae recovered, rinsed in physiological saline and transferred to 96% ethanol in 20 mL tubes. Larvae were collected from the sieve using a forceps and put in 15 mL tubes containing glycerol and 70% ethanol (proportion 1:4) prior to morphological identification (Figure 2.2.2).

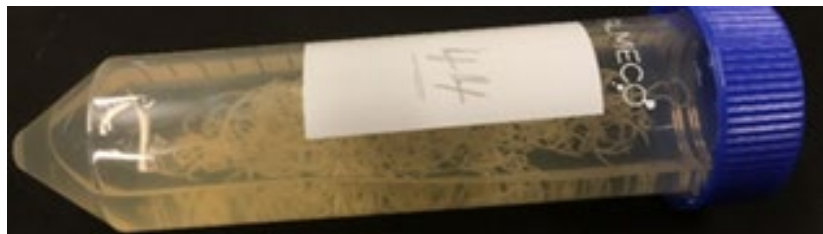


Figure 2.2.2. Nematodes collected from a single Åland cod liver and stored in glycerol and 70% ethanol.

Diagnosis of nematode larvae

Nematodes recovered were identified to the genus *Contracaecum*, based on their morphology: cephalic and caudal end morphology, presence of intestinal caecum, ventricular appendage, nerve-ring location, and excretory pore location (Koie and Fagerholm, 1995). Molecular diagnosis was performed on selected nematodes extracted from livers of the cod from both the Bornholm and Åland. The infection density (IFD), calculated as the number of nematodes per gram liver tissue (i.e. liver tissue = wet weight of the liver minus total weight of nematodes), was used to compensate for differences in the number of nematodes related to liver size (Ryberg et al., 2020).

Statistical analysis and Fulton condition

Fulton condition factor was calculated as:

$$\text{Fulton condition factor} = \left(\frac{\text{body weight}}{\text{total length}^3} \right) * 100$$

To test for difference in Fulton condition factor between cod from the Bornholm Basin and Åland Sea, a log-linear model including length as an explanatory variable was defined. Log-linear models were also used to describe the associations between infection density and Fulton condition factor for cod from each area. Length was included as an explanatory variable to account for any possible length effect on the result. Likelihood-ratio tests were used to test for significance levels in the models. Four models were performed in total, two with all data for each area and two where outliers were excluded. Outliers were defined based on visual inspection of model residuals. Further, the maximum value of Fulton condition factor of the whole data set and for the 95%, 90% and 85% quantiles for different levels of infection densities were calculated. All statistical tests were carried out using R with Rstudio (version 3.4.1; R Core Team, 2016).

Results

Infections with nematodes in cod livers

A total of 7721 nematodes were recovered from the 246 livers examined from Bornholm Basin cod (SD25), whereas a total of 9188 nematodes were recovered from the 98 Åland Sea cod livers. Nematode larvae isolated from livers of cod (both areas) corresponded by morphometric methods to the genus *Contracaecum* and molecular characterization to *C. osculatum* (GenBank accession no. JX467659). Prevalence of infection was high and comparable in both areas, being 92 and 96% in Bornholm and Åland Sea cod, respectively. Intensity of infection (i.e. mean number of parasites per liver, including only infected individuals) was on the contrary almost three times as high in Åland Sea cod (97 ± 12.9) as compared to cod from the Bornholm Basin (34 ± 2.1). The mean infection densities were $1.54 (\pm SE 0.12)$ nematodes per gram liver weight and $0.78 (\pm SE 0.12)$ for Bornholm and Åland Sea cod, respectively.

Fulton condition and statistical analysis

There was no effect of length in terms of variation in the Fulton condition factor of the fish from the two areas, but in both areas the total number of nematodes increased significantly with length of the cod, and the major part of the cod from the Åland Sea were substantially larger than their conspecifics from the Bornholm Basin (Figure 2.2.3). In addition, there was a significant difference in the slopes and intercepts between the two areas with the steepest slope found for cod in the Åland Sea (LM, slope = 2.6) compared to cod from the Bornholm Basin (LM, slope=2.5).

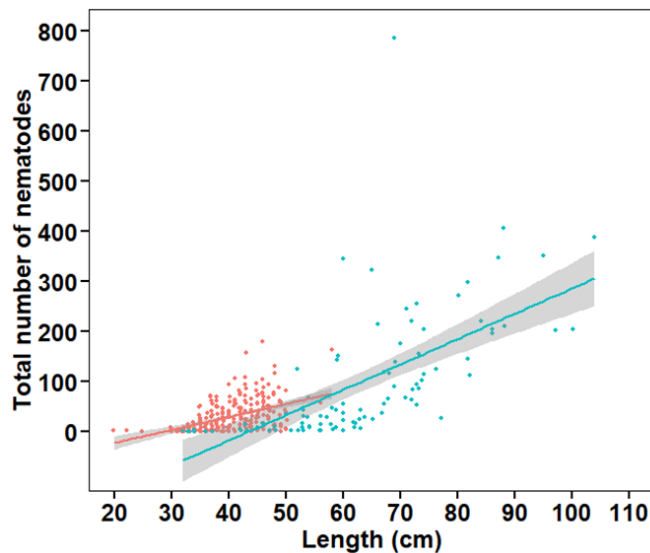


Figure 2.2.3. Total number of nematodes in relation to length of cod. Bornholm Basin cod: SD25, red dots; Åland Sea cod: SD29, blue dots. A linear fit (solid lines) and confidence interval (grey area) are provided for each of the two areas.

The Fulton condition factor was significantly lower ($p < 0.001$) in cod from the Bornholm Basin (SD25; 0.973 ± 0.009) as compared to cod from Åland Sea (SD29; 1.048 ± 0.012). Fulton condition factor of cod from the Bornholm Basin was negatively associated with infection density. The same trend was found for Åland cod, but the association was only significant when removing the outlier.

Conclusions

Size structure as well as nutritional condition differ for cod in the Bornholm Basin and Åland Sea. Cod from the Åland Sea are in better condition and tend to grow to larger sizes compared to cod from the Bornholm Basin. Interestingly, cod from both areas are heavily infected with the parasitic nematode, *C. osculatum*, in their livers. The intensity of infections of cod from the Åland Sea was almost three times as high compared to cod from the Bornholm Basin. Despite having much higher total number of nematodes and intensity of infection, cod from the Åland Sea nevertheless had become large and were in good condition. Nevertheless, our data also point to some effect of the nematodes on the nutritional condition of the most heavily infected Åland cod.

3. Cod recruitment production and survival

By Jonna Tomkiewicz, Sebastian N. Politis, Rikke Hagstrøm Bucholtz and Charlotte Jacobsen

Introduction

The prospects of the eastern Baltic cod stock depend largely on its reproductive potential and resulting recruitment. This chapter reports analyses elucidating the effects of parental quality on reproductive success and implications for cod recruitment. The composition of the spawning stock biomass of cod has changed from larger, highly fecund fishes to small, meagre fishes with fewer eggs per individual. This might affect egg and offspring quality and subsequently the recruitment, however the severity of such effects remains unclear. These questions were addressed by targeted small-scale studies of the present poor-condition cod and comparing these results with published data from former years, including periods where Baltic cod was in better condition.

The present investigation addresses fecundity of cod of different sizes and nutritional condition, building on methodology developed in an earlier EMFF project (33113-B-17-092, with the results published in Eero et al. 2021). Furthermore, a pilot shipboard experiment was conducted to assess fertilisation capacity of different egg batches from parents in poor condition as well as offspring survival and developmental characteristics. Lastly, egg lipid content and fatty acid composition are important predictors of offspring quality. Therefore, the change to small, poor condition fishes may influence recruitment through poorer egg quality. In this context, parental nutritional condition and egg quality was assessed in terms of egg size and lipid content.

3.1 Cod fecundity

Objective

The objective of this study was to a) conduct analyses of fecundity (i.e., egg quantity) in relation to female size, maturation and condition, using an accurate method combining systematic uniform random sampling (SURS) with the histologically based stereological analysis of the abundance of oocytes (developing eggs) in ovaries of individual cod and b) compare the results with existing comparable information for earlier times.

Materials & Methods

The fecundity analysis included ovaries from female cod sampled in the Bornholm Basin during research trawl surveys with R/V Alkor (AL521 and AL522) in April and May 2019 (Fig. 3.1.1). Only females with well-developed ovaries but not yet spawning were sampled, i.e., late vitellogenesis classified as maturity stage IV (Tomkiewicz et al. 2003). Data records included: length (cm), total body weight (g), liver (g) and ovary weight, and somatic weight, i.e., cleaned body weight (g). The complete ovaries were preserved in formaldehyde for the histological/stereological analysis.

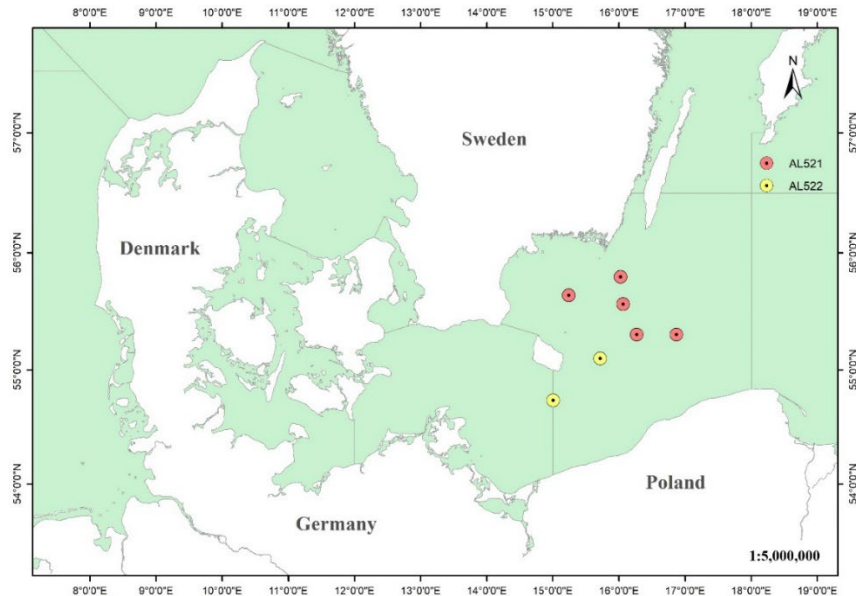


Figure 3.1.1. Trawl haul stations in the Bornholm Basin (ICES Sub-division 25) of the Baltic Sea, where the female cod were sampled during research surveys in 2019 with the German research vessel R/V Alkor: AL521 (n=36) and AL522 (n=6). ArcMap (version 10.4.0.5524).

In total, 42 females were sampled and ovaries from 26 specimens were applied in the present fecundity analysis (Table 3.1.1) including females of different size and nutritional condition. The fecundity analysis focused on the three groups with most specimens to analyse variability in relation to condition, while including a few distant sizes among samples to cover most of the range observed.

Table 3.1.1. Females sampled in total and for fecundity analysis in relation to length group including the numbers of females (N/n), Fulton's condition index (K), the hepatosomatic index (HSI) and the gonadosomatic index (GSI) per length group. All indices were based on gutted body weight.

Length group (cm)	All females sampled				Samples analysed for fecundity			
	N	K	HSI	GSI	n	K	HSI	GSI
16-19	0				0			
20-23	1	0.72	4.55	4.55	1	0.72	4.55	4.55
24-27	1	0.75	6.80	3.88	0			
28-31	12	0.73	7.77	9.47	11	0.73	7.54	9.70
32-35	13	0.74	8.71	12.89	8	0.64	7.52	9.41
36-39	9	0.74	9.42	14.71	5	0.76	7.80	12.42
40-43	5	0.80	8.56	9.66	1	0.74	7.64	8.00
44-47	2	0.69	8.48	16.32	0			

In the laboratory, the preserved ovaries were processed histologically for stereology using the smooth fractionator method as described in Eero et al. (2021). In short, both ovaries of each female were cut into slabs, which were paraffin embedded and sectioned using a microtome. For each block, 30 µm dissector pairs were sampled for every thousand 5 µm sections using a random start, until the block was fully sectioned, leading to 1 or 2 disector pairs of 30 µm from each block. This procedure was repeated for every block sampled from the individual fish. Sections were stained with H&E and mounted using Eukitt®. The slides were digitalised (Olympus Slideview VS200 or Zeiss Axio Scan.Z1) for stereological analysis of dissectors and estimation of total fecundity.

The number of oocytes from the scanned 30 µm disectors were counted in digital fractions sampled using VIS software (Visiopharm VIS 2020.08). All oocytes in developing stages were included: CA – cortical alveoli stage and vitellogenic stages VT1-3 (Tomkiewicz et al., 2003). The oocyte size of the most prominent cohort in the ovary was measured to evaluate potential influence of developmental stage on fecundity. The total fecundity was estimated from the fractionator equation:

$$N = 1/bsf \cdot 1/ssf \cdot 1/asf \cdot \sum Q^- / 2$$

where:

- N is the total number of oocyte nuclei i.e., oocytes;
- bsf the block sampling fraction, i.e., of blocks used from each individual;
- ssf the section sampling fraction, fraction of sections used from each individual, generally given by: $ssf = BA/T$. In this study, BA equals disector height (BA normally refers to the block advance of the cutting device i.e. microtome). T refers to the distance between sampling of two disectors;
- asf the area sampling fraction, fraction of area analysed given by: $asf = \text{total area of counting frames} / \text{area of section}$. In this study $asf = 0.1$;
- Q^- disector count i.e number of nuclei counted. As the procedure for disector counting involved counting in both directions, the total disector count was divided by 2.

Based on the morphometric data, Fulton's condition factor (K) was calculated as somatic body weight/length³*100, while the gonadosomatic index (GSI) was calculated as the total ovary weight/somatic body weight*100 and the hepatosomatic index (HSI) as total ovary weight/somatic body weight*100.

Results and discussion

The size of the females analysed ranged from 23 cm to 43 cm, which reflected the size range in the survey catches (Table 3.1.1). The average K-values ranging from 0.65-0.76 for the different size groups were low compared to K=1.05 reported for the same stage (Stage IV) in 1998-99 (Tomkiewicz et al., 2003) within the size range 30-65 cm. Similarly, the HSI in the range 4.55 to 7.80 was lower than, i.e., 8.25 on average in the same study.

The relative fecundity in relation to mean oocyte diameter varied. However, there was no indication of estimation errors that may occur, if recruitment of oocytes is not yet completed, numbers of developing oocytes have been downregulated, or spawning has started. The mean diameter was obtained by measuring the size of the 10 most developed oocytes within individual female ovaries.

The observed potential fecundity was linearly related to fish length (Fig. 3.1.2), while a logistic curve provided the best fit to the data for potential fecundity and female total body weight. The potential fecundity was similarly related to liver weight and to a lesser extent HSI. In this context, it should be considered that the liver weight and body weight are correlated. There was no relationship between potential fecundity and Fulton's condition factor ($y = 2E+06x - 800621$, $R^2 = 0.143$).

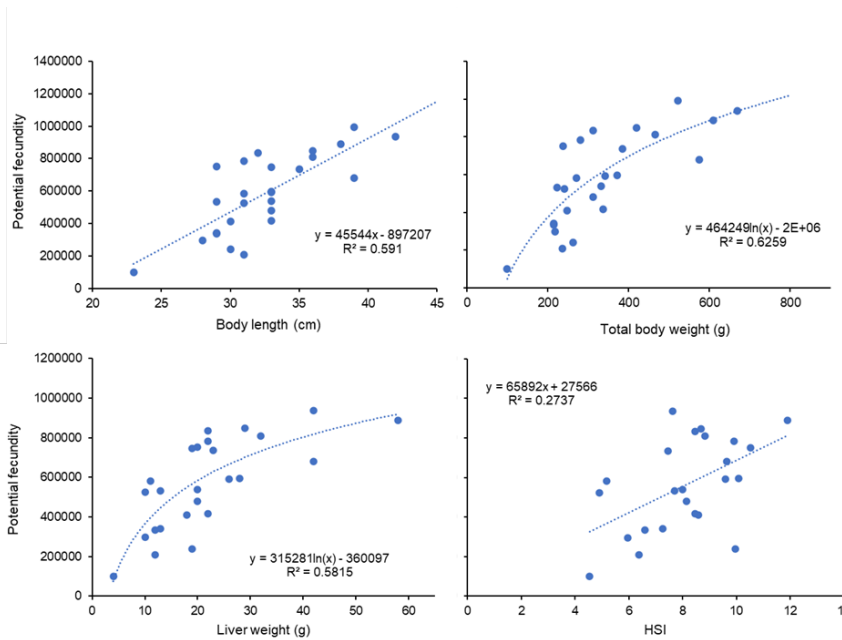


Figure 3.1.2. Potential fecundity in relation to female length (n=26), total body weight (n=25), liver weight (n=25) and HSI (n=24) of cod sampled in the Bornholm Basin in 2019.

Comparing present data with previously published Baltic cod fecundity records and models shows considerable differences between present and former times in reproductive output in relation to female size (Fig. 3.1.3). The relationships presented by Schopka (1971), Kosior et al. (2001) and Kraus et al. (2000) show considerably lower potential fecundity in relation to female length compared to current estimates (present study and Mion et al., 2018). For example, the potential fecundity of a 35 cm female in the present study was estimated to 735,800 eggs compared to 321,677 by Schopka (1971) and 376,345 by Kraus et al. (2000). The female potential fecundity thus appears to be around the double of what it was during 1970-2000 with an increasing trend during that period. The fecundity-length estimates of Mion et al. (2018) and the present study are similar with only slightly lower predicted fecundity at 30 cm.

Potential shortcomings in these comparisons include that the studies apply different methodologies to estimate fecundity. Over time, methods range from the gravimetric method based on manual counting via automated counting and the autodiometric method to stereology, which can generate differences in estimates. Also, the range of observations varies as cod has become much smaller on average and thus, extrapolations of equations in former times extends to smaller sizes than observations, while present extrapolation include larger sizes than observations cover. However, the change of the functional relationship between potential fecundity and female size supports the change that appears to have taken place. Moreover, Örey et al. (2016) provided intermediate potential fecundity estimates for the years 2005, 2007, 2009, 2011, 2013 and 2016 adapting the autodiometric methods to analysis of frozen samples.

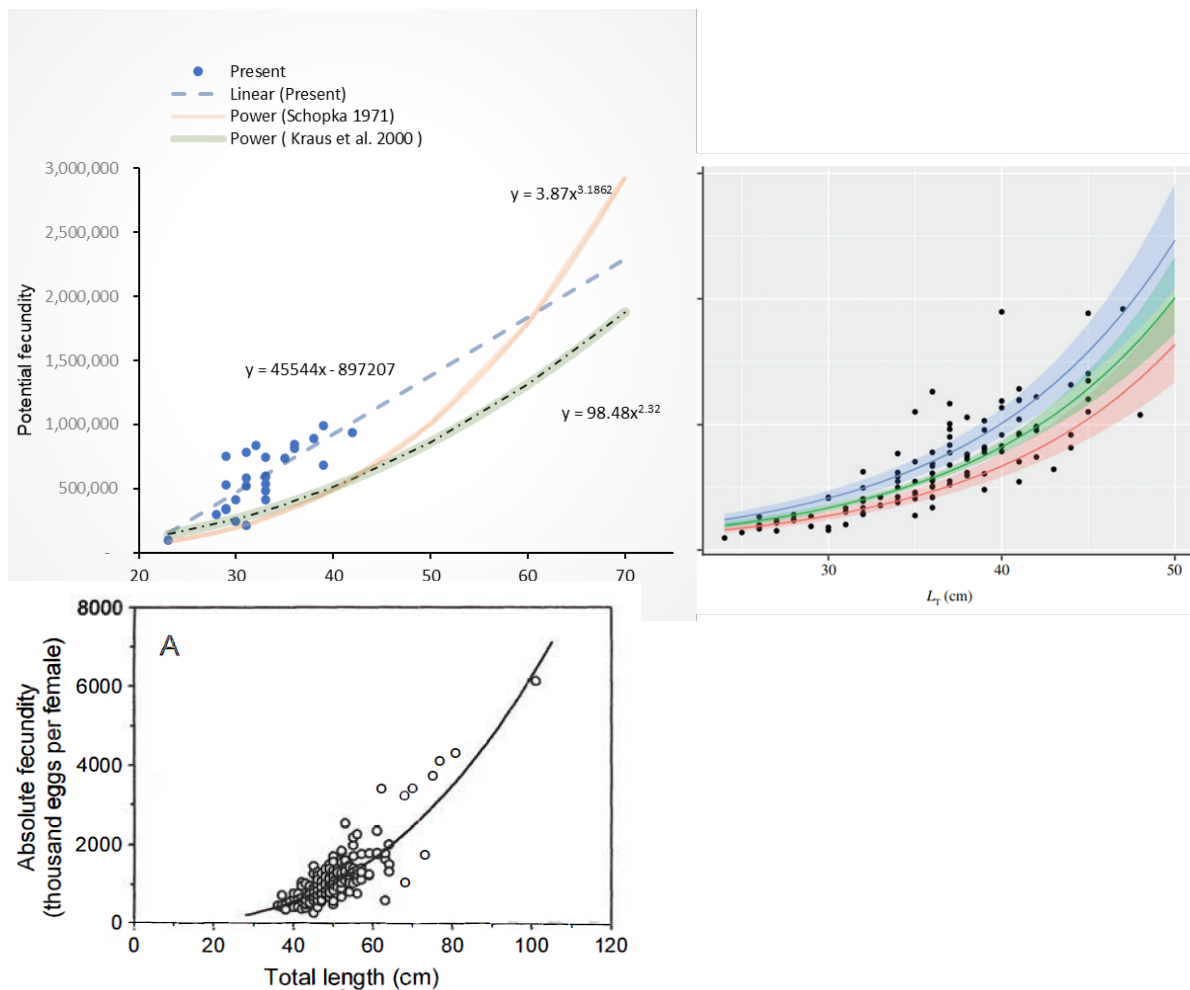


Figure 3.1.3. Potential fecundity-length relationships for Baltic cod. Upper panel left: Present data from 2019 and predicted relationship, equations by Schopka (1971) based on samples from different areas of the Baltic Sea and Kraus et al. (2000) based on samples from the Bornholm Basin, May 1995. Right upper panel: Mion et al. (2018) illustrating observations in SD 24 and 25 in 2015-2016 and predicted potential fecundity considering fish condition K (lowest red, highest blue), while HSI was set constant. Lower panel: Kosior et al. (2001) combining observations 1995, 1996 and 1995 in SD25 and fitting a regression equation (not specified).

Variation in female weight at length and nutritional state may influence the results positively or negatively. Still, potential fecundity at length provides the most reliable relationship for comparisons, as the two variables are used unambiguously by researchers. In contrast, relations to individual weight and condition are compromised by different use of variables, e.g., total weight, somatic weight, total weight minus organ weight etc. Nevertheless, the differences in the body weight range among the above mentioned studies are striking (Fig. 3.1.3). The results show the Baltic cod reproducing at a very small sizes with a high relative fecundity relative to their weight compared to previous years with a completely different size range, which to a larger degree resembled Atlantic cod in other areas.

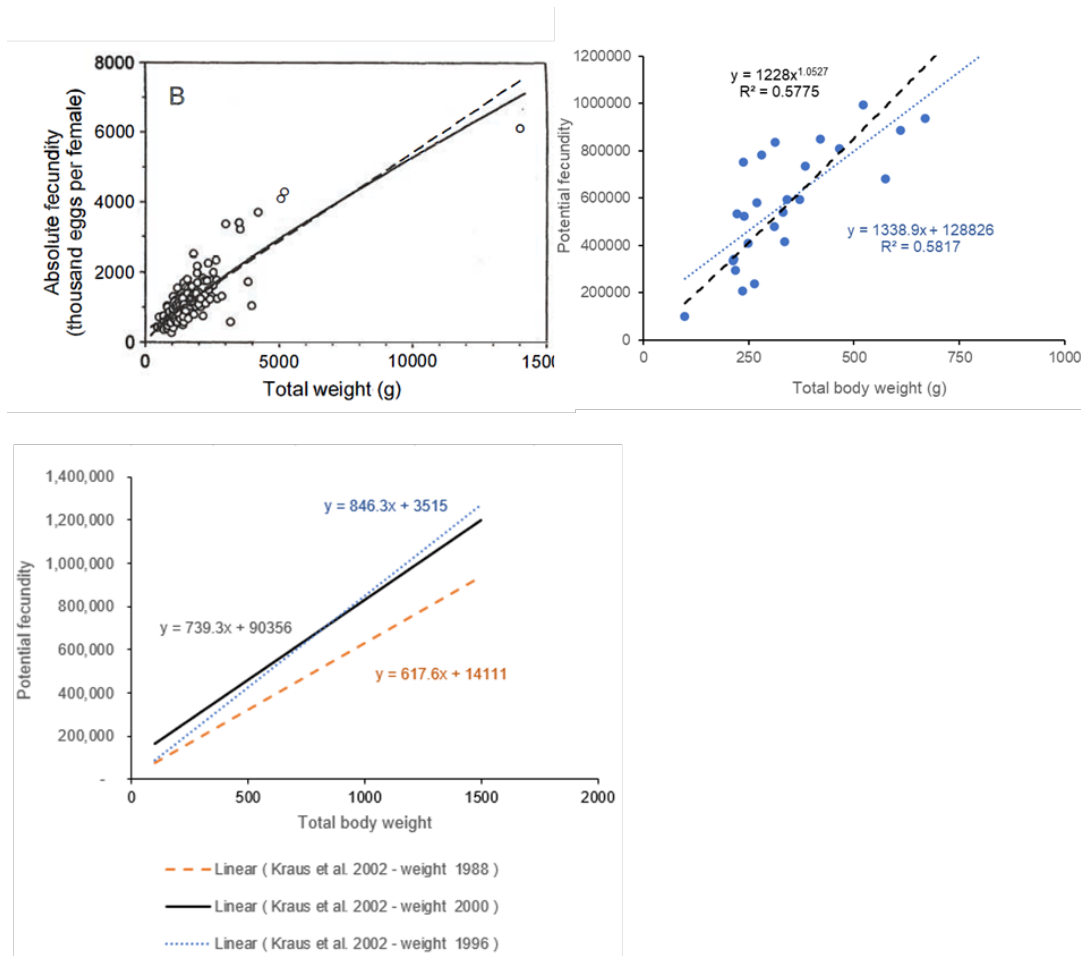


Figure 3.1.4. Potential fecundity (upper panels) in relation to total body weight of cod sampled in the Bornholm Basin 1995,1996 and 1999 (Kosior et al. 2001) and in 2019 (present study, same data as Fig. 3.1.2. but with similar fitting of equations to observations, i.e., linear fit and power function as in Kosior et al (2001) (equations not specified). Lower panel shows relationships estimated by Kraus et al. (2002) for different years, i.e., 1988, 1996 and 2000.

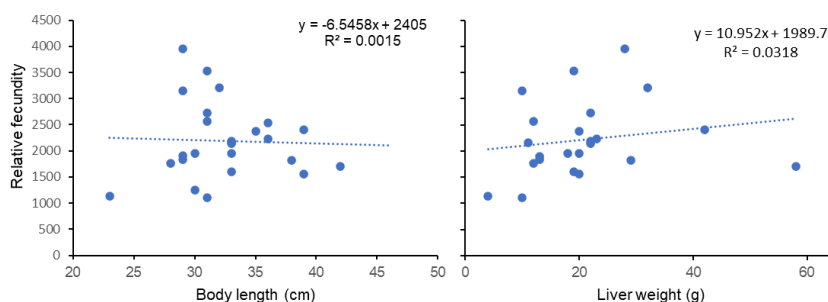


Figure 3.1.5. Relative fecundity based on somatic weight in relation to female length and liver weight of cod sampled in the Bornholm Basin in 2019 (N=26).

The relative fecundity of Baltic cod was independent of female length and liver weight (Fig.3.1.5), which complies with previous studies (Kraus et al. 2020; 2022). Like the potential fecundity, the relative fecundity has changed over time. Figure 3.1.6 compares the estimates of relative fecundity across size ranges available and sampled during 1987-2000 (Kraus et al., 2002), during 2005-2016 and the present study. These results suggest that the relative fecundity of the population in the present study was about twice the level of 1987-2000 with a gradual trend within the former studies.

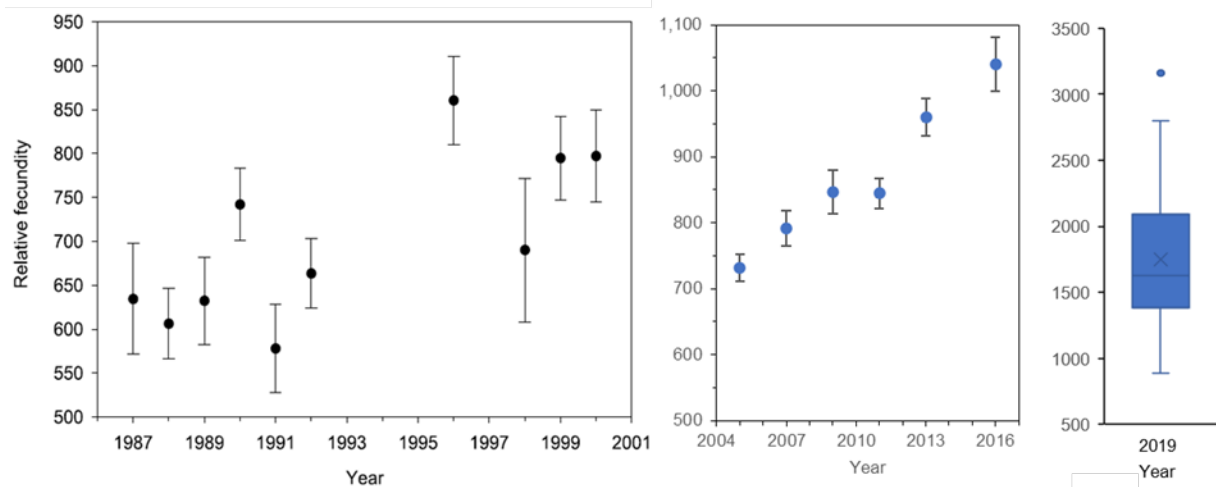


Figure 3.1.6. Relative fecundity (based on total body weight) of cod sampled in the Bornholm Basin estimated by Kraus et al. (2002) for different years during the period 1987-2001; by Örey et al. (2016) for the years 2005-2016; and in the present study for 2019. Error bars represents for Kraus et al. (2002) 95% confidence limits, Örey et al. (2016) standard error, while the present study shows the distribution of data into quartiles, highlighting the mean and outliers.

Conclusions

The most remarkable result is the high potential fecundity of the small sized females. The observed potential fecundity was linearly related to fish length, while a logistic curve fitted the data for potential fecundity versus total body weight better. This indicated a higher relative fecundity for smaller females compared to larger, in line with former studies. The comparison of present potential fecundity length relationships with previously published Baltic cod fecundity records and models showed that the female potential and relative fecundity is now around the double of what it was during 1970-2000, with a gradual increase over time. The relative fecundity of the Baltic cod population across the size range of the spawning stock showed a similar trend.

Overall, these results suggest that growth of Baltic cod is compromised by the investment in reproduction, substantiated by the extraordinary increase in fecundity, rendering the Baltic stock in a depressed state. Both, the change in fecundity over time in relation to total body weight and relative fecundity will have implication for estimates of spawning biomass based on egg production models. It will be difficult to verify independence of methodologies, however, the stereological method confirms that the recent fecundity results obtained by the autodiometric method are reliable.

3.2 Characteristics and survival of offspring

Objective

This section presents analyses of offspring quality and survival in relation to maternal size and condition via experiments to assess fertilisation capacity of eggs from different quality parents and assess implications for future recruitment.

Materials & Methods

Data collection and experimental studies were performed in collaboration with GEOMAR, Kiel. Cod were obtained during a trawl survey (AL573) with the German research vessel R/V Alkor, from the

14th to the 30th of May 2022. Fishing was conducted at 12 stations in the Bornholm Basin, but cod was only caught at 5 stations. Sampling included sex determination, length (g), total weight (g), liver weight (g), ovary weight (g), somatic weight (g) and maturity stage. Based on these records, the hepato-somatic index (HSI), Fulton's condition index (K) and the gonado-somatic index (GSI) were calculated. Most spawning specimens were caught at one station (50), close to the border of SDs 25 and 26. Therefore, *in vitro* reproduction experiments were conducted only at this station 50. At station 50, total weight, length, maturity stage and condition did not differ between females and males, while HSI and GSI was slightly higher for females compared to males.

Reproduction experiments

Gametes were collected from 22 females and 22 males in "running" maturity stage (V-VII). Parameters of these parental animals can be found in Table 3.2.1 and Table 3.2.2. A small sample of the female ovary was preserved in 4% buffered formalin using Biopsafe containers for histological analysis, while the entire liver was sampled for lipid analysis. Also, a sample of each stripped egg batch was collected for lipid and fatty acid analyses.

Gametes from each parent were collected in glass beakers and stored on ice until further use. Individual assisted fertilisations were attempted on each batch of eggs collected from the 22 females, using a pool of milt from the 22 males. Sperm to egg ratios were set according to Trippel et al., 2005. Fertilisations occurred within 2 hours of gamete collection. For activation of gametes, seawater was adjusted to 15 psu and 6.5°C (Politis et al., 2014; Dahlke et al., 2016).

Table 3.2.1. Information and records for male cod used for reproduction experiments in the present study.

Date	Ship Station	Station ID	Male ID	TL (cm)	Weight (g)	Liver (g)	Sex	Stage	Gonad (g)	Gutted (g)
21.05.2022	50	BB41	M1	42	716	12	M	VI	80	575
21.05.2022	50	BB41	M2	43	786	22	M	VI	131	600
21.05.2022	50	BB41	M3	49	951	14	M	VI	90	810
21.05.2022	50	BB41	M4	42	792	16	M	VI	68	550
21.05.2022	50	BB41	M5	35	402	18	M	VI	58	326
21.05.2022	50	BB41	M6	35	416	12	M	VI	24	360
21.05.2022	50	BB41	M7	33	302	8	M	VI	38	240
21.05.2022	50	BB41	M8	33	290	6	M	VI	32	244
21.05.2022	50	BB41	M9	40	522	14	M	VI	72	416
21.05.2022	50	BB41	M10	33	172	6	M	VI	26	132
21.05.2022	50	BB41	M11	31	236	4	M	VI	10	210
21.05.2022	50	BB41	M12	29	244	8	M	VI	26	202
21.05.2022	50	BB41	M13	32	288	6	M	VI	22	138
21.05.2022	50	BB41	M14	32	302	10	M	VI	52	236
21.05.2022	50	BB41	M15	42	634	24	M	VI	62	534
21.05.2022	50	BB41	M16	39	460	14	M	VI	62	360
21.05.2022	50	BB41	M17	34	294	8	M	VI	24	254
21.05.2022	50	BB41	M18	42	462	10	M	VI	40	394
21.05.2022	50	BB41	M19	31	256	10	M	VI	60	196
21.05.2022	50	BB41	M20	27	188	4	M	VI	20	158
21.05.2022	50	BB41	M21	35	326	10	M	VI	28	282
21.05.2022	50	BB41	M22	36	444	18	M	VI	68	338

Table 3.2.2 Information regarding female Baltic cod used for reproduction experiments in the present study.

Date	Ship Station	Station ID	Fish ID	TL (cm)	Weight (g)	Liver (g)	Sex	Stage	Gonad (g)	Gutted (g)
20220521	50	BB41	F1	54	1577	51	F	V	310	1077
21.05.2022	50	BB41	F2	36	417	16	F	V	80	306
21.05.2022	50	BB41	F3	44	786	16	F	V	199	544
21.05.2022	50	BB41	F4	32	315	13	F	V	67	208
21.05.2022	50	BB41	F5	32	303	11	F	V	44	242
21.05.2022	50	BB41	F6	31	283	7	F	V	49	215
21.05.2022	50	BB41	F7	30	236	7	F	V	60	164
21.05.2022	50	BB41	F8	31	285	17	F	V	55	206
21.05.2022	50	BB41	F9	29	251	11	F	V	48	187
21.05.2022	50	BB41	F10	32	294	12	F	V	52	221
21.05.2022	50	BB41	F11	38	374	11	F	VI	42	305
21.05.2022	50	BB41	F12	28	205	6	F	VI	42	144
21.05.2022	50	BB41	F13	35	375	8	F	VI	76	275
21.05.2022	50	BB41	F14	40	571	29	F	VI	127	393
21.05.2022	50	BB41	F15	32	342	10	F	VI	68	245
21.05.2022	50	BB41	F16	34	309	9	F	VI	67	217
21.05.2022	50	BB41	F17	31	262	17	F	VI	52	183
21.05.2022	50	BB41	F18	43	657	17	F	Vie	128	485
21.05.2022	50	BB41	F19	41	675	25	F	Vle	121	514
21.05.2022	50	BB41	F20	46	806	16	F/M	Vle	161	553
21.05.2022	50	BB41	F21	44	810	35	F	Vle	243	507
21.05.2022	50	BB41	F22	31	291	8	F	Vle	65	194

Floating eggs/embryos were then reared in customised 2 L incubators equipped with bottom inlets and with flow rates of ~150 mL/min and a 250 µm mesh subsurface outlet (Fig. 3.2.1). A steady upwelling flow created enough turbulence to keep the eggs/embryos/larvae in suspension and maintain optimal oxygen levels for rearing. Incubators were connected to mobile RAS units consisting of a header tank (including a biofilter filled with RK bio-elements ~30 m² surface area), a water reservoir tank and a sump tank hosting the main pump (Sicce Syncra Silent pump 3.5, 65W ~2500 L/h), a particle filter (5" PP cartridge housing w. 1 micron PP filter insert, Atlas Filtri, Limena, Italy) and a temperature regulating unit (TECO 500, 225W, Teco S.r.l. Fornace Zarattini, Italy). Moreover, each system, was supplied with a UV- C lamp placed in the header tank treating up to 430 L/h (Green Killing Machine 12V, 24W UV, AA-Aquarium, Unit 45, Essex, United Kingdom).

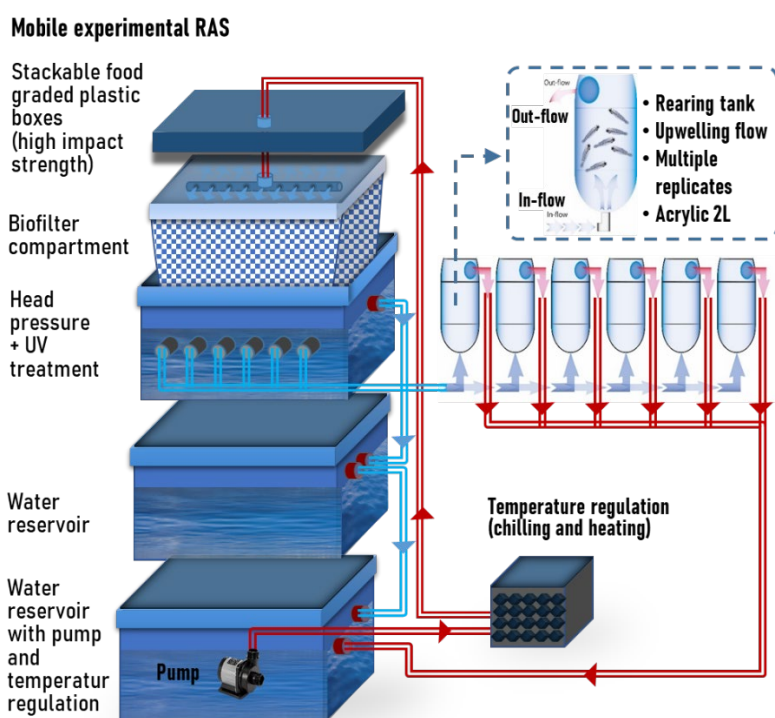


Figure 3.2.1. Mobile recirculating aquaculture system (RAS) and 2L incubation jars used to rear cod offspring, produced via assisted fertilisation on board the R/V Alkor cruise in May 2022.

Throughout rearing, water temperature was kept at 6.5°C and salinity at 15 psu to ensure optimal conditions for embryonic development and survival (Politis et al., 2014; Dahlke et al., 2016). Embryos were reared until hatching, which lasted up to 17 days post fertilisation (dpf). Thus, the experiments initiated on board of R/V Alkor were continued at GEOMAR (Kiel, Germany) by moving the mobile RAS units into a climate controlled experimental chamber at the location.

Data acquisition

Fertilisation success was assessed from digital images at the 4-8 cell stage. All images were taken using a digital camera (Digital Sight DS-Fi1, Nikon Corporation, Japan) attached to an objective microscope (Eclipse 55i, Nikon Corporation, Japan). Dead embryos were enumerated and removed daily. Embryos were categorised as dead if they turned white and/or sank to the bottom of the incubator. The first hatched larvae were observed on 12 dpf. From 14 dpf and onwards, for each incubator, daily cohorts of all hatched larvae were sampled and digitally imaged. This procedure was carried out each morning, completed within 6 h, and repeated every 24 h, which allowed us to study

asynchronous larval hatching throughout the hatching period. Once hatching was completed, all embryos and larvae within each incubator were counted and survival calculated. Moreover, offspring were photographed for morphological measurements (larval length (mm) and yolk area (mm²) at hatch) using the NIS-Elements-D analysis software (Nikon Corporation, Japan).

Results

Female length and hepato-somatic index (HSI) as well as condition (Fulton's K) was generally lower compared to historic data (Tomkiewicz et al., 2003) of female cod in the corresponding maturity stage (Fig. 3.2.2 A-C). On the other hand, the gonado-somatic index (GSI) was similar at the corresponding maturity stages and even higher for stage IV and V (Fig. 3.2.2 D).

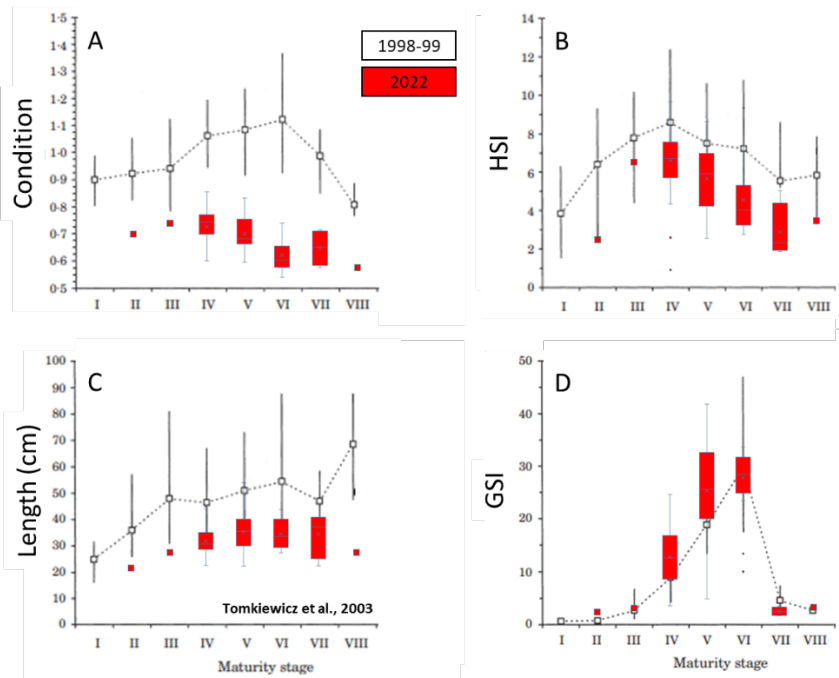


Figure 3.2.2. Comparison between current (2022) and historic (1998-99) variation in (a) Fulton's condition index, (b) hepato-somatic index (HSI), (c) Length and (d) gonado-somatic index (GSI) of female cod in the present study in relation to maturity stage.

Regarding the cod used in the reproduction experiments, all males were at maturity stage VI, while 10 females were at stage V and 12 at stage VI (Fig. 3.2.3 A). From the stage VI females, only 5 (VIe) produced eggs that were fertilisable, resulting in viable embryos that were further reared until hatching. Those females (VIe) were generally heavier and larger (Fig. 3.2.3 B-C). No noticeable difference was observed in condition or HSI (Fig. 3.2.3 D-E), while GSI of males was slightly lower than that of females (Fig. 3.2.3 F).

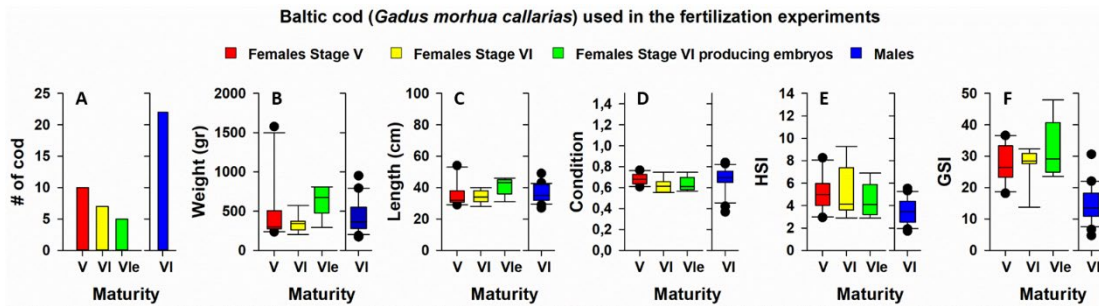


Figure 3.2.3. A) Number of fish per maturity stage, B) weight, C) length, D) Fulton's condition index, E) hepato-somatic index (HSI) and F) gonado-somatic index (GSI) of female and male cod caught at station 50 and used in fertilisation experiments.

Highest fertilisation success (~50%) was observed for F18, which was almost ~2-fold higher than for all other batches (Fig. 3.2.4 A). That batch also produced more than 4-fold more larvae (>2000 individuals) than the next best batch (Fig. 3.2.4 B). The first Baltic cod larvae hatched at 12 dpf and the last at 17 dpf, but the majority hatched on 15 and 16 dpf (Fig. 3.2.4 C). As such, overall, the hatching window spanned over 6 days, which agrees with previous findings (Politis et al., 2014). Peak hatch (>50% hatch reached) was observed at 15 dpf (Fig. 3.2.4 D).

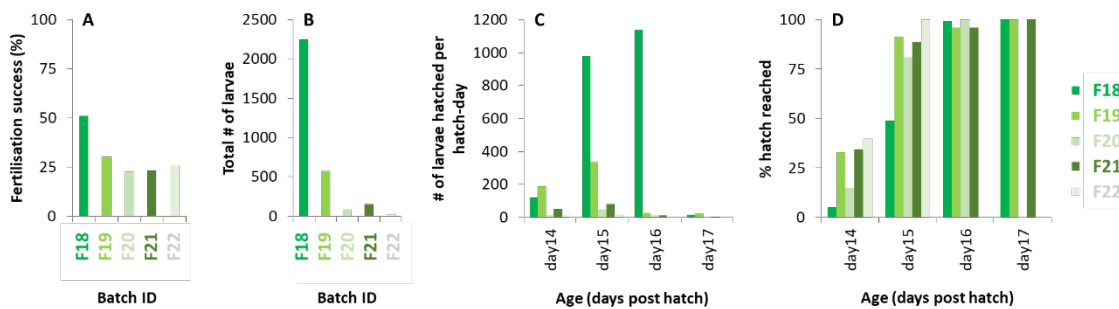


Figure 3.2.4 A) Fertilisation success, B) total amount of larvae hatching per batch, C) amount of larvae hatched per hatch-day, and D) % hatch reached for the cod offspring from the 5 batches produced via *in vitro* fertilisations on board R/V Alkor in May 2022.

When compared at peak hatch (15 dpf), F21 produced the largest larvae, while F22 the smallest (Fig. 3.2.4A). Interestingly though, the larvae produced here (from parental animals in poor condition) were generally bigger than larvae from different batches previously raised at comparable rearing conditions and originating from healthy broodstock held in a hatchery set-up (Bornholms Lakseklækkeri, Nexø, Denmark) and considered to be in good condition. On the other hand, amounts of energy reserves, maternally provided via the egg yolk to the offspring, were comparable between the offspring originating from good condition parents and those produced in this study: F18, F21 and F22, while lower for F19 but higher for F20 (Fig. 3.2.5 B).

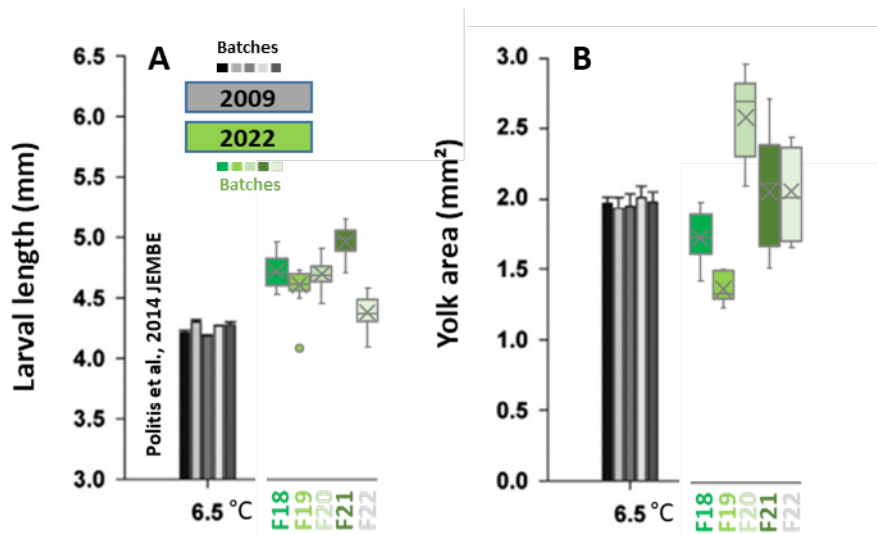


Figure 3.2.5. A) length and B) yolk area at peak hatch (15 dpf) of the 5 batches of Baltic cod larvae produced on board R/V Alkor in May 2022, in comparison to larvae from larval batches raised under comparable rearing conditions but originating from Baltic cod broodstock held at Bornholms Lakseklækkeri (Politis et al., 2014).

Generally, most of the observed mortality occurred during a critical period lasting until the end of gastrulation, whereas only few losses were recorded during the subsequent segmentation stage and the hatching period (Fig. 3.2.6). Highest larval survival was observed for F18 and F21, followed by F19, while F20 and F22 suffered from increased mortality.

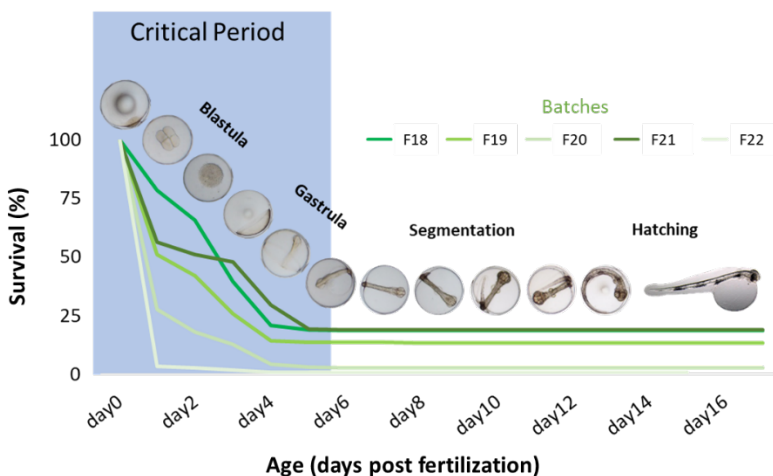


Figure 3.2.6. Survival of cod offspring from the 5 batches produced via *in vitro* fertilisations on board of R/V Alkor in May 2022.

Conclusions

The cod caught during the survey were small and in poor condition with much lower Fulton's K condition index compared to data from the beginning of the 2000s. Interestingly though, gonado-somatic index (GSI) was comparable to the historical level, which indicates high investment into reproduction at a small size. Unfortunately, only few of the cod caught during the survey were spawning and in "running" state, so only 5 specimens were able to produce viable offspring via *in vitro* fertilisation. This limits the conclusions that can be drawn from this pioneering experiment, however interesting observations were made.

From the five successfully fertilised batches of eggs, the majority produced only a negligible number of larvae, but one female (F18) showed 2-fold higher fertilisation success and more than 4-fold higher number of larvae hatching compared to the other females. These differences in egg quality may relate to the readiness of the eggs to be spawned at the time of catch as well as to maternal condition, however, viable offspring were produced from all five females. Notably, hatched larvae had comparable or even more energy reserves provided (in terms of yolk) compared to previous records of offspring originating from good condition broodstock (Politis et al., 2014). Combined with the measured larger larval size at hatch, the Baltic cod offspring produced in this study seemed to be of good quality, which indicate their potential in terms of recruitment. Hatching at a larger, more developed stage might increase the chances of survival, as predation mortality is inversely related to size (Bailey and Houde, 1989). The larger size might also involve changes in buoyancy, allowing the eggs to reach neutral buoyancy at a lower salinity and thereby avoiding the anoxic deeper waters in the spawning areas.

3.3 Quality of cod and unfertilized eggs

Objective

The purpose of this investigation was to analyse egg quality – egg size, lipid content of eggs and liver of the parental fish.

Materials & Methods

Image analysis: Photos of fertilised cod eggs from the 5 offspring batches obtained during the experiment onboard R/V Alkor in May 2022 (see Section 3.2) were taken at the 4-cell stage using a digital camera (Digital Sight DS-Fi1, Nikon Corporation, Japan) attached to an objective microscope (Eclipse 55i, Nikon Corporation, Japan). Later, the egg diameter was measured from these images using the NIS-Elements-D analysis software (Nikon Corporation, Japan).

Lipid extraction and determination of lipid content: Lipids in eggs and liver (1-5 g samples) were extracted with a homogeneous mixture of chloroform, methanol, and water (2:2:1.8) following the method of Bligh & Dyer (1959) with reduced solvent volumes. The lipid extracts were frozen at -40°C for the subsequent determination of lipid content, lipid class fractionation and determination of fatty acid composition. The lipid content was determined by gravimetry after evaporation of chloroform. For livers, two extractions were made on each sample. For eggs due to limited amounts of tissue, only one extraction was made for each sample.

Lipid class separation: Lipid extracts from both livers and eggs were analysed for their fatty acid composition as total lipids as described below. Moreover, a fraction of the extract from all livers and from one egg sample were separated into polar (PL) and neutral lipids (NL) by chromatography on a solid phase consisting of aminopropyl modified silica. Solvents with increasing polarity were used to separate the lipid classes. In short, a lipid extract corresponding to 10-50 mg lipid was used for the lipid class separation. Solvents from the lipid extraction were evaporated and the extract was resolubilised in 0.5 ml chloroform and transferred to a Sep-Pak column (Waters Corporation, Milford, Massachusetts). NL were eluted using 2x2 ml chloroform/2-pronanol (2:1), FFA were eluted with 3 x 2 ml diethyl ether / acetic acid (98:2) and PL were eluted with 3x2 ml methanol. NL and FFA fractions were pooled together and analysed together. One lipid class separation was made on each extract.

Preparation of fatty acid methyl esters and analysis of fatty acid composition: NL and PL fractions from liver and egg (only one) extracts as well as total lipid extracts from liver and eggs were used for

the preparation of fatty acid methyl esters. The NL and PL fractions were methylated in two steps including a boiling step as described by the AOCS Official Method Ce 2-66. Total lipid extracts were methylated using a slightly modified version of this method where all reagents were added in one step and the methylation was carried out in a microwave oven as described by Jacobsen et al. (2022). C23:0 methylester was used as internal standard. After methylation, the upper heptane phase was transferred into GC vials and analysed using gas chromatography (HP5890 A, Agilent Technologies, Santa Clara, CA, USA) according to AOCS official method Ce 1b-89. Fatty acid methyl esters were separated by the GC column Agilent DB wax 127–7012 (10 m _ 100 _m _ 0.1 _m) (Agilent technologies, Santa Clara, CA, USA). A standard mix of fatty acids methyl esters (Nu-Check-prep GLC 714, Nu-Check Prep. Inc., Elysian, MN, USA) was used for fatty acid identification. Fatty acids were quantified as area % of total fatty acids. Only one analysis was made on each extract.

Results

Egg size (diameter) increased with increasing maternal size, which agrees with previous findings (Valin and Nissling, 2000). More specifically, the egg diameter of F20 and F21 was the largest, while the diameter of F18 was intermediate and F19 and F22 the smallest (Fig. 3.3.1). Interestingly, % lipids in eggs were directly proportional to egg size for F22, F19 and F18, but not F21. Unfortunately, no sample of F20 was available for the lipid analysis.

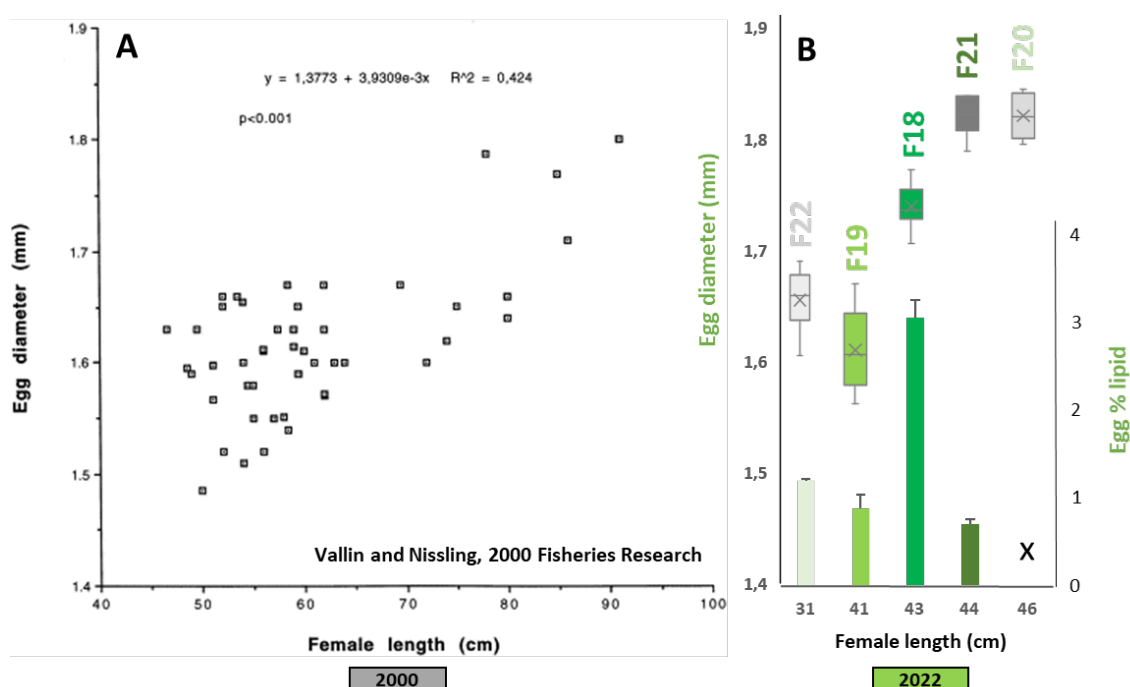
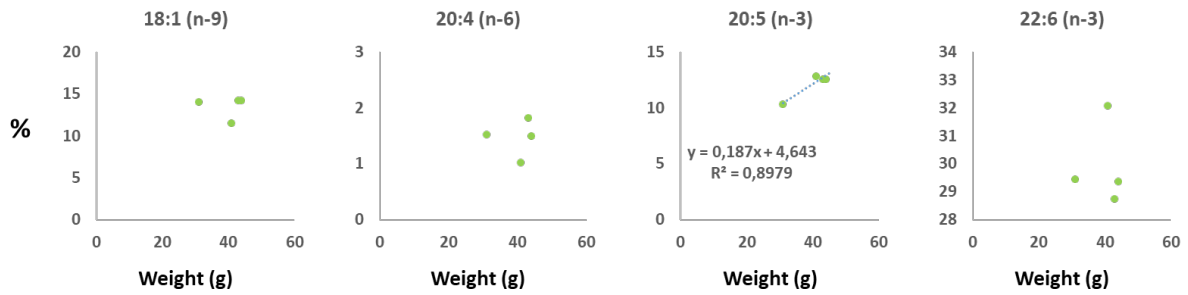


Figure 3.3.1. A) Diameters of Baltic cod eggs in relation to female length. B) Box plots show diameters (left y-axis) and bars show % lipids (right y-axis) of the eggs in relation to female length (x-axis) from the 5 batches produced via *in vitro* fertilisations on board R/V Alkor in May 2022.

Regarding fatty acid composition in eggs, we found a positive correlation between EPA (20:5 (n-3)) levels and total weight and length of female Baltic cod (Fig. 3.3.2).

A) Female weight vs egg fatty acids



B) Female length vs egg fatty acids

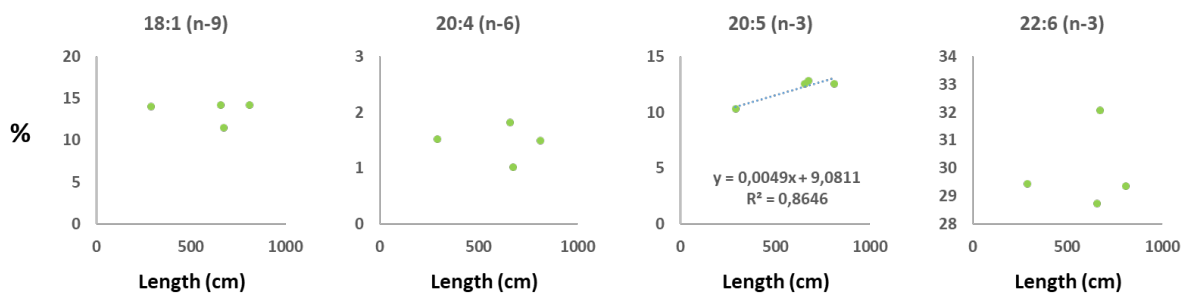
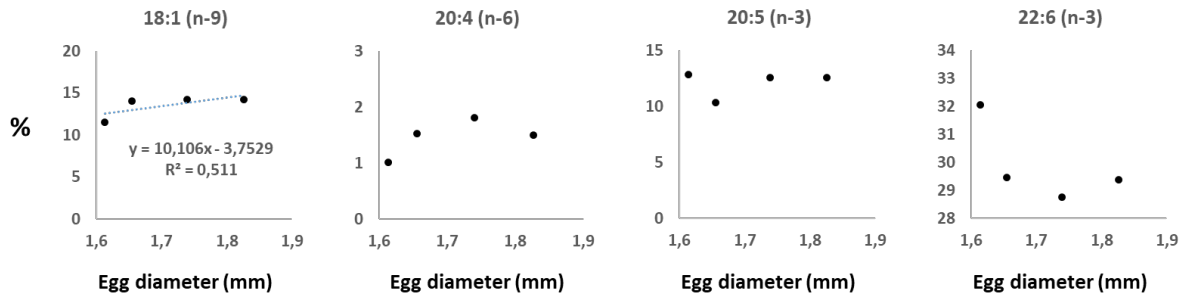


Figure 3.3.2. Correlations between egg fatty acids and total weight (A) or length (B) of female Baltic cod caught on station 50 during the R/V Alkor cruise during May 2022 and used for reproduction experiments.

Regarding fatty acid composition in female liver, intermediate levels of the essential acids arachidonic acid (ARA, 20:4 (n-6)) and eicosapentaenoic acid (EPA, 20:5 (n-3)), important for reproductive potential, were present in the female F18, which produced most larvae. On the other hand, highest oleic acid (OA, 18:1 (n-9)), used as fuel by the yolk sac larvae, was found in the female F21, which produced the largest larvae. Moreover, we found a positive correlation between the amount of OA in eggs and the corresponding egg diameter and larval yolk area (Fig. 3.3.3).

Among the stripped spawners, a positive correlation was found between the level of docosahexaenoic acid (DHA, 22:6 (n-3)) in livers and the total weight and length of the male Baltic cod applied in the reproduction experiment (Fig. 3.3.4). For example in mammals, sperm quality has been related to DHA level.

A) Egg diameter vs egg fatty acids



B) Larval yolk area vs egg fatty acids

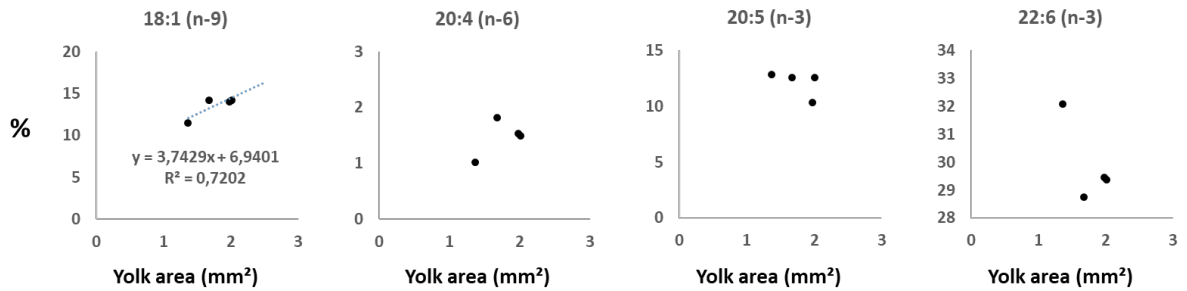
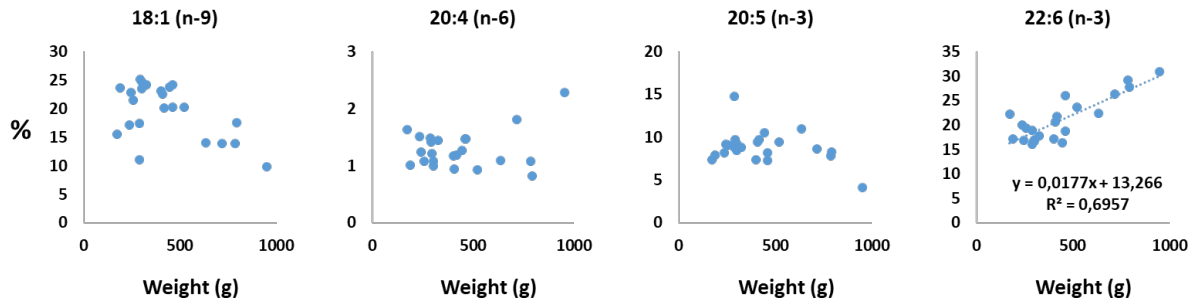


Figure 3.3.3. Correlations between Baltic cod egg fatty acids and egg diameter (mm) (A) and larval yolk area (mm²) (B) of offspring produced on board R/V Alkor, May 2022.

A) Male weight vs liver fatty acids



B) Male length vs liver fatty acids

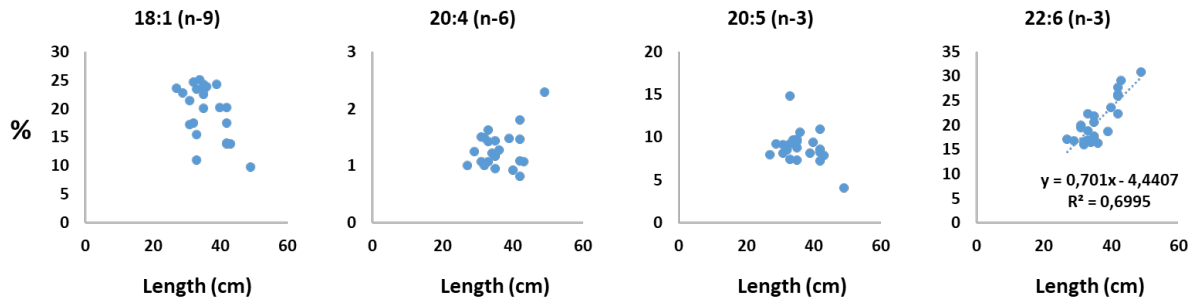


Figure 3.3.4. Correlations between liver fatty acids and total weight (A) or length (B) in male cod caught in station 50 during May 2022 with the German research vessel R/V Alkor during cruise # 573 and used for reproduction experiments.

Conclusions

Overall, the size of cod eggs produced via *in vitro* fertilisations was comparable to Baltic cod egg sizes previously reported. Generally, it is described that egg diameter can decrease with increasing batch number within the spawning season (Vallin and Nissling, 2000). However, the reproduction experiment and eggs studied in the study represent the beginning of the spawning period, while the egg diameters measured nevertheless corresponded to the upper known range.

Intermediate ARA and EPA levels were found in eggs that resulted in most larvae, while highest OA levels were found in eggs, which produced the largest larvae. Furthermore, there was a positive correlation between OA levels in eggs and the corresponding egg diameter and larval yolk area, which is in line with that % lipids in eggs is considered a good indicator for egg quality and later embryonic size and performance. Interestingly, male liver DHA level was related to male size, which might be associated with fertilisation capacity in Baltic cod.

Together, the studies of offspring quality in relation to parental quality call for further investigation.

4. Cod growth: new insights into environmental impacts

By Karin Hüsey

Background

Otoliths are structures located in the fish's head and grow through daily and seasonal growth rings, much like year rings in trees. These growth rings allow us to 1) derive the age of a fish, 2) identify the exact date when the fish has experienced e.g. a life stage transitions, undertaken migrations between different habitats or experienced specific environmental conditions, and 3) allow us to back-calculate how fast the fish has been growing over its entire life (Vigliola *et al.*, 2000; Hüsey *et al.*, 2003, 2016, 2018; Li *et al.*, 2008). Chronological records of elemental concentrations in the otoliths have become a widely used tool to infer the environmental conditions experienced by individual fish, and to reconstruct stock dynamics, migration phenology and connectivity patterns (Campana, 1999; Reis-Santos *et al.*, 2022). This is demonstrated, for example, in the EMFF project "Sustainable management of Kattegat cod; better knowledge of stock components and migration" (EMFF grant nr J. nr. 33113-B-16-034). Other elements allow us to infer patterns of age and growth (Limburg *et al.*, 2018; Heimbrand *et al.*, 2020; Hüsey *et al.*, 2021). The chronological records of element concentration from the core of the otolith (= birth) to the edge of the otolith (= death) therefore allows to infer life-long patterns of growth and habitat reconstruction on a sub-annual temporal resolution. In this study, we focused on the following elements as markers of growth, maturation and hypoxia exposure in order to identify temporal and spatial dynamics in growth and when the cod are most exposed to hypoxia.

Markers of growth: Phosphorus (P) and magnesium (Mg) are elements that are either essential constituents of the otoliths organic matrix, or co-factors in metabolic processes (Wojtas *et al.*, 2012; Sturrock *et al.*, 2013, 2014; Maret, 2017; Thomas and Swearer, 2019). Their ions also appear to be incorporated into the otolith randomly trapped in the crystal structure (Miller *et al.*, 2006; Izzo *et al.*, 2016; Thomas *et al.*, 2017). Previous studies have suggested positive relationships between growth rate and otolith P and Mg (Limburg *et al.*, 2018; Heimbrand *et al.*, 2020; Hüsey *et al.*, 2021).

Question addressed: Are there seasonal patterns in growth of eastern Baltic cod, and is growth impacted by temperature?

Markers of other physiological processes: Sturrock *et al.* (2015) speculated that the drop in plasma and otolith Zn among mature female plaice during the spawning season was caused by rerouting of Zn to the ovaries during vitellogenesis (Sturrock *et al.*, 2014). We therefore tested whether such a pattern was also evident in eastern Baltic cod.

Question addressed: Is there a season-dependent pattern in otolith Zn, particularly for mature females, that is associated with maturation?

Marker of hypoxia exposure: Manganese (Mn) is an active redox participant that cycles between dissolved and particulate phases as a function of pH and dissolved oxygen, with lower pH and oxygen favouring the dissolved forms (Slomp *et al.*, 1997; Trouwborst *et al.*, 2006). Dissolved Mn concentrations are thus elevated in the deep hypoxic areas in the eastern parts of the Baltic Sea, and in shallow coastal areas during summer throughout the Baltic Sea. As such, otolith Mn is becoming an increasingly popular marker to reconstruct past hypoxia-exposure in fish (Limburg *et al.*, 2011; Mohan *et al.*, 2012; Mohan and Walther, 2016; Altenritter *et al.*, 2018; Altenritter and Walther, 2019).

Question addressed: In which areas, and during which time of the year is exposure to hypoxia highest in eastern Baltic cod.

Materials & Methods

Samples

The samples used in this study originate from two tag-recapture programs carried out in the Baltic Sea: CODYSSEY („Cod spatial dynamics and vertical movements in European waters and implications for fishery management“, 2002-2006, <https://cordis.europa.eu/project/id/Q5RS-2002-00813>) and TABACOD (“Tagging Baltic Cod”, 2016-2020, <https://tabacod.dtu.dk/>). From CODYSSEY, $n = 146$ recaptured cod in the length range 435 – 960 mm were available and from TABACOD $n = 32$ recaptures in the length range 298 – 503 mm. Release and recapture locations are shown in Figure 4.1. All cod were tagged with an external tag with a unique identification number, and a chemical tag was induced on the otoliths by injection of Tetracycline. Tetracycline is an antibiotic that binds to proteins and is visible as a fluorescent band under UV light.

After recapture, fish total length (TL , mm), weight (g), sex (female, male), days at liberty (DAL) and maturity were recorded. Fish growth (G_{fish}) was calculated as growth per day:

$$G_{fish} = (TL_{recapture} - TL_{release}) \cdot DAL^{-1} \quad (1)$$

For all fish (total $n = 178$) paired otolith and DST records were available. Details on the tagging protocols of CODYSSEY may be found in Nielsen *et al.* (2013) and for TABACOD in Hüsey *et al.* (2020, 2021). All procedures were carried out under the necessary animal test permissions: German DST tagging: AZ 7221.3.1-007/18; Danish T-bar and DST tagging: 016-15-0201-00929, Swedish T-bar and DST tagging: Dnr 5.8.18-14823/2018.

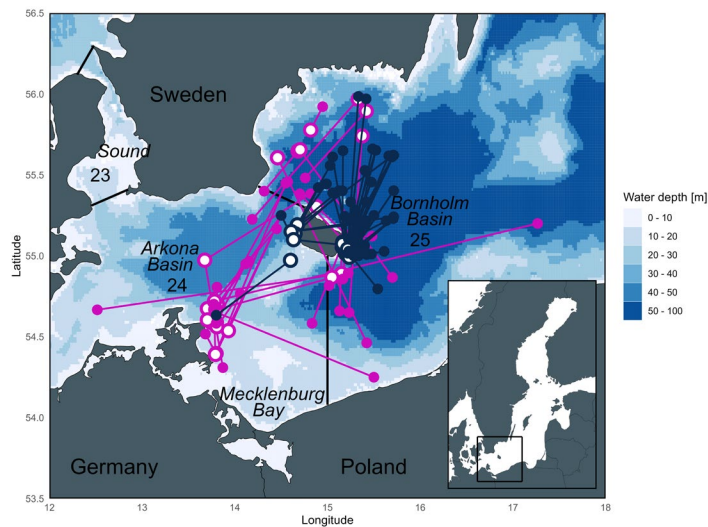


Figure 4.1. Map of the release and recapture positions of the cod from the TABACOD (pink) and CODYSSEY (blue) tagging programs used in this study. Open circles = release positions, closed symbols = recapture positions. Numbers represent ICES Subdivisions (SD) and SD boundaries are outlined by straight lines. The Bornholm Basin is the main spawning area of eastern Baltic cod.

Otolith preparation

Otolith preparation procedures have been described in detail in Hüsey *et al.* (2020, 2021). In brief, otoliths were embedded in Epoxy resin (Struers®) and sectioned through the core using an Accutom-100 multicut sectioning machine. The otolith sections were viewed under UV light using a Leica DMLB microscope to identify the Tetracycline mark (see Figure 4.2). The distance from the mark to the edge of the otolith (G_{oto}), corresponding to the time the fish was at liberty after tagging, was measured.

Trace element analyses were carried out by laser ablation inductively coupled plasma mass spectrometry (LA-ICP-MS) at the Geological Survey of Denmark and Greenland, using a NWR213 laser system from Elemental Scientific Lasers that was coupled to an ELEMENT 2 mass spectrometer from Thermo-Fisher Scientific. The otoliths were analysed along a transect from the nucleus to the dorsal edge of the otolith. The data corresponding to the time at liberty was identified from the otolith growth measurements (the black line in Figure 4.2). Each chemical measurement was assigned to a date of formation:

$$Date_{formation} = Date_{release} + Distance_{mark\ to\ measurement} \cdot G_{oto}^{-1} \cdot DAL \quad (2)$$

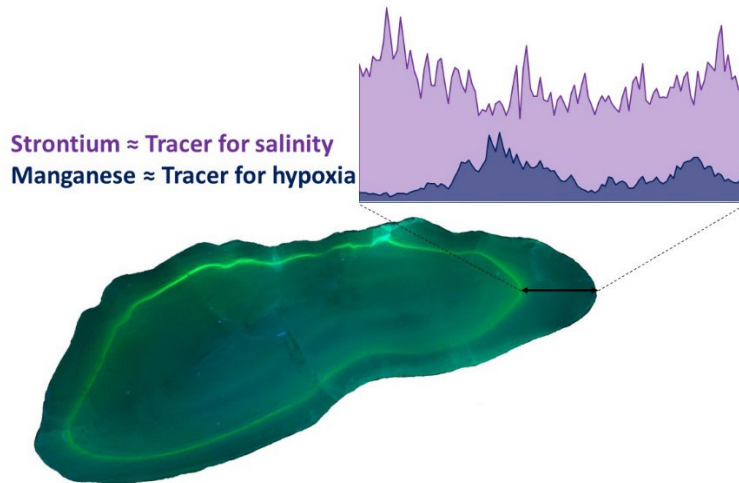


Figure 4.2. Image of cross section of cod otolith viewed under UV light showing the fluorescent tetracycline-hydrochloride mark (green), where the black line indicates the laser transect and growth measure (G_{oto}) and an example of Sr:Ca and P:Ca profiles during the time from tagging to recapture.

DST data

The tags used in both projects were DST-CTD, micro-TD and milli-TD from Star-Oddi. Tags were programmed to record ambient conditions every hour. The data of mean daily depth and temperature experience of all individuals from the two tagging programs are shown in Figure 4.3. To correlate DST data with the otolith chemical measurements (that have far lower temporal resolution), salinity, temperature and depth records were averaged by day for each fish to match the date of formation of each chemical measurement.

Owing to the spatial differences in hydrographic regimes between the two areas in the Baltic Sea used by the eastern stock (SD 24: shallow, higher salinity and larger seasonal temperature amplitude; SD 25: deep basins, low salinity and lower seasonal temperature amplitude), it is possible to estimate the approximate geographic position of each fish from these DST records using various geolocation tools described in (Haase, 2021; Haase *et al.*, 2021) (Andersen *et al.*, 2007; Neuenfeldt *et al.*, 2007)

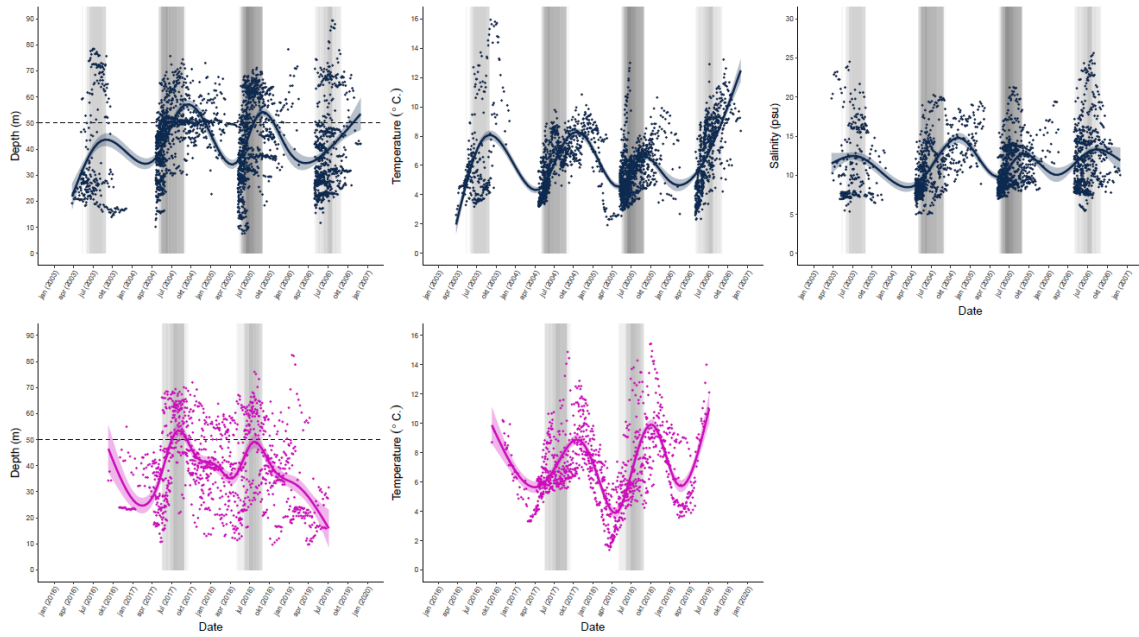


Figure 4.3. Depth, temperature, and salinity profiles obtained from the archival tags of all individual data points for all fish including loess-smoothed means and confidence interval bands, and represented for the two tagging projects separately, CODYSSEY (blue) and TABACOD (pink) tagging programs. Salinity was only measured by the tags used in the CODYSSEY program. Years differ between tagging programs, but measurements are aligned by month to facilitate visual interpretation of the graphs. Shaded bars indicate the duration of the spawning season, where the season of individual fish are superimposed on each other. The darker the colour, the more individuals are in the spawning area. The horizontal line indicates the 50 m depth line, which is used for the identification of the onset of spawning migration of individual fish. CODYSSEY fish were released in April of all years, while TABACOD fish were released throughout the year.

Drivers of otolith chemical composition

To examine how much variation in otolith elemental concentrations were explained by environmental and/or physiological variables we fitted linear mixed-effects (LME) models similar to (Sturrock *et al.*, 2015) using the “lme4” package (Bates et al. 2015) in R. Models were fitted using individual fish and release year as random variable to allow variable intercepts, accounting for inter-individual differences and differences between tagging years.

The full model (model (3)) included all fixed effects, including *area* (each individual geolocation assigned to eastern or western Baltic Sea based on SD boundary), *season* (spawning/feeding based on individual depth profiles – see methods), *month* (month of formation 1 – 12), *T* (temperature), *D* (depth), *sex* (males/females), *age* (years), *TL* (total length), G_{fish} (fish somatic growth between release and recapture), and *opacity* (0 - 255), with subscripts *i* representing individual fish and *j* individual chemistry measurements. For the CODYSSEY samples, where measurements of salinity were also available, the analysis was repeated by including S_{ij} (salinity) in model (3) as well.

$$E_{ij} = \text{factor}(area_{ij}) + \text{factor}(season_{ij}) + \text{factor}(month_{ij}) + T_{ij} + D_{ij} + \text{factor}(sex_i) + age_i + TL_i + G_{fish_i} + opacity_{ij} + (1|fish_i) + (1|year_i) + \varepsilon_i, \text{ where } \varepsilon_i = N(0, \sigma^2) \quad (3)$$

Finally, the most parsimonious model was identified by ranking all possible models by the Akaike information criterion (AIC) using the “dredge” function of the MuMIn package (Burnham and Anderson, 2002). The final model was selected as the model with an AIC difference > 2 compared to all other models.

Results

Markers of growth (P, Mg)

Otolith concentration of all elements that are related to growth showed similar responses across environmental and biological variables (Figure 4.4). Both P and Mg showed a distinct seasonal pattern with lowest concentration in late spring (April-May) and highest concentrations in winter (November-February) – corresponding to the seasons of lowest and fastest growth. P and Mg were also positively correlated with temperature, and higher element concentrations during the feeding season compared to the spawning season in P only, while Mg showed no response. Neither P nor Mg were related with fish growth between release and recapture. This however is not surprising, considering the seasonality in growth (correspondingly in P and Mg incorporation) and the fact that somatic growth is measured across variable seasons and days at liberty.

Further significant effects were an increase in Mg with depth and higher concentrations in P and Mg in the eastern than in the western Baltic Sea. Dissolved organic phosphate is highest in the eastern parts of the central Baltic Sea (Conley *et al.*, 2002, 2009; Naumann *et al.*, 2020). The higher concentrations of otolith P in the east may be the result of higher environmental bioavailability (which is typically related to hypoxia). For Mg, freshwater runoff is known to create a coast to offshore gradient in concentration (Cox, 1989; Lebrato *et al.*, 2020). This depth-related environmental Mg gradient may explain the effect of depth occupied by the fish observed in this study.

Marker of other physiological processes (Zn)

Otolith Zn concentrations are thought to be regulated by physiological processes related to maturation and spawning. Otolith Zn showed a seasonal pattern similar to the response of Mg and P (Figure 4.4). Plasma concentrations of Zn are known to decrease during spawning migrations in sockeye salmon (*Oncorhynchus nerka*) (Fletcher *et al.*, 1975; Fletcher and Fletcher, 1980), as maternal Zn is rerouted to embryogenesis (Riggio *et al.*, 2003; Thompson *et al.*, 2012). However, otolith Zn concentrations were higher during the spawning season, and lower during the feeding season. Zn occurs primarily in particulate form in freshwater with a higher degree of dissolved ions occurring in marine water (Sylva, 1976). The bio-availability of Zn, occurring as free ions that can be absorbed across the gills, thus decreases from marine to freshwater environments (Sylva, 1976). It is not possible to identify whether the significant spawning/feeding season signal is attributable to spawning or more likely to the environment the cod is exposed to during its spawning migration.

In all the physiologically regulated elements, the fixed effects explained a considerably lower proportion of the observed variability than the random effects tagging year and fish (P: marginal $r^2 = 23.2\%$, conditional $r^2 = 79.4\%$; Mg: marginal $r^2 = 6.3\%$, conditional $r^2 = 72.0\%$; Zn: marginal $r^2 = 5.9\%$, conditional $r^2 = 60.7\%$).

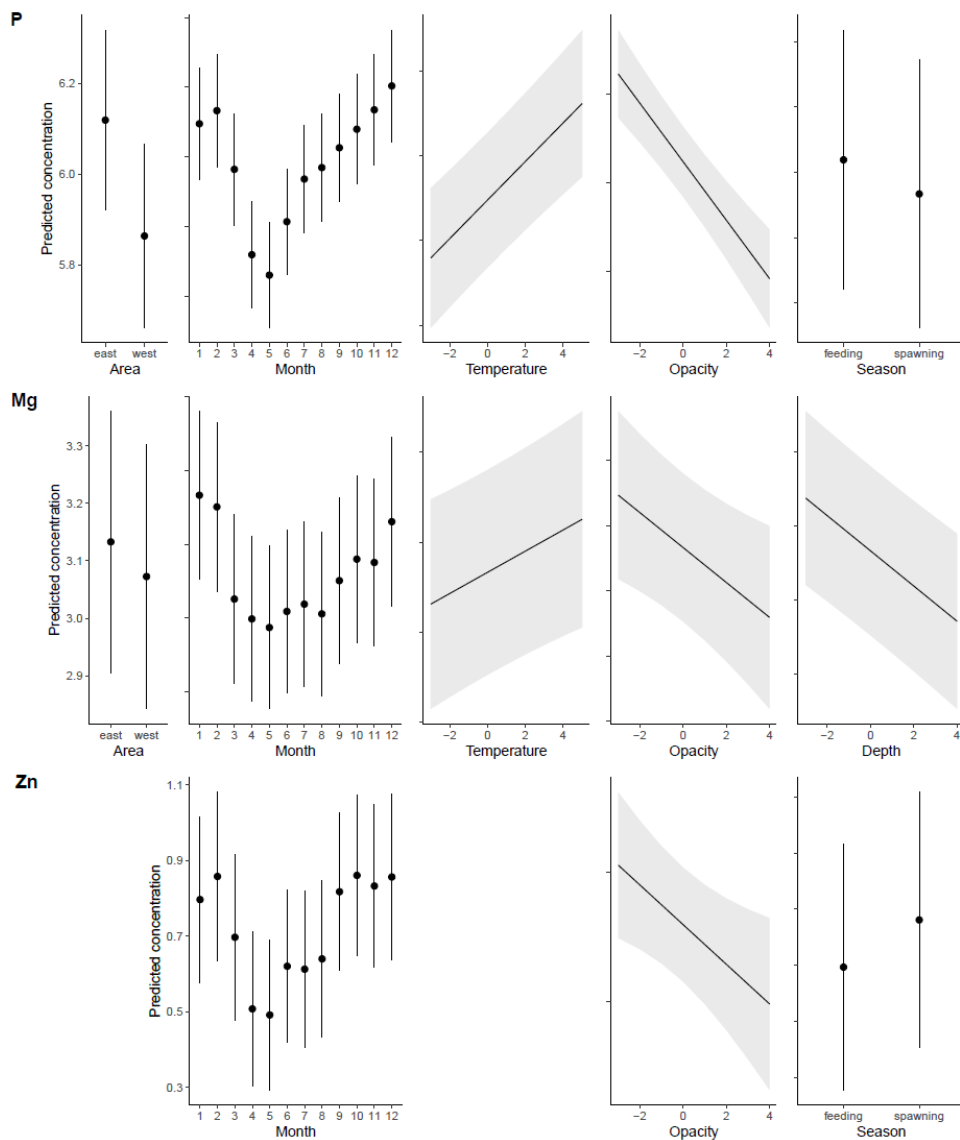


Figure 4.4. Predicted response of P, Mg and Zn to significant drivers: Area (east or west of Bornholm), Month (numbered as month of the year), Temperature (°C.), and Opacity (otolith light absorption). Note that all effects (Area, Month, Temperature and Opacity) for all three elements are shown in the same order from left to right. Only the effects shown in the last column differ between elements (P and Zn: Season (feeding or spawning), Mg: Depth (water depth)). Element concentrations are log+1 transformed predicted ppm values, and continuous variables (temperature, depth and opacity) were centred and scaled prior to analysis.

Marker of hypoxia exposure (Mn)

Otolith Mn concentrations were significantly lower in the western than in the eastern Baltic Sea (Figure 4.5), which is consistent with a higher extent of hypoxic areas in the eastern Baltic Sea. One of the most notable results of this study is that otolith Mn concentrations were higher in shallow water during the feeding season. It is thus not when the cod are moving into the deep areas for spawning that they are exposed to the highest hypoxia levels, but rather during the post-spawning time spent feeding in shallow water. We also detected a size-related pattern, where otolith Mn decreases with fish size. Given the size-related depth distribution of Baltic cod (Sparholt et al., 1991; Pihl and Ulmestrand, 1993; Oeberst, 2008) and seasonal depth movements associated with spawning, these results indicate that the highest Mn concentrations in Baltic cod are found during the feeding season

from late summer to winter at shallow depths, with smaller fish having higher Mn concentrations than larger fish.

The fixed effects explained a considerably lower proportion of the observed variability than the random effects tagging year and fish (marginal $r^2 = 10.0\%$, conditional $r^2 = 58.9\%$), meaning that there is a considerable degree of unexplained variability in otolith Mn concentration.

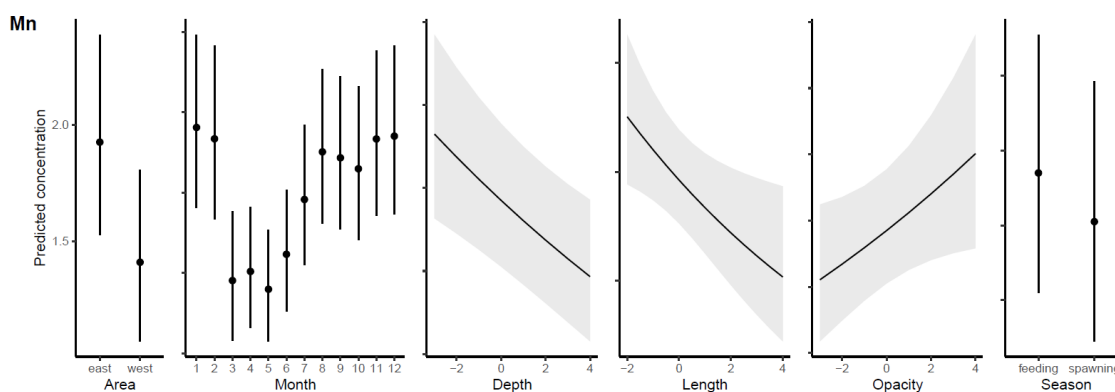


Figure 4.5. Predicted response of Mn to significant drivers: Area (east or west of Bornholm), Month (numbered as month of the year), Depth (water depth), Length (fish length at recapture), Opacity (otolith light absorption) and season (feeding or spawning). Element concentrations are log+1 transformed predicted ppm values, and continuous variables (temperature, depth and opacity) were centred and scaled prior to analysis.

Conclusions

Markers of growth (*P*, *Mg*)

- Growth of eastern Baltic cod (as assessed by the concentrations of otolith *P* and *Mg*) is subject to seasonal variations, with fastest growth rates in November-February and lowest growth rates in April-May. Growth increases with increasing temperature. Growth is thus highest in the feeding season at higher temperatures from late summer to winter.
- Maximum temperatures experienced by eastern Baltic cod during this study was $< 12\text{ }^{\circ}\text{C}$, which is generally considered the optimum temperature for growth. Since cod in the eastern Baltic Sea seldom experience temperatures above their tolerance level, climate-related increases in water temperatures will not be the direct cause for reductions in growth in the near future - given that abundant food is available to sustain metabolic cost of living and growth.

Marker of other physiological processes (*Zn*)

- Otolith *Zn* concentrations show a similar seasonal pattern as *P* and *Mg*. Together with the highest *Zn* concentrations during the spawning season (contrary to other literature studies), this suggests that *Zn* in cod reflects growth-related physiological activity rather than maturation patterns.

Marker of hypoxia exposure (*Mn*)

- Highest hypoxia exposure in eastern Baltic cod occurs during the feeding season from late summer to winter at shallow depths, with smaller fish being more exposed than larger fish.
- The increasing frequency of extensive summer hypoxia events in shallow water may thus have negative effects on growth (and ultimately survival) of particularly smaller cod.

5. Feeding of cod and its interactions with the pelagic fisheries

Background

Sprat is a major fish prey for adult cod in the eastern Baltic Sea. In last decades, sprat spatial distribution in the Baltic Sea has shifted northwards; especially during autumn, as recorded in acoustic surveys (ICES 2020). This has resulted in limited spatial overlap with cod, as cod is distributed mostly in the southern Baltic Sea. Neuenfeldt et al. (2020) revealed that decreased growth and survival of small cod may be an extension of the juvenile, post-settlement bottleneck, and that feeding levels of small cod have been critically low in recent years, at or even below minimum fish maintenance levels. This has raised concerns whether cod may be lacking prey, in the light of the deteriorating nutritional condition of cod. If this is the case, spatial management measures for sprat fisheries could be beneficial for cod (Eero et al. 2012), as also pointed out by ICES (e.g. 2020). However, as many factors likely contribute to the currently poor state of the cod stock, it is unclear whether reduced sprat fishing in the cod distribution area would improve the state of the cod stock and to what extent. In the following chapters we provide new insights regarding this question by exploring changes in cod and sprat overlap (section 5.1), cod feeding (section 5.2) as well as spatio-temporal patterns in sprat fisheries (section 5.3).

5.1 Sprat biomass in cod distribution area

By Margit Eero

Materials and methods

Sprat data

Sprat biomass by ICES Subdivisions (SDs) in the Baltic Sea was calculated using biomass estimates for the entire stock, obtained from ICES stock assessment, combined with spatial distribution information from acoustic surveys conducted in quarter 4 (Q4). The acoustic abundances are quite noisy and variable from year to year. For this reason, the acoustic stock estimates were not used directly for biomass, but only for relative stock distribution information. The distributions from Q4 acoustic surveys were combined with absolute biomass estimates for January 1 in the following year, to minimize the seasonal gap between stock biomass and distribution data. The SD-specific sprat biomass used here represent biomass in Q4, under the assumption that stock biomass in Q4 is similar to that in January 1 in the following year. In acoustic surveys in Q2, large part of the sprat stock is distributed more in the southern Baltic Sea, and the surveys do not cover the northernmost SDs. It could be assumed that larger fraction of the entire Baltic sprat stock is overlapping spatially with cod distribution area during spring. Therefore, we focused our analyses mainly on Q4, when overlap between cod and sprat is most limited, but which is an important season for cod feeding and growth.

Data on biomass and numbers at age for the entire Baltic sprat stock were available from ICES (2022). Sprat numbers at age by SDs from acoustic survey were compiled by ICES survey working group for the Baltic Sea WGBIFS (ICES 2021). Sprat weights at age in Q4 by SDs were obtained from annual ICES WGBFAS reports, and were based on commercial catch sampling. The numbers at age from acoustics in Q4 were converted to biomass, by multiplying the numbers with SD-specific mean weights at age. The proportions of the sprat biomass in different SDs in acoustic data, by age, were then applied to distribute stock biomass at age into SDs.

The SD-specific sprat biomasses were only used from 2000 onwards. In earlier years, the acoustic surveys did not cover the northernmost areas of the Baltic Sea, where part of the sprat stock is distributed, which likely introduces a bias in the distribution keys and resulting SD-specific biomass estimates for earlier years. Since 2000, the trends in total biomass from ICES stock assessment and from the acoustics were similar.

Cod data

Eastern Baltic cod abundance at length was available from ICES stock assessment (ICES 2022). The data are available on quarterly basis and we used cod abundance for Q4, to correspond to the sprat SD-specific estimates that were only available for Q4. We used abundance of >20 cm cod, as from this size cod has been found to start preying on sprat, based on stomach content information (Neuenfeldt et al. 2020). In later decades, eastern Baltic cod is mainly distributed in SDs 24-26 (more than 95% of the landings came from this area). Thus, the analyses focusing on overlap used data for the entire cod stock in comparison with sprat biomass in SDs 24-26.

Results

Sprat distribution

Since the late 2000s, in Q4, more than a half of the total sprat biomass in the Baltic Sea has been concentrated in the northern areas, i.e. SDs 29-32 (Fig. 5.1.1). About 25% of the sprat biomass in Q4 is found in cod distribution area, in SDs 24-26. In the early 2000s, the proportion of the sprat stock in SDs 24-26 was up to 50%, with correspondingly lesser proportion in the northern Baltic Sea (Fig. 5.1.1).

The distribution of sprat in Q4 differs somewhat for the different age-groups (Fig. 5.1.2). The distribution of age 0 has been most variable, with occasional years of more than 50% being found in cod distribution area (SDs 24-26), and other years with high proportions found further north (SDs 29-32). There is a slight tendency towards higher proportions of age 0 in the north and correspondingly less in SDs 24-26 over the time series since 2000. Distributions of age 1-2 are relatively similar to the total biomass distribution. The proportion of ages 3+ in SDs 24-26 in Q4 has increased since 2010s to up to 40%, compared to less than 20% in 2005-2010 (Fig. 5.1.2).



Figure 5.1.1. Sprat biomass (left panel) and relative distribution of the biomass in sub-areas (right panel) in the Baltic Sea, in Q4.

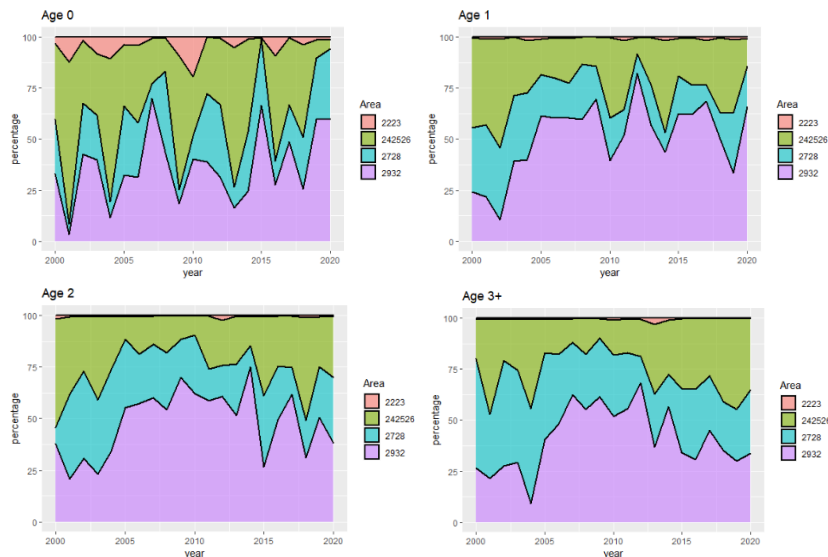


Figure 5.1.2. Relative distribution of sprat biomass in Q4 in subareas in the Baltic Sea, for age- groups 0, 1, 2 and 3+ combined.

Sprat biomass relative to cod abundance

Biomass of sprat stock in the entire Baltic Sea (SDs 22-32) was record high in the mid-1990s, after which is declined. This resulted in a decline in sprat biomass relative to the abundance of Eastern Baltic cod (> 20cm in length) (Fig. 5.1.3). The lowest level of sprat per cod in the Baltic Sea occurred in the early 2010s, which was due to a decline in sprat stock accompanied with a slight increase in cod abundance. Since 2015, sprat biomass per cod has increased again to the level observed in the early 2000s, which is mostly because of a pronounced decline in cod abundance.

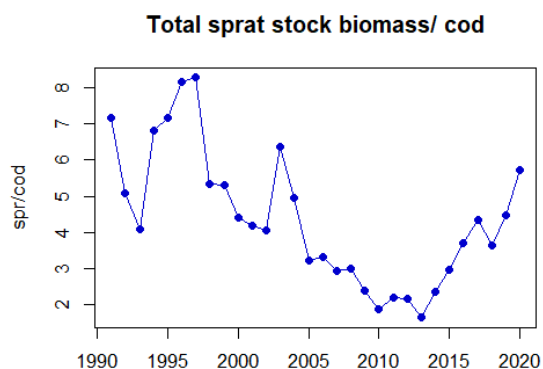


Figure 5.1.3. Biomass of sprat in the entire Baltic Sea relative to the abundance of >20 cm cod, in Q4.

Since the Eastern Baltic cod is mostly distributed in SDs 24-26, we also looked at sprat biomass relative to cod within the area of cod distribution. The biomass of sprat in the distribution area of cod (SDs 24-26) in Q4 declined sharply in the early 2000s to a low level where it remained until the early 2010s (Fig. 5.1.4). Since about 2013, sprat biomass in this area increased, though has remained at a lower level compared to the early 2000s, and shows a large inter-annual variability. The estimate for 2020 was as low as observed in the late 2000s-early 2010s. The abundance of >20cm eastern Baltic cod was low in the early 2000s after which it increased to a relatively higher level in around 2005-2015, before a sharp decline to the present record low abundance (Fig. 5.1.4).

Following from the dynamics of the two species in the distribution area of cod (SDs 24-26) in Q4, sprat biomass relative to cod in this area declined sharply in the early 2000s and remained at a low

level until about 2015 (Fig. 5.1.5). In later years, sprat biomass relative to cod in this area has increased, though it has not reached the level prior to the decline in the early 2000s. In last few years in the time series, sprat biomass relative to cod abundance has shown a declining trend (Fig.5.1.5), due to a lower sprat biomass in SDs 24-26 (Fig. 5.1.4).

When looking at sprat biomass in SDs 24-26 in Q4 separately for age-groups, it is apparent that biomass of age 0 sprat relative to >20cm cod abundance has not increased in later years, in contrast to older ages, but in fact the values in 2019-2020 were the lowest in the time series. Biomass of age 3+ sprat relative to cod has increased most since 2017, and has reached close to the highest values recorded since 2000. An increase in sprat age 2 biomass relative to cod is also apparent, while the increase is less pronounced for age 1 sprat (Fig. 5.1.5).

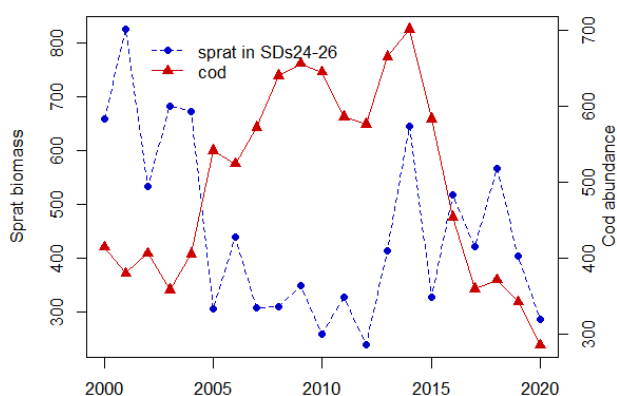


Figure 5.1.4. Sprat biomass in SDs 24-26 in Q4 and abundance of >20cm eastern Baltic cod.

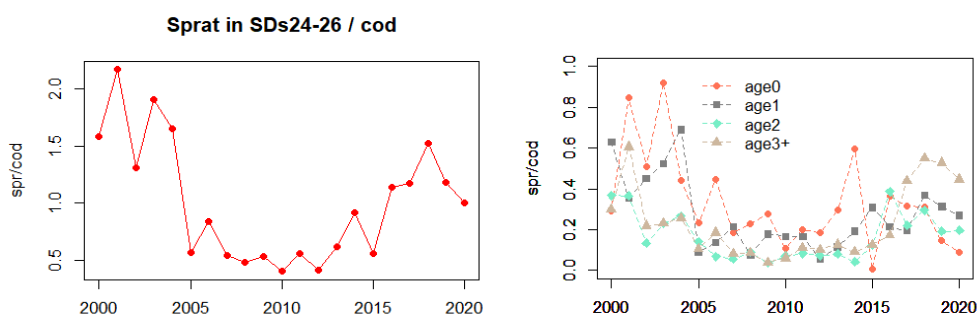


Figure 5.1.5. Sprat biomass in SDs 24-26 in Q4 relative to the abundance of >20cm eastern Baltic cod, for all sprat age groups combined (left panel) and separately for sprat age-groups (right panel).

Conclusions

The early 2010s, when many indicators of the Eastern Baltic cod stock health deteriorated to their worst levels, corresponds to the period of lowest biomass of sprat in the distribution area of cod in autumn, since the 2000s. This is both in terms of absolute biomass of sprat as well as relative to the abundance of adult cod. Since then sprat biomass in the cod area in autumn has generally increased, however, there are differences by age-groups. An increase in older sprat (especially age 3+) biomass relative to cod abundance is observed since 2015, which is mainly due to a shift in relative distribution of older ages of sprat towards the south. However, this increase is not apparent for age 0, and there

is a slight tendency towards a lower proportion of age 0 in the cod area in later years. Thus, it is plausible that limited availability of age 0 sprat in autumn is among the factors preventing improvements in cod condition, despite the increased biomass of older sprat in the distribution area of cod.

5.2 Cod feeding on sprat: is there enough prey available?

By Stefan Neuenfeldt

Material and methods

Cod daily consumption rates were calculated assuming a feeding level of 0.3 (Figure 5.2.1), which is the average feeding level in 1964-2004 (Neuenfeldt et al. 2020), when cod growth was not impaired.

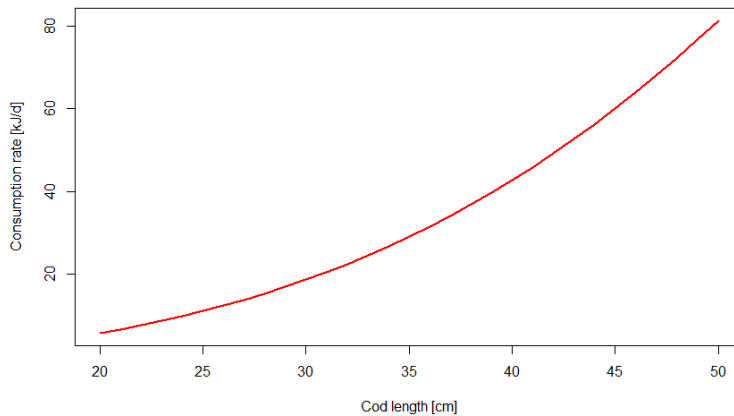


Figure 5.2.1. Consumption rate, expressed as kJoule per day at given length.

To calculate annual energy demand for the whole cod stock, first prey dependent growth over the year must be considered. Applying a feeding level that corresponds to the period 1964 to 2004, the growth model for 20 cm to 80 cm was run in 10 cm steps, to estimate the empirical relationship between start length (at the beginning of the year) and annual consumption rate integrating continuous growth (Fig. 5.2.2). Numbers per length class in the beginning of the year were calculated using the biomass per length group in Q1, which was transformed to numbers using $W = 6.838 L^{3.07} \cdot 10^{-3}$ from Neuenfeldt et al. (2020).

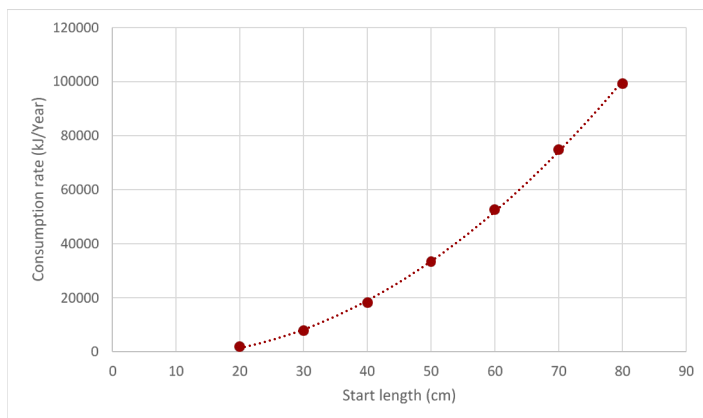


Figure 5.2.2: Empirical growth models for cod.

Results

Cod total energy demand in the Eastern Baltic Sea almost in all years has been higher than the energy available in the total sprat stock in the Eastern Baltic (Figure 5.1.3). Sprat energy density was assumed to average 7.5 kJ/g. However, changing this value within the realistic range of energy density for sprat between 5 and 12 7.5 kJ/g over the annual cycle does not change the discrepancy between the energy available in sprat and cod demands (Fig 5.2.3).

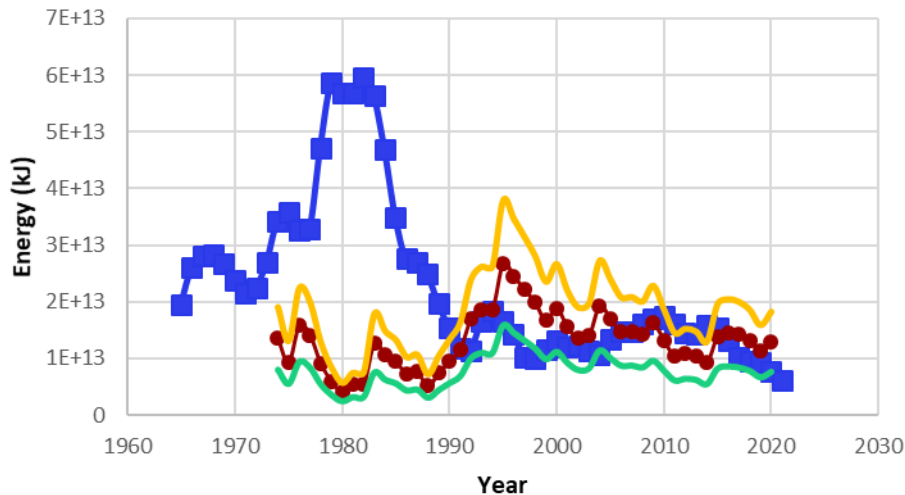


Figure 5.2.3. Energy content of the entire sprat stock in the Baltic (dark red) and cod energy demand (blue), both in kJ. Green line: sprat energy minimum of 5 kJ/g; yellow line: sprat energy maximum of 12 kJ/g.

Cod diet composition (Figure 5.2.4) has differed between the periods 1965-2004 and 2005-2014. Note that in the first period, low growth or condition of cod were less pronounced compared to the recent period. While the proportion of sprat in the stomachs of cod >40 cm was slightly higher in the earlier period, there is a clear difference towards relatively more sprat in the stomachs of smaller cod in the latter period (Figure 5.2.5, red dots). In the period 1965-2004, the average proportion of sprat in the diet of cod (averaged over all lengths of cod) was 30%. This implies that around 30% of the energy intake of cod consisted of sprat, when assuming similar energy density of the different prey types (they all approximately vary between 5 and 12 kJ/g over the year).

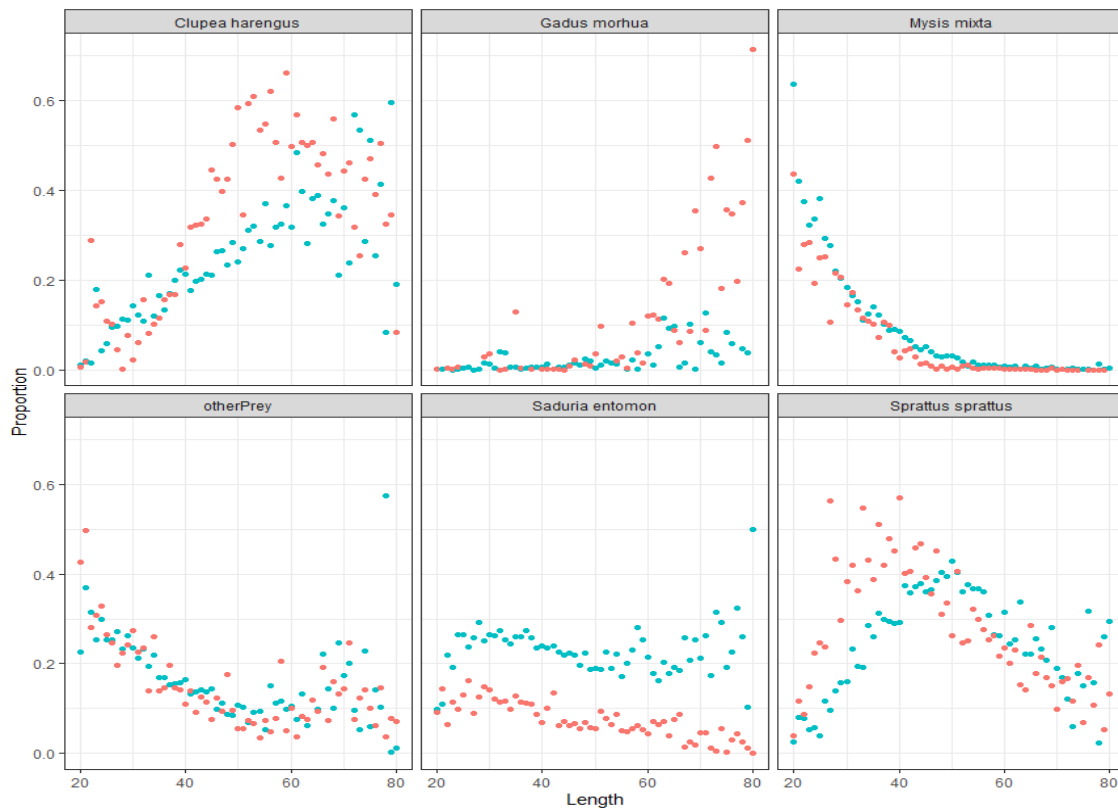


Figure 5.2.4. Diet composition (Proportion between 0 and 1) of cod over cod length for the periods 1965-2004 (blue) and 2005-2014 (red).

As mentioned in section 5.1, sprat distribution has changed over time. To address the sprat availability in the area overlapping with cod, the sprat total biomass was multiplied with the fraction of the stock that resides in the same area as the cod, roughly corresponding to ICES Sub-divisions 25 and 26 in the Eastern Baltic Sea. This could be done for Q4 (see the section 5.1 for calculation of area-specific sprat biomasses). After adjusting the amount of energy available in sprat to represent the fraction of the stock spatially overlapping with cod (SDs 25-26), it became apparent that cod energy demand for sprat in most years since 2004 has been about twice as high as the available energy in sprat within the area (Figure 5.2.5). This is when assuming the same proportion of sprat in cod diet (30%) as historically.

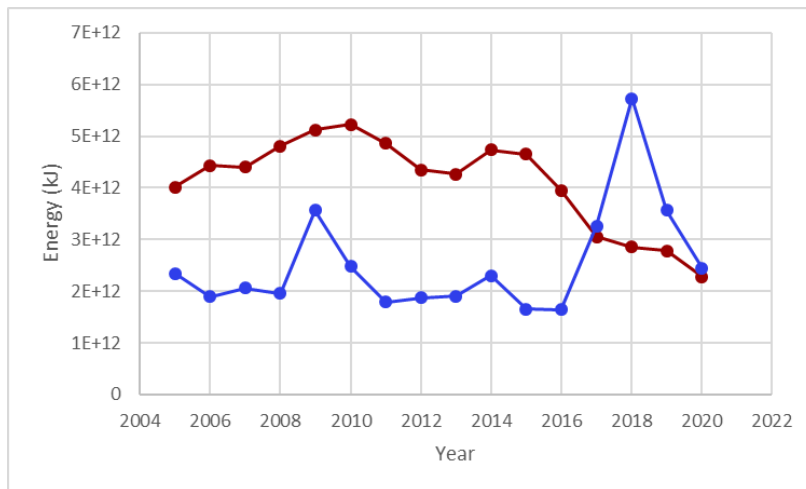


Figure 5.2.5. Sprat total energy content in ICES Sub-divisions 25 & 26 in Q4 (based on sprat relative distribution in Q4 acoustic survey and absolute biomass from the assessment (blue)) and cod energy demand (red). Cod energy demand shown here represents the energy demand concerning sprat only, and is derived applying the overall feeding level from 1964-2004 and that sprat consists 30% of the diet of cod.

The decreased availability of energy conserved in sprat is underlined by independently sampled stomach content data (Fig. 5.2.6). The feeding level of cod became more heterogeneous in space after the regime shift. Furthermore, the feeding level of juveniles (but not of adults) has considerably decreased in the later period (2005-2016) compared to the historical average (1965-2004) in the Bornholm basin and the western side of the Gdansk basin.

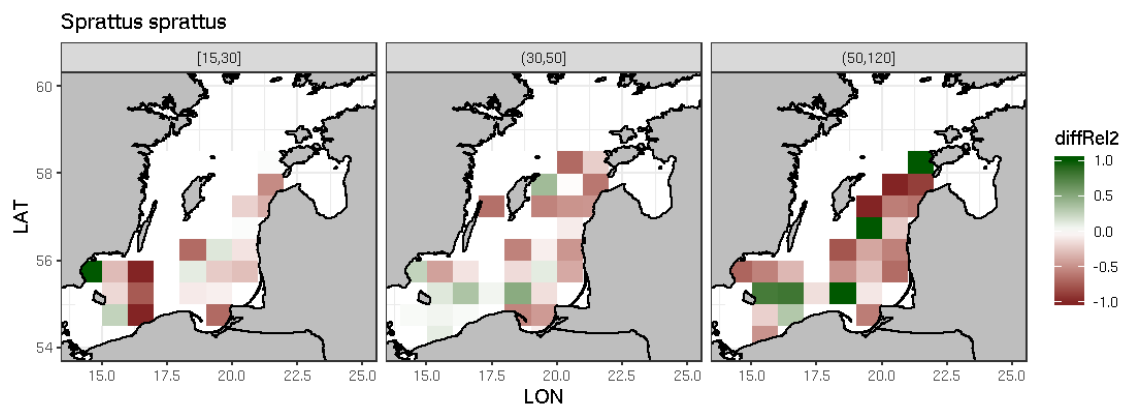


Figure 5.2.6. Changes in cod feeding level of sprat (observed consumption rate versus maximum consumption from lab experiments) in 2005-2016 compared to 1965-2004, for different size groups of cod (15-30 cm, 30-50 cm and 50-120 cm). The colour scale shows the relative difference in cod feeding level before and after 2004 scaled to a range between -1 and 1.

The relative decrease of sprat in the stomachs of small cod might be due to the lack of small sprat in the distribution area of cod. Alternatively, small cod are in recent years, on average, in so low condition, that they may not be able to forage on sprat during the predation windows at dawn and dusk (Figure 5.2.7), where cod ascend to catch sprat on their decrease from surface waters. Here, attack success and encounter rate depend on the locomotive capabilities of the cod, especially their potential for swimming burst. If this is limited, capture success decreases independent of prey abundance.

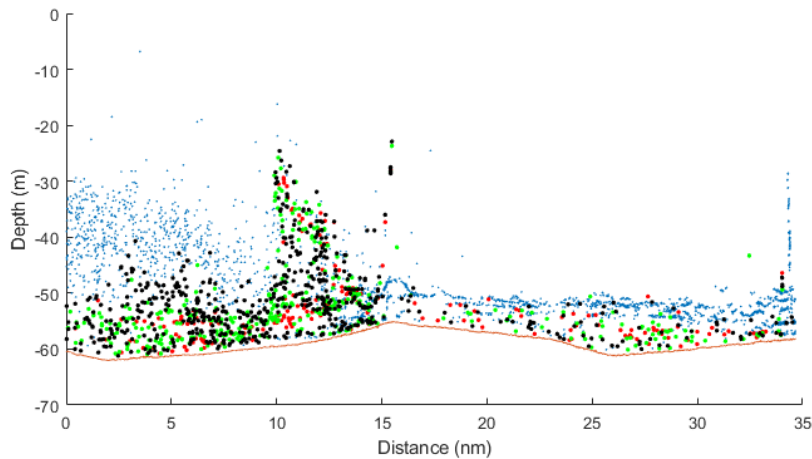


Figure 5.2.7. Single target echoes from the north-eastern edge of the Bornholm Basin in March 2005. Increasing distance corresponds to increasing time, sunrise was around 7:00 am, corresponding to 5 nautical miles steamed distance. Blue dots: Individual sprat decreasing from surface waters at dawn. Black dots: 15-30 cm cod; Green dots 30-50 cm cod, red dots: cod >50 cm.

Conclusions

Sprat is the main fish prey of cod, and cod consumes a significant part of the sprat stock annually. We can only observe the outcome of this process, not the original sprat biomass 'before' cod start preying on them. The available data indicate that sprat alone cannot accommodate the energy demands of the Eastern Baltic cod population. Furthermore, cod energy demand for sprat in most years since 2004 has been higher than the available energy in sprat within the area of cod. The relative contribution of sprat in the diet of cod <50 cm has increased in recent years. At the same time, for cod >50 cm, the contribution of sprat to the diet decreased slightly at decreasing consumption rates for the whole population. Stomach data are in agreement with these findings and imply additionally, that mainly smaller cod show decreased sprat consumption. Linking sprat availability to cod condition is not straightforward. Small-scale investigations of the predation process are recommended, to elucidate, if the presently poorly conditioned small cod are at all able to forage on sprat, independent of the total sprat energy availability on the population scale.

5.3 Changes in sprat fishing patterns

By Margit Eero

Material and Methods

Data on sprat catch by sub-areas in the Baltic Sea were compiled back to 1950, based on data from the reports of the ICES working groups conducting Baltic sprat assessments through time, as well as national statistics for the earliest decades in the time series (see also Eero 2011 for historical data sources). For the earliest decades in the time series, data for some countries were not available for every SD, but only as aggregated, including more than one SD. Thus, we grouped the data to sub-areas according to the resolution available in the data. Sprat catch data in the presently main distribution area of cod (SDs 24-26) was not possible to separate out for all the years back to 1950. The areas of SDs 24-25 and 26+28 are considered as most relevant in relation to cod, in the long time series of catch data. From 1995 onwards, data were available by quarter and SD allowing for analyses of both seasonal and spatial patterns in sprat catch. We additionally looked at spatio-temporal changes in harvest rate (catch/biomass) of sprat in Q4, using area-specific sprat biomass in Q4 (calculated in section 5.1) from 2000 onwards.

Results

Sprat catch distribution

The proportion of total Baltic sprat catch taken in the historically main distribution area of the Eastern Baltic cod (SDs 24-26 & 28) has varied between 60-80% in most years since the 1950s (Fig. 5.3.1). The share of sprat catches from these areas was largest (80-90%) in the late 1980s-early 1990s. In later years, the proportion of catch from SDs 24-26& 28 has increased again from a relatively lower level (ca 60% in 2010) to around 80% in 2020. Within this area, most of the sprat has generally been caught in SDs 26 and 28. The contribution of SDs 24-25 to the total Baltic sprat catch was highest in the 1990s, when it reached up to 40%. In the late 2000s-early 2010s, only 10-15% of the sprat catch was taken in SDs 24-25, but it increased to over 20% in recent years. The northern areas, i.e. SDs 27 & 29-32, where cod abundance is generally low, have contributed 10-40% of the Baltic sprat catches throughout the time-series since the 1950s, with a declining trends in last decade from ca 30 to 20 %.

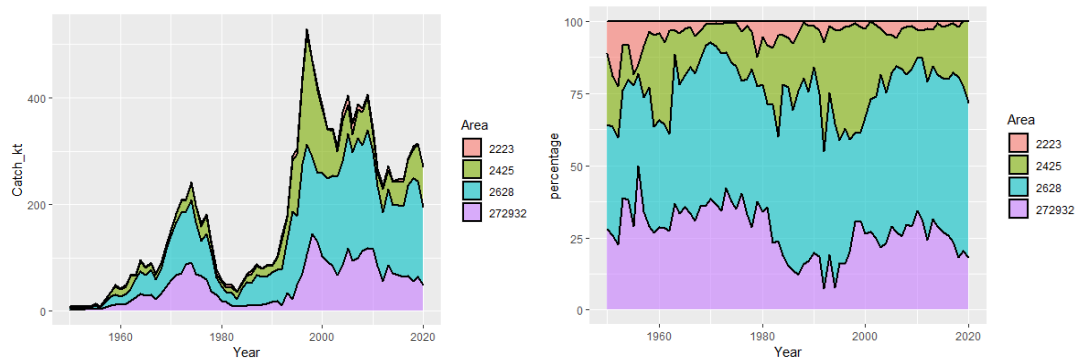


Figure 5.3.1. Sprat commercial catch by areas in the Baltic Sea, as absolute values (left panel) and relative distribution between the areas (right panel).

The quarterly distribution of total Baltic sprat catch has been relatively stable since 1995. About 40-50% of the sprat catch has generally been taken in Q1, whereas Q2 and Q4 have contributed roughly 20-25% each. The catches in Q3 have been low (3-8%) throughout the time-series (Fig. 5.3.2).

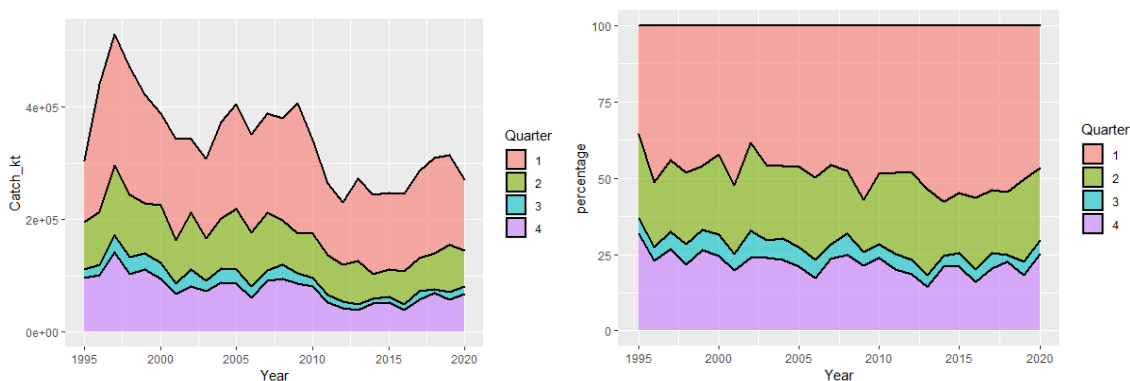


Figure 5.3.2. Total sprat commercial catch in the Baltic Sea (SDs 22-32) by quarter, as absolute values (left panel) and relative distribution between the quarters (right panel).

In the entire time series since 1995, sprat fishery in the main cod distribution area (SDs 24-26) has been concentrated mainly in Q1-Q2. Furthermore, more than 50% of the sprat catch taken in Q1-Q2 has been caught in SDs 25-26 (Fig. 5.3.3, Fig. 5.3.4). In Q1, the proportion of sprat catch taken in

SDs 25-26 increased since around 2015 to approx. 70%. Correspondingly, the annual catches taken in SDs 25-26 are largely concentrated in Q1 and Q2 (over 75 %) (Fig. 5.3.3, Fig. 5.3.4).

In Q4, about 40% of sprat catches are taken in the northern areas, in SDs 27&29-32, while these areas contribute lesser and more variable share to sprat catch in other quarters (about 20-30%). In most years, largest proportion of sprat catch in SDs 27&29-32 has been taken in Q1 (50% or more), apart from mid 1990s and most recent years, when Q4 fishery has been equally or more important than Q1 (Fig. 5.3.3).

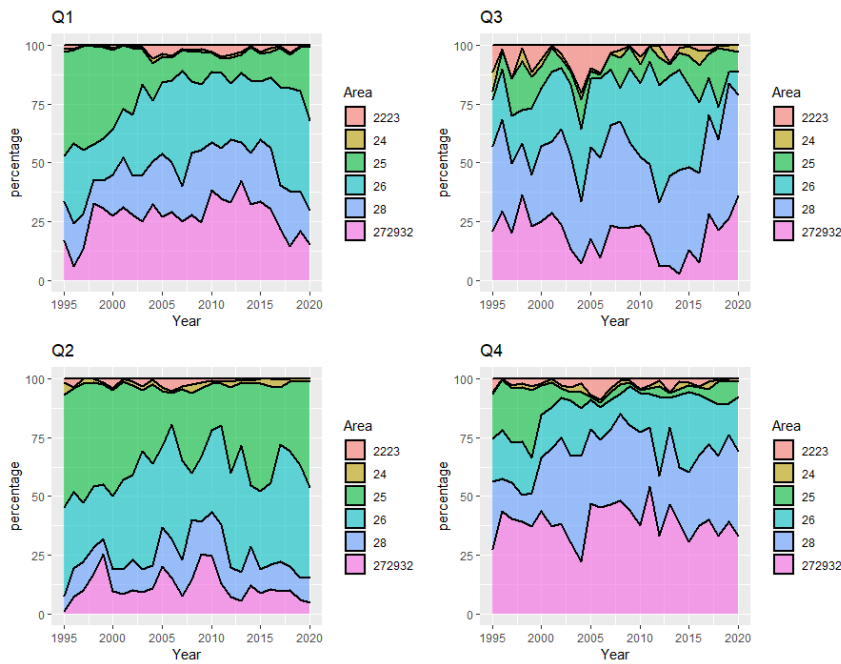


Figure 5.3.3. Distribution of sprat commercial catch in sub-areas (ICES Subdivisions), shown separately for quarters (Q).

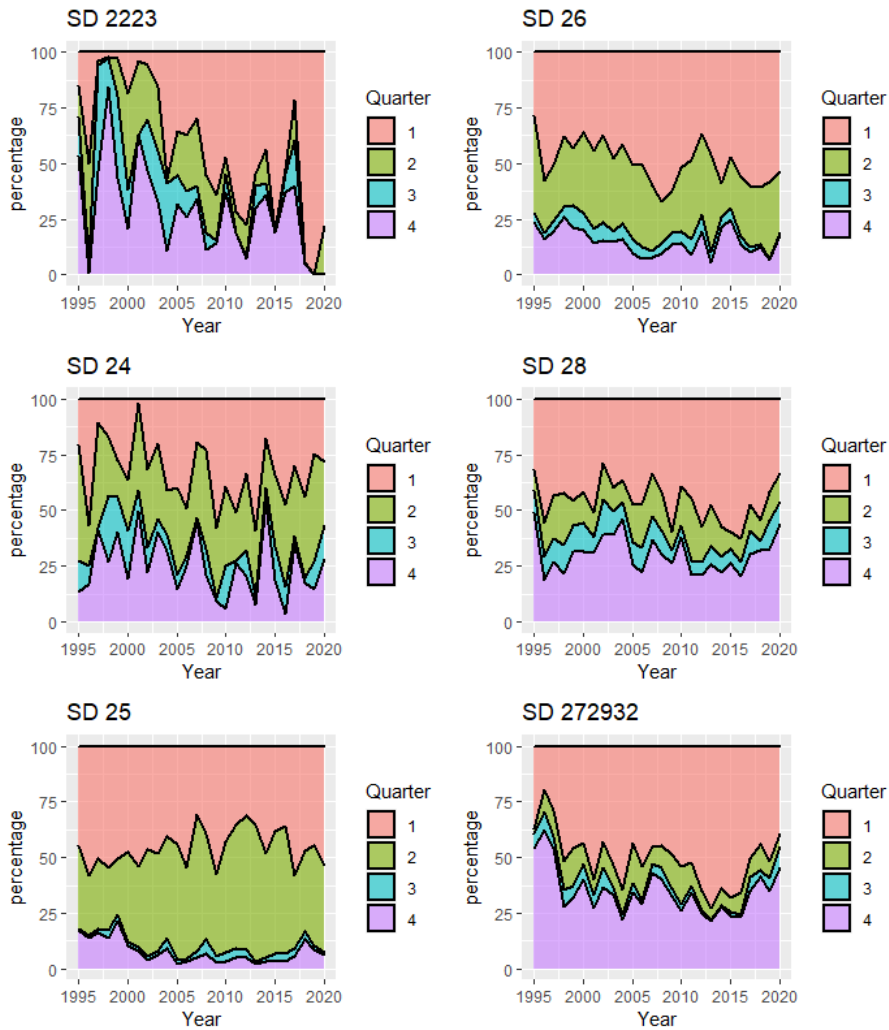


Figure 5.3.4. Distribution of sprat commercial catch between quarters, shown separately for ICES Subdivisions.

Sprat harvest rate

The harvest rate of sprat in Q4 in the distribution area of cod (SDs 24-26) is generally low, and relatively similar for all age-groups (Fig. 5.3.5). This is because the main part of sprat annual fisheries catch is taken in Q1-Q2, and the fishery in Q4 is to a larger extent concentrated in SDs 27& 29-32, i.e. further north of the distribution area of cod. Occasionally higher fishing mortality in SDs24-26 is apparent for age 0 in Q4, e.g. in 2015-2017. Age 0 harvest rate in Q4 is generally highest in SDs 25-26 (Fig. 5.3.6). For age-groups 1 and 2, harvest rates are generally highest in SDs 26 and 28, and relatively low in SD 25. For older sprat (ages 3+), the harvest rate is highest in SD 28 in Q4. These patterns are relatively stable since the 2000s, with no clear spatio-temporal trends in the harvest rate, though a considerable variability (Fig. 5.3.6).

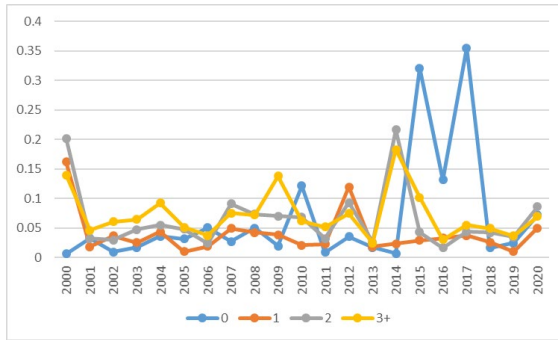


Figure 5.3.5. Average harvest rate of sprat in SDs 24-26, in Q4, for age-groups 0,1,2, and 3+.

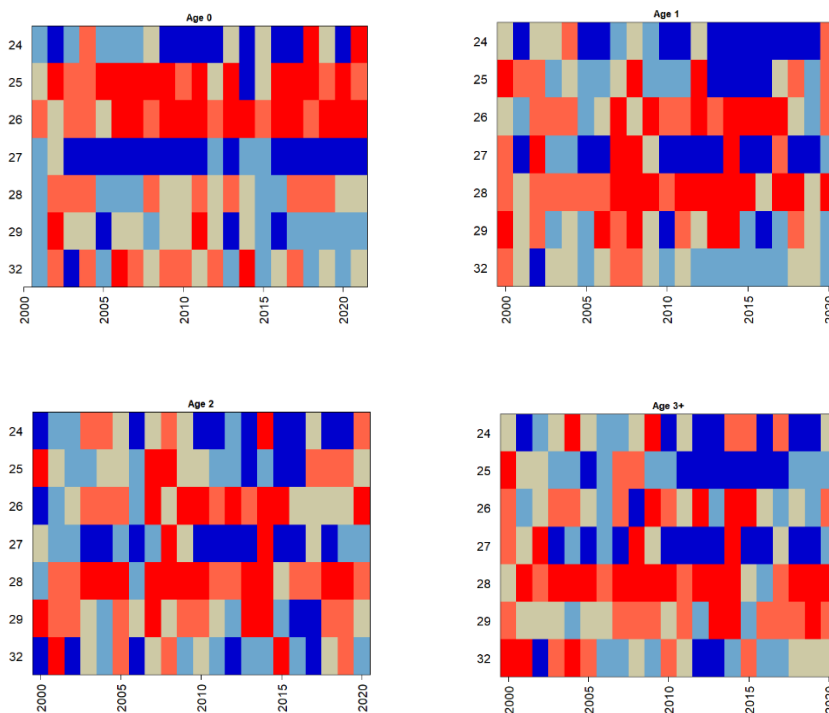


Figure 5.3.6. Relative harvest rate (catch/biomass) of sprat in different Subdivisions (y-axis) since the year 2000, for age groups 0, 1, 2 and 3+. The colors represent 20th percentiles of the range of values in the time series, with the blue representing the lowest and red the highest harvest rate.

Conclusions

There are no apparent major changes in spatial distribution of sprat commercial catches over time. Thus, there is no clear indication that fishery could be responsible for the more northerly distribution of sprat in last decades, resulting in reduced overlap between sprat and cod in Q4. Also, the Q4 sprat fishery in cod distribution area is relatively limited, as the main part of the fishery is taking place in Q1-Q2. Thus, overall fishing impact on sprat biomass in the distribution area of cod in Q4 is relatively limited. However, the fishing pressure on age 0 sprat in Q4 is highest within the main cod distribution area in SDs 25-26, with occasionally relatively high catches. This maybe important to consider, especially given the limited availability of especially age 0 sprat for cod in Q4 (see section 5.1) and low feeding level and sprat consumption of small cod (see section 5.2), which would mainly feed on small sprat.

6. Synthesis of knowledge

6.1 Drivers and processes associated with the state of the cod stock

The biomass of Eastern Baltic cod is currently at the lowest level recorded since 1946. The current low level of biomass is especially pronounced for commercial sized cod (> 35 cm in length; ICES 2022) while the spawning stock biomass trends in later years are much influenced by the substantial decline in size at first maturity that partly masks the decline in the number of larger individuals in the stock. Spawning stock biomass is a primary indicator used to measure the status of a fish stock, and together with fishing mortality, provides basis for fisheries management advice in ICES.

Biomass of a fish stock is determined by incoming recruitment and growth of individual fish, as well as mortality due to fisheries and natural causes (predation etc) (Fig. 6.1). In Eastern Baltic cod, according to the latest stock assessment, recruitment has a declining trend since 2012. Recent analyses of tagging data have shown that growth of the fish is currently lowest since the 1950s (Mion et al. 2021). Overall mortality of the stock (fishing+natural mortality) is currently estimated lower than it has been in the 1990s and early 2000s, when fishing mortality was high (Fig. 6.2). However, differently from the past, the present mortality of the stock is largely due to other causes than fishing, as natural mortality is estimated to have increased substantially since the 2000s, while fishing mortality has declined to a very low level (Fig. 6.2).

Recruitment, growth and natural mortality are thus all contributing to the present low biomass. In addition, several other biological parameters of the Eastern Baltic cod have deteriorated in recent years, which are likely interacting with one another, and reducing recruitment, growth and/or increasing natural mortality, thereby contributing to a low biomass (Fig. 6.1). Furthermore, a number of ecosystem and environmental drivers are hypothesized to be involved, the ones most discussed and debated in literature include poor oxygen conditions, limited food availability and quality and increasing number of grey seals.

Number of recent publications have addressed individual indicators and drivers of the Eastern Baltic cod stock health and a recent review is provided in Birgersson et al. (2022). In the sections below, we briefly describe the key drivers and processes that have been suggested in literature to potentially contribute to the poor state of the Eastern Baltic cod, and for which this project, together with earlier related EMFF projects, has provided additional information. We note that the list of issues covered here is not exhaustive and additional drivers and processes may be involved in the current poor state of cod. The order of the topics in the following sections does not reflect their relative importance.

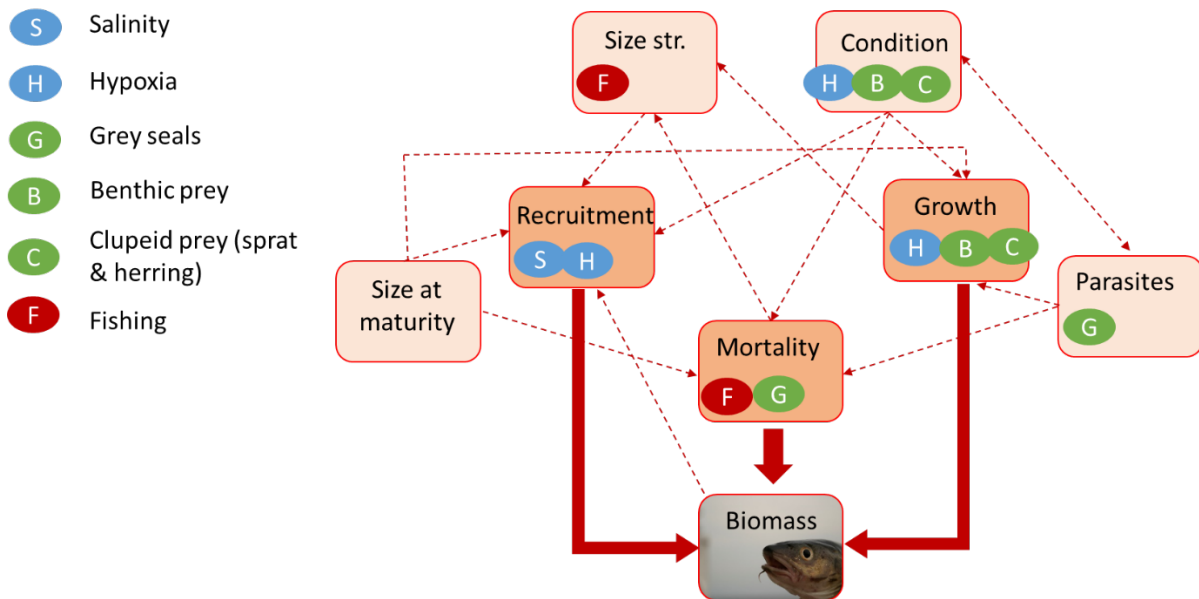


Figure 6.1. Schematic illustration of external drivers and interactions between biological parameters, directly or indirectly influencing stock biomass of the Eastern Baltic cod.

External drivers

Fishing

Fishing has been historically a dominant driver for the dynamics of Eastern Baltic cod biomass, being a major source of mortality. However, targeted fisheries for Eastern Baltic cod in EU has been banned since 2019. Fishing mortality has sharply declined since the 2000s and reached a historic low level in recent years. Consequently, fishing mortality is currently much lower than the mortality from other causes (Fig. 6.2).

In addition to removing stock biomass, fishing generally truncates population size structure (Berkeley et al. 2004; Hutchings and Baum, 2005). The newly constructed long time series of L95 for the Eastern Baltic cod (Fig. 1.4) provides a rare opportunity to demonstrate how this indicator has both increased and declined over time, roughly inversely to changes in fishing pressure. We note that L95 increased in the 1960s–1970s while fishing mortality was high, indicating that fishing was not the only factor affecting L95. Nevertheless, at least some association between L95 and fishing pressure is apparent until about the 2000s (Fig. 1.4). It is noteworthy that since the 2000s, L95 declined sharply, in parallel to and despite of the large reduction in fishing pressure. This indicates that a pronounced increase in natural mortality (ICES 2022) in combination with low growth (Mion et al. 2021) are responsible for the current low proportion of large individuals in the stock.

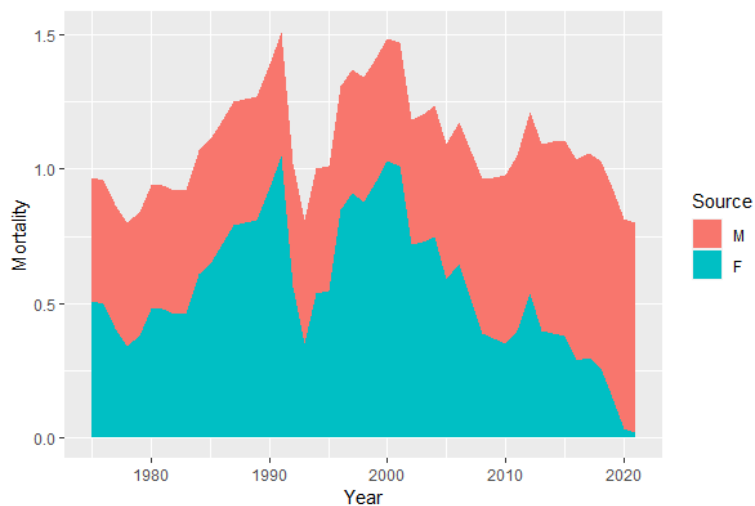


Figure 6.2. Dynamics of fishing (F) and natural mortality (M) of the Eastern Baltic cod, estimated from ICES stock assessment (ICES 2022).

Hypoxia

Oxygen deficiency in the Baltic Sea is associated to eutrophication, further amplified by increasing water temperatures. Oxygen conditions, together with salinity, are well-known to influence reproductive success of cod in the Eastern Baltic Sea (Köster et al. 2005). Compared to the well-known effects on recruitment, the effects of oxygen deficiency on other biological parameters of Eastern Baltic cod are less investigated, and the contribution of hypoxia to the current poor state of the stock is therefore still debated. It is suggested that hypoxia could affect cod body condition and growth directly by altering metabolism (Plambech et al. 2013) and causing physiological stress including loss of appetite (Brander, 2020; Chabot & Dutil, 1999). Moreover, hypoxia could affect cod growth and condition indirectly by reducing the availability of benthic prey (Neuenfeldt et al., 2020; Conley et al. 2009); and/or by contraction of suitable habitat which may induce density-dependent responses (Casini et al., 2016a; Limburg and Casini 2019). In contrast to recent decades, hypoxia is unlikely to have been responsible for the poor condition of cod in the 1940s–1950s (Fig. 1.1), because the oxygen status in the Baltic Sea was generally considerably better, and only started to gradually deteriorate after the 1950s (Carstensen et al. 2014).

Prey availability

Limited food availability could affect growth and body condition of the fish. Sprat and herring are important prey species for larger cod, while both small and larger individuals consume benthic organisms. Intake of benthic prey has reduced in recent decades, estimated from stomach data (Neuenfeldt et al. 2020), which is possibly interconnected with hypoxia (Neuenfeldt et al. 2020; Brander 2020).

Since 2000s, there is limited spatial overlap between cod and sprat, especially in autumn (Casini et al. 2011, 2016a; Eero et al. 2012), which may lead to food limitation for cod, and reduce its growth and condition. The analyses presented in Section 5.2 indicate that cod energy demand for sprat in most years since 2004 has been considerably higher than the available energy in sprat within the distribution area of cod (Fig. 5.2.5). Furthermore, the feeding level of smaller cod has considerably decreased in the 2000s compared to historical level (5.2.6). Some increase in older sprat in cod distribution area is observed in latest years (Fig. 5.1.5). However, the abundance of smallest sprat, which may be important prey for the presently small -sized cod, has remained low (Fig. 5.1.5).

Some association between sprat and cod condition is supported by historical data as the biomass of sprat was relatively low also in the, on average, low-condition periods in the 1980s (ICES 2022), in the 1940s–1950s (Eero 2012). Thus, it is plausible that prey availability has been involved in all cases, when deterioration of average condition of Eastern Baltic cod has been observed in the past 80 years (Fig. 1.1).

Grey seals

Grey seal (*Halichoerus grypus*) population has increased in the Baltic Sea since the 2000s. Grey seals are top predators and substantial part of their prey in the southwestern Baltic Sea has been estimated to comprise of cod (results from EMFF 33113_B_16_047; published in Eero 2019). However, the level of overall natural mortality of the cod stock caused by seal predation is unclear (Bryhn et al. 2022). An attempt to calculate possible cod mortality levels associated with seal predation suggested it to be a rather small fraction of the presently high overall natural mortality of cod, based on the recent level of grey seals and the fraction of these found in the southern Baltic Sea overlapping with cod (Eero 2019).

Another factor affecting cod is infection of parasitic nematode *Contracaecum osculatum* in cod livers. Grey seal is a final host for this parasite in the Baltic Sea. An increase in infections with the trophically transmitted *C. osculatum* in Eastern Baltic cod livers has been observed in the last decade concurrent with the increase in the grey seal population in the Baltic Sea (Haarder et al. 2014; Nadolna and Podolska, 2014). Several factors likely influence transmission rate of *C. osculatum* to cod livers (Sokolova et al. 2018), while some association between grey seal abundance and infection rate in cod is to be expected. This is supported by concurrent changes in these variables not only in recent years, but also previously in the historic record (Fig. 1.3).

The effects of *C. osculatum* on cod have been addressed in several earlier EMFF projects (33113-B16-070; 33113-B-16-071; 33113-B-17-110; 33113-B-20-161). The results of these studies have shown that cod that are heavily infected with *C. osculatum* in their liver have poorer body condition, destroyed liver tissue and show signs of a chronic liver disease, potentially contributing to increased natural mortality (Ryberg et al. 2020, 2022). A modelling study suggests that also growth rate of the fish decreases with increased infection load (Ryberg et al. 2023). Other studies have also noted a pattern of high numbers of *C. osculatum* in cod livers coinciding with low body condition of the fish (Sokolova et al. 2018; Horbowy et al. 2016). A connection between these indicators is plausible, as a high average *C. osculatum* load in cod corresponded to, on average, low body condition both in recent years and in the 1940s–1950s (Figures 1.1 and 1.3).

The degree to which there is a direct causal link between body condition and *C. osculatum* load is difficult to prove, as cod that are already in a poor condition may be more susceptible to liver worm – a ‘chicken or the egg’ dilemma. A study combining field data and laboratory experiments, suggests that the metabolic function of the liver is compromised by high parasite loads, which in turn may negatively affect the nutritional condition and overall health of the fish (Ryberg et al. 2020). On the other hand, cod in Åland Sea, which are even heavier infected with *C. osculatum* than the specimen in Bornholm Basin, are in a better condition (Section 2.2). One reason behind the less strong response to the infections of Åland cod could be that, in contrast to the cod from Bornholm Basin, the cod from Åland are in a good nutritional condition when infected, meaning that their immune system may be stronger and hence better at dealing with the nematode. This is supported by other investigations in the Åland Sea that found that when food availability was high, the effects of liver worm infection on cod condi-

tion or growth were small or insignificant (Birgersson et al. 2022 and references therein). These observations suggest that the initial condition at infection time may have a crucial influence on the severity of the infections to the host.

Interactions between indicators of stock health

Interactions between different biological parameters of a fish stock and associated effects are generally difficult to prove and relatively little information is available on some of these aspects. In the following sections, we describe some possible links (Fig. 6.1), either based on research on Eastern Baltic cod in particular or based on general knowledge on other stocks. We structure this section around recruitment, growth and natural mortality, which are the parameters directly determining biomass dynamics, and discuss how adverse developments in other stock health indicators may influence these parameters, with the effects propagating to biomass.

We note that the list of cod health indicators and their possible interactions covered here is not exhaustive. For example, we recognize that thiamine deficiency in Eastern Baltic cod has been reported (Engelhardt et al. 2020), which is not further elaborated on in the present report. Thiamine deficiency could reduce growth, condition and recruitment and increase natural mortality (Engelhardt et al. 2020), however studies on thiamine in Baltic cod are limited and more research is needed to determine whether there is a link to poor state of the Eastern Baltic cod stock (Birgersson et al. 2022).

Recruitment

Recruitment of the fish is generally considered at least to some extent associated with biomass of the spawning stock. Accordingly, at a critically low stock sizes, recruitment is impaired, and respective spawning stock biomass levels are considered as limit reference points for biomass in the context of fisheries management advice. The spawning stock biomass of Eastern Baltic cod stock is currently considered below such level (ICES 2022). Besides the stock size, recruitment of the Eastern Baltic cod is known to be largely environmentally driven, mainly by salinity and oxygen conditions affecting recruitment via different processes (Köster et al. 2005; 2017). At the present small size and poor condition of the fish, parental effects may have become important for reproduction as well.

Low maternal condition has been shown to impact not only the quantity but also the quality of spawning products and viability of offspring in other cod stocks (Marteinsdottir and Begg, 2002). Larger female cod produce higher number of eggs, and offspring quality may increase with parent age or reproductive experience (e.g., Marteinsdottir and Steinarsson, 1998; Trippel, 1998). Potential fecundity of Eastern Baltic cod is documented to be related to fish size and additionally affected by nutritional condition (Mion et al. 2018). Furthermore, the on average larger eggs of larger Eastern Baltic cod are neutrally buoyant at a lower salinity, and therefore have a greater survival probability under low salinity conditions compared to the eggs of smaller individuals (Vallin and Nissling, 2000; Hinrichsen et al., 2016).

Interestingly, the analyses conducted in the present project show that the small sized females have a remarkably high potential fecundity, around the double of what it was during 1970-2000 (Section 3.1). Thus, the Baltic cod is currently reproducing at a very small size with a high fecundity relative to their weight compared to previous years and compared to Atlantic cod in general. Also, gonadosomatic index was found to have remained high, while body condition of the fish has much deteriorated. Experimental investigations suggest that good quality viable offspring can be produced by these cod (Section 3.2), though this result is currently based on very few individuals. Altogether, the available knowledge indicates a high investment into reproduction, which likely occurs at the expense of growth, and probably also leading to increased mortality.

Growth

Long-term temporal trends in cod growth, estimated from tagging data (Mion et al., 2021) have been relatively similar to the developments in body condition (Fig. 1.1), and both growth and condition of the Eastern Baltic cod are considered to be influenced by the same external drivers (e.g. hypoxia, prey availability etc). Thus, some association between condition and growth is plausible and likely, also supported by knowledge on other stocks (EMFF 33113_B_16_047 published in Eero 2019). Furthermore, reduced size at maturation, in combination with high reproductive investment (Section 3), is expected to lower growth due to energy being allocated to maturation. In addition, a high liver worm load is associated with low body condition and presumably also growth of the fish (Ryberg et al. 2023). Low growth, in turn, contributes to truncated size structure (Fig. 6.1).

Natural mortality

Poor condition/growth has been suggested to increase natural mortality for a number of species (Adams et al., 1982; Henderson et al., 1988; Gislason et al., 2010). Critically low body condition is suggested to also contribute to the increased natural mortality of the Eastern Baltic cod (Casini et al. 2016b), based on the experimental results of Dutil and Lambert (2000). In addition, a high infection load of *C. osculatum* in cod livers likely causes mortality (Horbowy et al. 2016; Ryberg et al. 2020; 2022; 2023). Furthermore, the present unprecedentedly small size at maturation (Fig. 1.2), in combination with poor body condition (Fig. 1.1), is expected to cause mortality due to energy costs associated with reproduction (Lambert and Dutil, 2000; Brosset et al. 2016). The high natural mortality, in turn, contributes to the truncated size structure of the stock (Fig. 6.1).

6.2 Future perspectives & management challenges

The Eastern Baltic cod stock is currently in an unprecedentedly poor state, in a time scale of the past 80 years. This is concerning not only biomass, but also all other investigated biological parameters that provide an indication of the health of the stock, including body condition, size at maturity, liver worm load, length structure and spatial distribution of the stock (Section 1; Fig. 6.3; Eero et al. 2023). The present exceptionally poor state of the stock on all metrics suggests that more drivers and mechanisms are having simultaneous adverse effects than has been the case in the past, which complicates our understanding of the recovery potential of the stock.

Similar poor levels have occurred for some of the indicators (body condition, *C. osculatum* load) in the 1940s-1950s and subsequently improved, suggesting that recovery from such indicator states is possible. Also, the fact that healthier cod are still found in some parts of the Baltic Sea today (Åland; Section 2.2) provides some optimism. However, these healthier cod in Åland Sea are relatively few in numbers and it is unclear whether the apparently better conditions in this area could support the improvement of the health status of the overall population in the Eastern Baltic Sea. Furthermore, the current poor state of cod by all metrics in the main distribution area of the stock may compound the difficulty of recovery of the stock, as the poor states of individual indicators may re-inforce one another (Fig. 6.1). This is especially in the light of a high natural mortality, which has been considered as one of the reasons hampering recovery of other collapsed cod stocks (Swain and Benoît, 2015).

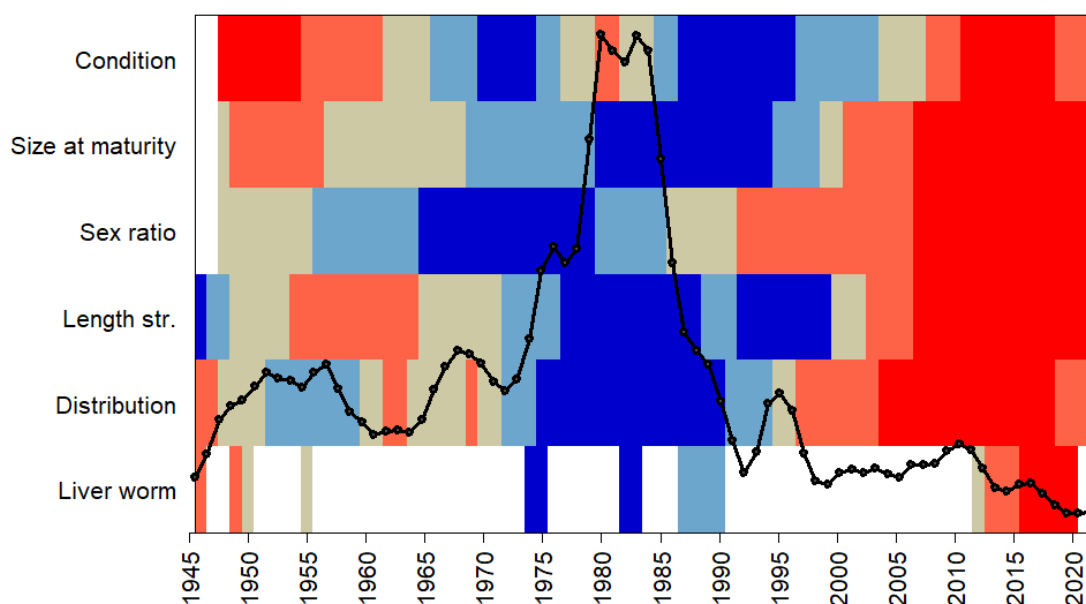


Figure 6.3. Long-term relative changes in health indicators of Eastern Baltic cod. The colors represent 20th percentiles of the range of smoothed average values observed in the time series, with the blue representing the best and red the worst state. These are overlaid with trends in biomass of commercial sized cod (≥ 35 cm; black line), estimated from stock assessment (Based on Eero et al. 2023).

In contrast to recent years, the environmental-ecological conditions that prevailed in the Baltic Sea in the period from the late 1970s to early 1990s benefitted the cod stock in nearly all aspects, with generally the most favorable indicator states recorded (Fig. 6.3). From the long-term data, it is apparent that the good state of the stock in this period was exceptional rather than representing the average historical baseline. It is therefore unrealistic to regard such indicator levels as targets for stock recovery. The period from the 1940s–1970s is generally characterized by an intermediate health status of the stock, and is probably more realistic as a recovery target, as argued by Tomczak et al. (2022), who suggested this time period as a reference for the Baltic Sea ecosystem.

Future developments in the Eastern Baltic cod stock and its recovery potential are primarily dependent on growth, recruitment and natural mortality, and the associated drivers and processes. Recruitment development in recent years is a concern as it has generally a declining trend since 2012 (ICES 2022). This is not only because of low biomass, as also recruitment produced per unit of spawning stock biomass has declined in later years (Fig. 1.2 a). The results presented in Section 3 suggest that production of viable offspring is still possible, at the presently small size and poor condition of spawners, which provides some optimism regarding recruitment in coming years. However, in a long term, conditions for cod reproduction in the Eastern Baltic Sea are forecasted to further deteriorate, which would reduce recovery potential of the stock. This is in relation to climate change and associated anticipated further decline in salinity in the Baltic Sea, and increase in temperature (MacKenzie et al. 2007; Lindegren et al. 2010), while higher water temperatures will increase oxygen consumption rates, thereby further reducing the size of cod spawning habitats (MacKenzie et al. 2007).

Poor oxygen conditions are considered to also lower cod body condition and growth. The increasing frequency of extensive summer hypoxia events in shallow water may have negative effects on growth (and ultimately survival) of particularly smaller cod (Section 4). On the other hand, increasing temper-

ature generally increases growth. Since cod in the eastern Baltic Sea seldom experience temperatures above their tolerance level, climate-related increases in water temperatures will likely not be the direct cause for reductions in growth in the near future - given that abundant food is available to sustain metabolic cost of living and growth (Section 4). However, even if sufficient food abundance is available, it is unclear whether the presently poorly conditioned small cod are at all able to forage on, for example, sprat, which requires small-scale investigations of the predation process (Section 5.2).

Management of the Eastern Baltic cod stock has traditionally focused on fisheries, in line with the dominant role of fishing in determining overall mortality of the stock back in time (Fig. 6.2). In recent years, when targeted cod fishing has been banned, fishing mortality has declined to a historic low level. Discards of cod still occur (ICES 2022) and cod is caught as bycatch in demersal fisheries for flatfish. Also, Eastern Baltic cod are caught together with the Western Baltic cod in SD 24. There are some uncertainties in the catch amounts in recent years, for example, due to low quotas that may have given incentives for misreporting of landings. However, these uncertainties are unlikely to change the current perception from stock assessment that fishing mortality in recent years is much lower compared to natural mortality that has increased substantially (Fig. 6.2). Thus, any further reductions in fisheries removals of the Eastern Baltic cod can have only a limited impact on overall mortality of the stock. At present low growth and high natural mortality, the stock biomass is projected to remain low, even in the absence of fishing (Eero et al. 2020). Furthermore, modified size selection of cod in fisheries catches can unlikely result in notable improvement in the size structure of the cod stock. It is because the fishing mortality is generally low and the lack of larger individuals is currently mainly due to low growth and high natural mortality.

As illustrated in Figure 6.1, the Eastern Baltic cod stock situation is currently considered influenced by a number of environmental and ecosystem drivers, as well as interactions between different parameters of stock health. Because of the complexity of the processes involved, it is difficult to predict whether and to what extent the stock status could be improved by management actions, regarding the drivers and processes that are at least to some extent under management control.

One of such factors that could be influenced by fisheries management is the availability of fish prey (especially sprat) in the distribution area of cod (Birgersson et al. 2022). Spatial overlap between cod and sprat is limited especially in autumn. The analyses of sprat fishing patterns showed that sprat fishery in the cod distribution area in autumn (Q4) is also relatively limited, as the main part of the sprat fishery is taking place in Q1-Q2 (Section 5.3). Thus, overall fishing impact on sprat biomass in the distribution area of cod in Q4 is relatively limited. However, the harvest rate and catches of smallest sprat (age 0) in Q4 are occasionally relatively high within the main cod distribution area in SDs 25-26. Furthermore, the available data on cod and sprat distribution (Section 5.1) as well as stomach data (Section 5.2) suggest that prey limitation for cod may be most pronounced regarding smaller sprat. Thus, the potential management regulations regarding sprat availability for cod could focus on reducing fishing pressure for the smallest sprat within the distribution area of cod. However, any possible improvement of cod stock situation resulting from spatial management of sprat fisheries is not possible to quantify. This is due to the complexity of food web processes, where cod growth and condition do not only depend on prey abundance (Neuenfeldt et al., 2020; Section 5.2 and Fig. 6.1).

Science is generally lagging behind in being able to quantify possible benefits to the stock resulting from management interventions influencing the ecosystem conditions (Eero et al. 2020). This is due to complexity of the factors involved, as illustrated in Fig 6.1, as several external factors and possible connections between different aspects of stock health are interacting with one another influencing recruitment, growth and/or mortality and ultimately stock biomass. No quantitative models are presently

available that could simultaneously consider the processes and drivers potentially involved (Fig. 6.1), and compare their relative impacts on fish growth, mortality and reproduction, and evaluate the effects of possible management measures.

Dedicated research may eventually improve our understanding of the processes involved in the present state of the Eastern Baltic cod and provide better guidance regarding aspects that are at least to some extent under management control. However, to track any progress towards recovery, continued regular monitoring of a wider range of stock health indicators is recommended. Furthermore, future stock assessment and management should consider multiple indicators of stock health, not only biomass, in defining overall stock status and appropriate management measures.

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