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Food for Thought

Eastern Baltic cod in distress: biological changes and challenges for stock assessment

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The eastern Baltic (EB) cod (*Gadus morhua*) stock was depleted and overexploited for decades until the mid-2000s, when fishing mortality rapidly declined and biomass started to increase, as shown by stock assessments. These positive developments were partly assigned to effective management measures, and the EB cod was considered one of the most successful stock recoveries in recent times. In contrast to this optimistic view, the analytical stock assessment failed in 2014, leaving the present stock status unclear. Deteriorated quality of some basic input data for stock assessment in combination with changes in environmental and ecological conditions has led to an unusual situation for cod in the Baltic Sea, which poses new challenges for stock assessment and management advice. A number of adverse developments such as low nutritional condition and disappearance of larger individuals indicate that the stock is in distress. In this study, we (i) summarize the knowledge of recent changes in cod biology and ecosystem conditions, (ii) describe the subsequent challenges for stock assessment, and (iii) highlight the key questions where answers are urgently needed to understand the present stock status and provide scientifically solid support for cod management in the Baltic Sea.

Keywords: data quality, eastern Baltic cod, ecosystem understanding, stock assessment.

Introduction

The Baltic Sea is known for being a data-rich region, with long time-series from biological and environmental monitoring. Stock assessment of the eastern Baltic (EB) cod (*Gadus morhua*) conducted by ICES extends back to the 1960s. The quantity and quality of data used in fish stock assessments have generally increased in recent years in conjunction with the introduction of the data collection regulation (EC, 2000) and framework (EC, 2008) in Europe. The models used to assess EB cod have developed over time, and in more recent years, an advanced state–space assessment model (SAM) has been applied (Nielsen and Berg, 2014).

Ecosystem processes, including environmental and ecological impacts on Baltic cod, have been studied for decades, resulting in a relatively comprehensive understanding of ecosystem functioning. Given the comparatively simple structure of the central Baltic foodweb, multispecies studies are well advanced (Horbowy, 2005; Casini *et al.*, 2009; ICES, 2012), and the Baltic Sea has been chosen as a forerunner for developing management plans taking into account species interactions. The exploitation status of EB cod was considered to have substantially improved since the stock assessment pointed to a rapid decline in fishing mortality below the management target in 2008. Moreover, cod abundance began to increase despite generally unfavourable ecosystem conditions for cod (Cardinale and Svedäng, 2011; Eero *et al.*, 2012a).

In light of recent positive trends in cod abundance and exploitations status, solid data collection, and in-depth knowledge of ecosystem interactions, it seems surprising that the analytical assessment of EB cod failed in 2014 (ICES, 2014a). Owing to large inconsistencies in the model outputs (e.g. retrospective bias) and unexplained trends in the available biological data (e.g. absence of larger cod), a reliable analytical assessment could not be conducted leaving the present stock status unclear. In this study, we summarize the biological factors and data issues that have so far been considered to contribute to poor understanding of the present stock status (ICES, 2014a, b, 2015). The process to understanding the present ecology of cod in the Baltic Sea and solving the issues with stock assessment is ongoing and will likely continue in the coming years. Thus, our aim in this study is not to provide answers to the issues identified, but to facilitate a common view of the challenges being faced and highlight the key questions, particularly those relevant to stock assessment, to assist in prioritization of research efforts.

Biological changes in the EB cod stock

Increase in recruitment

The abundance and biomass of <30-cm cod (proxy for juveniles, ICES, 2014a) has increased up to fivefold in recent years and is currently among the highest since the 2000s (Figure 1). This is despite the absence of major Baltic inflows in this period (Lehmann *et al.*, 2014; Plikshs, 2014), which is expected to impact negatively on cod egg survival and suggests that the recruitment dynamics of cod in the Baltic Sea are more complex than previously thought (Köster *et al.*, 2005). Evidence from recent hydrographic and ichthyoplankton surveys suggests that the following processes may have contributed to increased recruitment success: (i) regularly occurring minor inflows into the Bornholm Basin (Lehmann *et al.*, 2014); (ii) regular utilization of the Arkona Basin for spawning by the eastern stock (Bleil *et al.*, 2009; Hüssy, 2011); (iii) extended spawning season (Neumann *et al.*, 2014) with high larval survival in certain months, i.e. spreading risk (ICES, 2015); (iv) improved nutritional condition/growth of larvae in certain years and areas

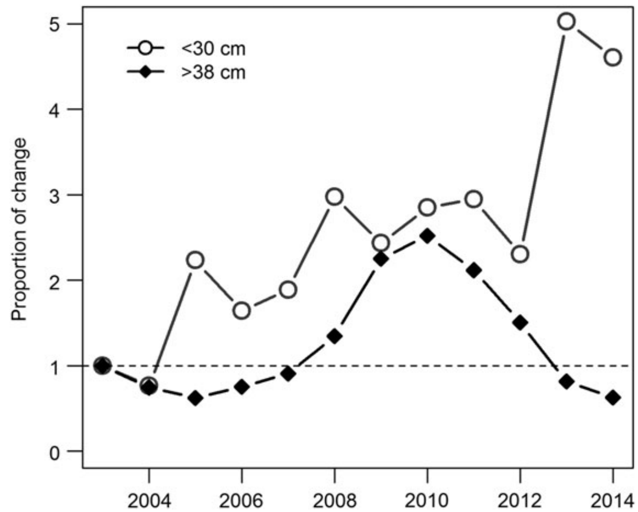

Figure 1. Change in biomass of juvenile (<30 cm) and market-size cod (>38 cm) in 2004–2014 relative to 2003, based on data from International Bottom Trawl Surveys (geometric mean of Q1 and Q4 surveys) in the entire central Baltic Sea.

(Huwer *et al.*, 2011, 2014); and (v) a decline in cod egg predation by sprat (*Sprattus sprattus*) and herring (*Clupea harengus membras*) (Neumann *et al.*, 2014).

Limited distribution range

In the Bornholm Basin, cod densities in the late 2000s were estimated to be close to the historically highest level observed since the 1970s (Eero *et al.*, 2012b). Yet, the recent increase in cod abundance and locally high densities have not resulted in an expansion of the stock to the northeast (e.g. Gotland Basin), where cod have historically been abundant. Possible hypotheses why cod is not expanding its distribution range in the Baltic Sea include: (i) low oxygen in deeper waters in the EB basins impedes a northeastward expansion of cod (Köster *et al.*, 2009); (ii) local subpopulations in the northeast are extinct; and (iii) homing behaviour characteristic for Atlantic cod (e.g. Zemeckis *et al.*, 2014) hampers occupying other areas because successful reproduction of EB cod is currently largely limited to the Bornholm Basin (Köster *et al.*, 2009).

Decline in nutritional condition of adult cod

Nutritional condition of adult cod has been continuously declining since the early 1990s. However, since the mid-2000s, when cod abundance began to increase, the proportion of cod with a very low condition index (Fulton's $K < 0.8$) increased rapidly to 20% in recent years in the Bornholm Basin (Figure 2), where cod densities are highest (Eero *et al.*, 2012b). The decline in cod condition is evident in all offshore areas of the central Baltic. It has been suggested that growth in terms of length-at-age has also declined (Svedäng and Hornborg, 2014). Hypothesized reasons for deteriorating nutritional condition include: (i) low availability of fish prey in the main distribution area of cod (Eero *et al.*, 2012b); (ii) shortage of benthic prey given the stagnation period and frequent oxygen depletion at the bottom (Carstensen *et al.*, 2014); (iii) increased extent of low oxygen areas that could affect cod growth directly via altering metabolism (Plambech *et al.*, 2013) and reducing food intake (Teschner *et al.*, 2010; ICES, 2014c, 2015); (iv) increased infestation with parasites (Petrushevski and Shulman, 1955; Mehrdana *et al.*,

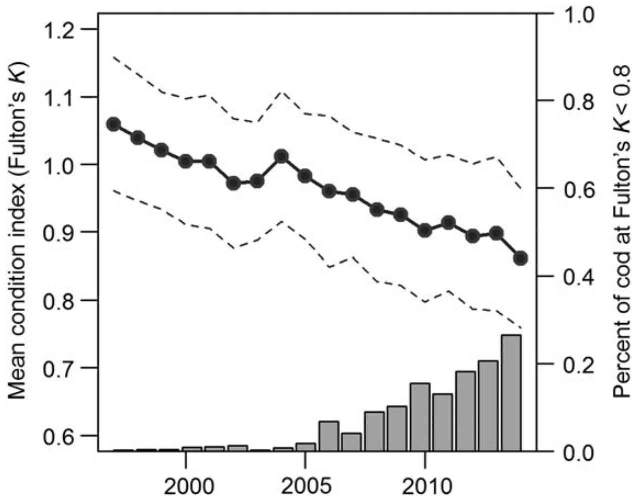

Figure 2. Average condition (Fulton's K) of 40–60 cm cod in Bornholm Basin with the standard deviation (the lines) and the proportion of cod with Fulton's $K < 0.8$ (the bars).

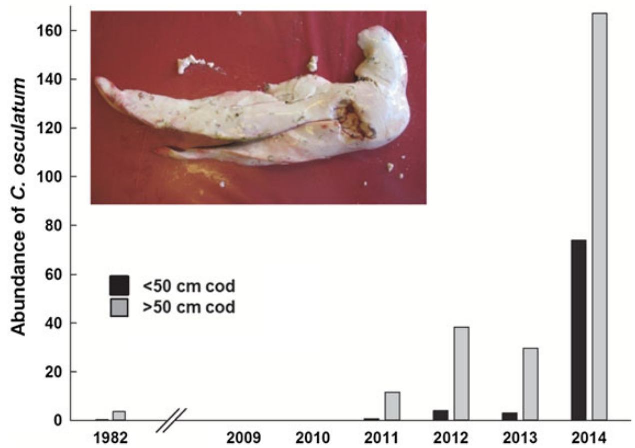

Figure 3. Abundance (number of parasites per fish with infected and uninfected included) of the parasite *C. osculatum* in cod liver [data from Bornholm and Gdańsk Basins, ca.100–300 cod sampled year^{-1}; modified from Haarder *et al.* (2014), Mehrdana *et al.* (2014), and M. Podolska *et al.* (pers. comm.); no data available for 2009–2010]. Photo shows a cod liver infected with *C. osculatum* (K. Buchmann).

2014), although this connection is not supported in all available studies (e.g. Lunneryd *et al.*, 2015); and (v) size selectivity in commercial fisheries, which may have contributed to a larger proportion of smaller fish in the stock that may have led to density-dependent effects (Svedäng and Hornborg, 2014).

Increased parasite infestation due to seals

During most years covered by stock assessment, the abundance of natural enemies for cod in the Baltic Sea, i.e. grey seals (*Halichoerus grypus*), has been low. Since the beginning of the 2000s, the grey seal population has increased threefold and was estimated to be ca. 28 000 individuals in 2012 in the entire Baltic (Härkönen *et al.*, 2013). Cod is a transport host for two seal parasite species: cod worm (*Pseudoterranova decipiens*) and liver worm (*Contracaecum osculatum*; Mehrdana *et al.*, 2014). Recent investigations have documented a marked increase in prevalence and intensity of infestation for both parasites (Figure 3), compared with the 1980s when seal abundance was lower (Buchmann and Kania, 2012; Haarder *et al.*, 2014; Mehrdana *et al.*, 2014; Nadolna and Podolska, 2014).

Absence of larger cod

Standard research surveys covering the entire central Baltic Sea suggest that the abundance of market-sized (>38 cm) cod started to increase in 2007, consistent with the observed increase in recruitment and anticipated reduction in fishing mortality. In contrast, in 2013–2014, the numbers and biomass of larger cod in survey catches dropped to the levels observed before the stock increase in the mid-2000s (Figure 1), and the absence of larger cod is confirmed by the fisheries. Reasons for the reduced abundance of larger cod are unclear because the extent to which it is associated with increased mortality of older cod and/or low individual growth is unknown. The key to distinguishing between the potential effects of reduced growth and increased mortality lies in accurate age information, which, unfortunately, is not available (see below).

Overall ecosystem conditions for adult cod

One of the key events leading to the present unusual ecological situation for cod in the Baltic Sea was the relatively high reproductive success in the mid-2000s, despite the lack of major inflows of saline and oxygen-rich water from the North Sea. For adult cod, low oxygen concentration, which is characteristic for a stagnation period, is associated with several adverse influences including: (i) reduced habitat size (Köster *et al.*, 2009; Casini *et al.*, 2012) with an increasing risk for density-dependence effects; (ii) reduced metabolism and food intake with direct negative impacts on growth and condition (Hinrichsen *et al.*, 2011; ICES, 2014c); and (iii) deterioration of benthic prey availability (Carstensen *et al.*, 2014). This situation coincided with reduced abundance of clupeid prey in the main distribution area of cod compared with the 1990s (Eero *et al.*, 2012b), i.e. benthic and fish prey availability being low at the same time. In addition, the parasite infestation rate of cod due to seals has increased (e.g. Haarder *et al.*, 2014). This combination of relatively high recruitment with a number of adverse ecosystem conditions for adult cod (Figure 4) has, to our knowledge, not occurred earlier during the history of the EB cod assessment, causing limited understanding of present ecology and new challenges for stock assessment.

Challenges for stock assessment and management advice

The basic input data for an age-based stock assessment include commercial catch-at-age, relative abundance index at age (e.g. from research surveys), and biological information on natural mortality, mean weight, and maturity-at-age. Additionally, assessment models rely on certain assumptions, one of which is time-invariant catchability in the surveys used in the assessment. In the sections below, we describe how this input information to stock assessment is challenged by the recent changes in cod life history parameters and the Baltic Sea ecosystem described above.

Age information

Age reading of EB cod has always been considered difficult because of low contrast between seasonal growth zones and irregular growth patterns, resulting in significant differences in age interpretation between and within age readers (e.g. ICES, 1973, 2000, 2006).

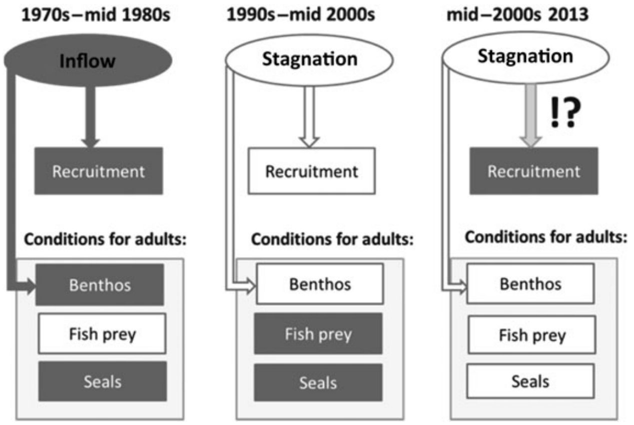

Figure 4. Schematic illustration of the unusual combination of ecological factors affecting cod in recent years (from mid-2000s to 2013) compared with earlier decades. Inflow and stagnation refer to hydrographical conditions (salinity and oxygen) of the Baltic Sea. Dark and white cells denote positive and negative status of a given factor for cod, respectively.

A simulation study that investigated the effect of national differences in age interpretation occurring before the 2000s on stock assessment concluded that the overall trends in stock status were broadly unaffected by age-reading errors (Reeves, 2003). Consequently, the application of standard age-based assessment methods has continued. Since 2007, inconsistencies in age data among countries have become more severe (Supplementary Figure 1). This was confirmed in a new age-reading calibration exercise in 2014 that documented even more pronounced disagreement in age interpretation among readers than the earlier exercises [see ICES (2014b) for details]. The reasons for increased discrepancies in age interpretation are not clear. Deteriorating condition and growth of cod is hypothesized to have aggravated the age-determination problems in recent years. A validation exercise where true age of small cod was determined by counting daily increments of otoliths indicated that some age readers were unbiased with respect to actual ages, i.e. their age readings of the young known-age fish below 3 years were, on average, accurate [see ICES (2014b) for details]. However, precision in age readings was low always. Furthermore, no age validations are available for cod older than 2 years to evaluate respective ageing errors. Sensitivity analyses of survey indices demonstrated a widely different perception of recent stock trends depending on the national origin of age information used (Supplementary Figure 2). Furthermore, differences in age interpretation led to contrasting mortality trajectories and more than threefold differences in current mortality levels obtained from survey analyses (Supplementary Figure 3). Similarly, fishing mortality estimates for recent years from exploratory analytical assessment analyses were sensitive to age information (ICES, 2014b).

Commercial catch

The quality of landings data of EB cod has historically suffered from underreporting; however, this is considered to have improved in recent years (ICES, 2014a). The situation may be different for discards, which are generally associated with uncertainties in the entire time-series. Discards of EB cod have increased in recent years (ICES, 2014a), possibly due in part to the poor nutritional condition and a large proportion of undersized cod. Anecdotal evidence from the fishery suggests that real discards may be higher than those reported through the discard sampling programmes and used in stock assessment. However, as the magnitude of real discards can currently not be quantified, it is unknown to what extent this is an issue for stock assessment.

Survey indices and catchability

Ambient hydrographic conditions can influence the horizontal (Köster *et al.*, 2003) and vertical (Schaber *et al.*, 2009) distribution of cod in the Baltic Sea that may introduce a positive or negative bias to catch rates in bottom trawl surveys used in the assessment. It is recognized that part of the cod stock is regularly found in pelagic waters; however, analyses conducted thus far have been inconclusive in quantifying the potential bias introduced to the indices from bottom trawl surveys. In recent years, catchability of cod may additionally be impacted by low nutritional condition. If length-/weight-at-age has also declined, this has likely changed catchability-at-age, invalidating the assumption of time-invariant catchability used in most stock assessment models (ICES, 2014b).

Growth

Undoubtedly, nutritional condition of EB cod has declined. However, due to uncertainties in age interpretation, it is not possible to reliably quantify the associated change in mean length-/weight-at-age. Some age interpretations suggest a substantial decline in mean weight-/length-at-age in recent years, which is not apparent in other data (Supplementary Figure 4). In an age-based stock assessment, data on mean weights are not directly used in the estimation procedure; however, these are applied to translate estimated stock abundance to biomass. In this way, uncertainties in weight-at-age also affect the calculation of fishing quotas corresponding to management options. To circumvent the age-reading issues, length-based and production models may be considered, which, however, still rely on growth parameters. Given the lack of validated age data to determine growth, the results from such models may be sensitive to the assumptions on growth applied (ICES, 2015).

Natural mortality

Natural mortality (an instantaneous annual rate for age groups 2 and older) of EB cod has been assumed constant and relatively low (0.2) in the entire time-series since 1966. In the present situation, natural mortality can be expected to have increased due to increased parasite infestation, which has been suggested to cause mortality in cod (Haarder *et al.*, 2014; Mehrdana *et al.*, 2014; M. Podolska *et al.* pers. comm.). Furthermore, low condition has been shown to increase natural mortality in cod (Dutil and Lambert, 2000). Linking natural mortality to condition of the EB cod has been considered (ICES, 2015), though the relationships available from laboratory experiments (e.g. Dutil and Lambert, 2000) may not be directly transferable to the field. Historically, a higher natural mortality ($\sim$0.4) was estimated for EB cod in the period before the start of the official stock assessment in the 1960s (Thurow, 1974), when cod condition was reported to be low. Assumptions on both the level and temporal changes in natural mortality interfere with the perception of current fishing mortality and stock size estimated from stock assessments.

Maturity

The present low nutritional condition and a relatively high parasite loading can be expected to affect reproductive potential for the stock (Kraus *et al.*, 2000). The present time-invariant maturity index applied in stock assessment for EB cod does not influence the perception of stock status in terms of fishing mortality or stock abundance. However, uncertainties in maturity may lead to a false perception of reproductive potential for the stock, influence reference points used in fisheries management, and bias expectations of future recruitment.

Bottlenecks in resolving the trouble

Large changes in ecosystem conditions and fish stocks regularly occur, and the recent developments with EB cod are not unique in this respect. For example, increased parasite infestation due to seals was observed in cod in Newfoundland and Labrador before the collapse of those stocks (Brattey *et al.*, 1990). A rapid increase in natural mortality and absence of larger individuals has been recorded for several demersal stocks in the Northwest Atlantic (Swain and Benoit, 2015). Furthermore, the example of Pacific halibut (*Hippoglossus stenolepis*) demonstrates large changes in growth as well as booms and busts in recruitment (Clark and Hare, 2002). These and similar experiences from elsewhere would be important to consider in seeking solutions to the present situation with EB cod.

It is also recognized that the solutions for improving the management of fish stocks under changing ecosystem conditions may not be entirely science-based, but involve developing management strategies and structure of the fisheries, which are more robust to the type of changes described. In this study, we focus on highlighting the key issues that should be given high priority from a scientific perspective to improve the assessment and management of EB cod. One such issue is information on the true age of cod that is required to be able to answer some of the key questions related to growth and mortality.

From a stock assessment perspective, age-based models are sensitive to age information, and a different perception of current stock size and mortality of EB cod can be obtained depending on the age data used. Non-age-structured assessment models (e.g. length-based or production models) exist and have also been explored for the EB cod (ICES, 2015). However, age information is still crucial to non-age-structured models where growth is an important parameter, and information on true age is needed to validate recent developments in growth. Alternatively, ageing errors can be taken into account or estimated in an age-based model (e.g. Punt *et al.*, 2008). Such an approach is also being explored for the EB cod (ICES, 2015). Nevertheless, information on true age would be useful to quantify the ageing errors, especially in a case like the EB cod, where ageing errors are mixed with other uncertainties in the assessment input and model parameters, such as natural mortality and the assumption of constant catchability. These uncertainties could possibly also be reduced if validated age information was available. Technically, it is possible to implement time-varying survey catchability in the SAM model that has been used to assess the EB cod. However, the potential changes in catchability-at-age are interlinked to inconsistent age readings, which would need to be solved first (ICES, 2014b). Furthermore, application of some of the existing methods for estimating natural mortality (e.g. Pauly, 1980) is currently hampered due to a lack of reliable growth information.

From a management perspective, the decline in the abundance of larger cod is one of the most significant stock developments observed in recent years, independent of stock assessment uncertainties. For adequate management advice, it must be emphasized to understand the extent to which this decline is associated with the absence of older individuals. Low abundance of older cod in combination with relatively high abundance of juveniles would imply that mortality must be substantially higher than previously anticipated. In contrast, if the present abundant smaller individuals include older fish, this would suggest a substantial reduction in growth. Depending on the guiding mechanism, appropriate management actions could go in opposite directions. Lessons from some of the most dramatic stock collapses in history, such as the groundfish stocks in Atlantic Canada from the late 1980s to the early 1990s, warn against being overly optimistic in cases of uncertainties in stock assessment (Walters and Maguire, 1996; Lilly *et al.*, 2008). Thus, a precautionary approach is generally recommended, which would be appropriate if mortality is suspected to be high. On the other hand, if the absence of larger cod is mainly due to low growth, lowering fishing pressure may not be helpful in such a situation.

From an ecological perspective, a number of new questions have emerged that need to be investigated to understand the mechanisms and ecosystem processes behind the recent developments in cod, including the causes for low nutritional condition/growth, and likely increase in natural mortality. Furthermore, relating growth and condition to individual egg production as well as viability of offspring is relevant to be able to foresee future developments for Baltic cod. Explaining the absence of larger cod and being able to quantify growth are essential for understanding the present ecology and drivers of the central Baltic Sea ecosystem, where cod is the main predator fish species. Thus, knowledge of whether there is massive mortality of larger cod taking place or drastic reduction in growth has implications for interpreting the present foodweb and ecosystem interactions. Consequently, obtaining validated age/growth information is also important in the context of ecosystem-based management.

Why is age determination in EB cod so difficult? The problems interpreting EB cod otoliths are likely caused by the coupled effects of specific hydrographic characteristics of the Baltic Sea in terms of thermal stratification, large seasonal variability in food consumption of cod, and vertical migration behaviour (Hüssy *et al.*, 2009, 2010; Hüssy, 2010). Furthermore, the long spawning season of Baltic cod could contribute to different otolith structures depending on hatch date (Rehberg-Haas *et al.*, 2012). Over the last four decades, different expert groups have tried to determine the magnitude of this problem, and attempts have been made to standardize age interpretation through calibration exercises (e.g. ICES, 1973, 2000, 2006), but without success. Unfortunately, age information has further deteriorated in recent years just when accurate growth information is urgently required, given the unusual ecological situation for cod and the developments in the stock that need to be understood.

This calls for direct age-validation methods. One such method is counting daily otolith increments, which is, however, only possible for cod up to 3 years of age (Hüssy, 2010; Hüssy *et al.*, 2010). For larger cod, a suite of methods based on otolith isotope composition is known to have great potential. These include bomb radiocarbon (Campana, 1997; Campana and Jones, 1998), radiochemical dating of the nucleus, based on the decay of naturally occurring radioisotopes (Burton *et al.*, 1999; Cailliet *et al.*, 2001), as well as patterns in stable oxygen isotopes owing to the link between $\delta^{18}O$ incorporation and environmental temperature (Høie and Folkvord, 2006). One of the most reliable approaches would likely be external tagging of fish and concurrent chemical marking of the otolith. This approach was used, for example, for European hake (*Merluccius merluccius*), where age reading was a similar problem and age validation was eventually achieved through a large-scale tag–recapture programme which ended decades of discussion regarding otolith zone interpretation (de Pontual *et al.*, 2006). For EB cod, tagging experiments have earlier been suggested in response to historically known difficulties with age interpretation (e.g. ICES, 2006), but have so far not been implemented in practice. The present situation calls for international mark-and-recapture programmes for Baltic cod to be initiated to evaluate traditional age readings and calibrate alternative methods such as those listed above. This would be an important step in reaching long-term sustainable solutions to many of the present challenges with the cod assessment and management and enhancing ecosystem understanding.

Supplementary data

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

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References

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

Brattey, J., Bishop, C. A., and Myers, R. A. 1990. Geographic distribution and abundance of *Pseudoterranoua decipiens* (Nematoda: Ascaridoidea) in the musculature of Atlantic cod, *Gadus morhua*, from Newfoundland and Labrador. *In* Population Biology of Sealworm (*Pseudoterranova decipiens*) in relation to its intermediate and seal hosts, pp. 67–82. Ed. by W. D. Bowen. Canadian Bulletin of Fisheries and Aquatic Sciences, 222.

Buchmann, K., and Kania, P. W. 2012. Emerging *Pseudoterranova decipiens* (Krabbe, 1878) problems in Baltic cod, *Gadus morhua* L., associated with grey seal colonization of spawning grounds. Journal of Fish Diseases, 35: 861–866.

Burton, E. J., Andrews, A. H., Coale, K. H., and Cailliet, G. M. 1999. Application of radiometric age determination to three long-lived fishes using 210Pb:226Ra disequilibria in calcified structures: A review. American Fisheries Society Symposium, 23: 77–87.

Cailliet, G. M., Andres, A. H., Burton, E. J., Watters, D. L., Kline, D. E., and Ferry-Graham, L. A. 2001. Age determination and validation studies of marine fishes: Do deep-dwellers live longer? Experimental Gerontology, 36: 739–764.

Campana, S. E. 1997. Use of radiocarbon from nuclear fallout as a dated marker in the otoliths of haddock, *Melanogrammus aeglefinus.* Marine Ecology Progress Series, 150: 49–56.

Campana, S. E., and Jones, C. M. 1998. Radiocarbon from nuclear testing applied to age validation of black drum, *Pogonias cromis*. Fishery Bulletin US, 96: 185–192.

Cardinale, M., and Svedäng, H. 2011. The beauty of simplicity in science: Baltic cod stock improves rapidly in a "cod hostile" ecosystem state. Marine Ecology Progress Series, 425: 297–301.

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

Casini, M., Blenckner, T., Möllmann, C., Gårdmark, A., Lindegren, M., Llope, M., Kornilovs, G., *et al.* 2012. Predator transitory spillover indices trophic cascades in ecological sinks. Proceedings of the National Academy of Sciences of the USA, 109: 8185–8189.

Casini, M., Hjelm, J., Molinero, J. C., Lövgren, J., Cardinale, M., Bartolino, V., Belgrano, A., *et al.* 2009. Trophic cascades promote threshold-like shifts in pelagic marine ecosystems. Proceedings of the National Academy of Sciences of the USA, 106: 197–202.

Clark, W. G., and Hare, S. R. 2002. Effects of climate and stock size on recruitment and growth of Pacific halibut. North American Journal of Fisheries Management, 22: 852–862.

de Pontual, H., Groison, A-L., Piñeiro, C., and Bertignac, M. 2006. Evidence of underestimation of European hake growth in the Bay of Biscay, and its relationship with bias in the agreed method of age estimation. ICES Journal of Marine Science, 63: 1674–1681.

Dutil, J. D., and Lambert, Y. 2000. Natural mortality from poor condition in Atlantic cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciences, 57: 826–836.

European Commission (EC). 2000. Council regulation no. 1543/2000 establishing a community framework for the collection and management of the data needed to conduct the common fisheries policy. Official Journal of the European Union, L 176: 1–16.

European Commission (EC). 2008. EC Council Regulation No. 199/2008 of 25 February 2008 concerning the establishment of a community framework for the collection, management and use of data in the fisheries sector and support for scientific advice regarding the Common Fisheries Policy. Official Journal of the European Union, L 60: 1–12.

Eero, M., Köster, F. W., and Vinther, M. 2012a. Why is the eastern Baltic cod recovering? Marine Policy, 36: 235–240.

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

Haarder, S., Kania, P. W., Galatius, A., and Buchmann, K. 2014. Increased *Contracaecum osculatum* infection in Baltic cod (*Gadus morhua*) livers (1982–2012) associated with increasing grey seal (*Halichoerus gryphus*) populations. Journal of Wildlife Diseases, 50: 537–543.

Härkönen, T., Galatius, A., Bräeger, S., Karlsson, O., and Ahola, M. 2013. HELCOM Core Indicator of Biodiversity: Population growth rate, abundance and distribution of marine mammals. HELCOM, www.helcom.fi.

Hinrichsen, H-H., Huwer, B., Makarchouk, A., Petereit, C., Schaber, M., and Voss, R. 2011. Climate-driven long-term trends in Baltic Sea oxygen concentrations and the potential consequences for eastern Baltic cod (*Gadus morhua*). ICES Journal of Marine Science, 68: 2019–2028.

Horbowy, J. 2005. The dynamics of Baltic fish stocks based on a multispecies stock production model. Journal of Applied Ichthyology, 21: 198–204.

Høie, H., and Folkvord, A. 2006. Estimating the timing of growth rings in Atlantic cod otoliths using stable oxygen isotopes. Journal of Fish Biology, 68: 826–837.

Huwer, B., Clemmesen, C., Grønkjær, P., and Köster, F. W. 2011. Vertical distribution and growth performance of Baltic cod larvae—Field evidence for starvation-induced recruitment regulation during the larval stage? Progress in Oceanography, 91: 382–396.

Huwer, B., Hinrichsen, H. H., Böttcher, U., Voss, R., and Köster, F. W. 2014. Characteristics of juvenile survivors reveal spatio-temporal differences in early life stage survival of Baltic cod. Marine Ecology Progress Series, 511: 165–180.

Hüssy, K. 2010. Why is age determination in Baltic cod (*Gadus morhua* L.) so difficult? ICES Journal of Marine Science, 67: 1198–1205.

Hüssy, K. 2011. Review of western Baltic cod (*Gadus morhua*) recruitment dynamics. ICES Journal of Marine Science, 68: 1459–1471.

Hüssy, K., Hinrichsen, H. H., Fey, D. P., Walther, Y., and Velasco, A. 2010. The use of otolith microstructure to estimate age in adult Eastern Baltic cod (*Gadus morhua* L.). Journal of Fish Biology, 76: 1640–1654.

Hüssy, K., Mosegaard, H., Nielsen, B., and Worsøe Clausen, L. 2009. Using data storage tags to link otolith macrostructure in Baltic cod (*Gadus morhua* L.) with environmental conditions. Marine Ecology Progress Series, 378: 161–170.

ICES. 1973. Report of the Working Group for Assessment of Demersal Stocks in the Baltic. ICES Document CM 1973/F: 6. Charlottenlund, Denmark. 32 pp.

ICES. 2000. Report of the Study Group on Baltic Cod Age Reading (SGBCAR). ICES Document CM 2000/H: 01. Karlskrona, Sweden. 35 pp.

ICES. 2006. Report of the Study Group on Ageing Issues of Baltic Cod (SGABC). ICES Document CM 2006/BCC: 08. Gdynia, Poland. 49 pp.

ICES. 2012. Report of the Workshop on Integrated/Multispecies Advice for Baltic Fisheries (WKMULTBAL), 6–8 March 2012. ICES Document CM 2012/ACOM: 43, Charlottenlund, Denmark.

ICES. 2014a. Report of the Baltic Fisheries Assessment Working Group (WGBFAS), 3–10 April 2014 ICES HQ. ICES Document CM 2014/ACOM: 10. Copenhagen, Denmark.

ICES. 2014b. Report of the Workshop on Scoping for Integrated Baltic Cod Assessment (WKSIBCA), 1–3 October 2014. ICES Document CM 2014/ACOM: 62. Gdynia, Poland.

ICES. 2014c. Report of the Study Group on Spatial Analyses for the Baltic Sea (SGSPATIAL), 4–6 November 2014. ICES Document CM 2014/SSGRSP: 08. Gothenburg, Sweden.

ICES. 2015. Report of the Benchmark Workshop on Baltic Cod Stocks (WKBALTCOD), 2–6 March. ICES Document CM 2015/ACOM: XX. Rostock, Germany.

Kraus, G., Müller, A., Trella, K., and Köster, F. W. 2000. Fecundity of Baltic cod: Temporal and spatial variation. Journal of Fish Biology, 56: 1327–1341.

Köster, F. W., Möllmann, C., Hinrichsen, H-H., Tomkiewicz, J., Wieland, K., Kraus, G., Voss, R., *et al.* 2005. Baltic cod recruitment—The impact of climate and species interaction. ICES Journal of Marine Science, 62: 1408–1425.

Köster, F. W., Schnack, D., and Möllmann, C. 2003. Scientific knowledge on biological processes potentially useful in fish stock predictions. Scientia Marina, 67 (Suppl 1): 101–127.

Köster, F. W., Vinther, M., MacKenzie, B. R., Eero, M., and Plikshs, M. 2009. Environmental effects on recruitment and implications for biological reference points of eastern Baltic cod (*Gadus morhua*). Journal of Northwest Atlantic Fishery Science, 41: 205–220.

Lehmann, A., Hinrichsen, H-H., Getzlaff, K., and Myrberg, K. 2014. Quantifying the heterogeneity of hypoxic and anoxic areas in the Baltic Sea by a simplified coupled hydrodynamic-oxygen consumption model approach. Journal of Marine Systems, 134: 20–28.

Lilly, G. R., Wieland, K., Rothschild, B. J., Sundby, S., Drinkwater, K., Brander, K. M., Ottersen, G., *et al.* 2008. Decline and recovery of Atlantic cod (*Gadus morhua*) stocks throughout the North Atlantic. *In* Resiliency of Gadid Stocks to Fishing and Climate Change, pp. 39–66. Ed. by Kruse, G. H., Drinkwater, K., Ianelli, J. N., Link, J. S., Stram, D. L., Wespestad, V., and Woodby, D.. Alaska Sea Grant College Program, Fairbanks, AK. 364 pp.

Lunneryd, S -G., Ljungberg, P., Ovegård, M., Bernt, K., and Boström, M. 2015. Sälmask och spiralmask i torsk och rötsimpa i svenska kustvatten. Aqua Reports, 2015: 1 (in Swedish).

Mehrdana, F., Bahlool, Q. Z., Skov, J., Marana, M. H., Sindberg, D., Mundeling, M., Overgaard, B. C., *et al.* 2014. Occurrence of zoonotic nematodes *Pseudoterranova decipiens*, *Contracaecum osculatum* and *Anisakis simp*lex in cod (*Gadus morhua*) from the Baltic Sea. Veterinary Parasitology, 205: 581–587.

Nadolna, K., and Podolska, M. 2014. Anisakid larvae in the liver of cod (*Gadus morhua* L.) from the Southern Baltic Sea. Journal of Helminthology, 88: 237–246.

Neumann, V., Köster, F. W., Schaber, M., and Eero, M. 2014. Recovery in eastern Baltic cod: Is increased recruitment caused by decreased predation on early life stages? ICES Journal of Marine Science, 71: 1382–1392.

Nielsen, A., and Berg, C. W. 2014. Estimation of time-varying selectivity in stock assessments using state-space models. Fisheries Research, 158: 96–101.

Pauly, D. 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. Journal du Conseil International pour l'Exploration de la Mer, 39: 175–192.

Petrushevski, G. K., and Shulman, G. G. 1955. Infection of Baltic cod liver with roundworms. Trudy Akademii Nauk Litovskoj SSR Ser. B, 2: 119–125 (in Russian).

Plambech, M., van Deurs, M., Steffensen, J. F., Tirsgaard, B., and Behrens, J. W. 2013. Excess post-hypoxic oxygen consumption in Atlantic cod *Gadus morhua.* Journal of Fish Biology, 83: 396–403.

Plikshs, M. 2014. Impact of environmental variability on year class strength of Baltic cod (*Gadus morhua callarias* L.). Doctoral thesis. University of Latvia, Riga. 49 pp.

Punt, A. E., Smith, D. C., KrusicGolub, K., and Robertson, S. 2008. Quantifying age-reading error for use in fisheries stock assessment, with application to species in Australia's southern and eastern scalefish and shark fishery. Canadian Journal of Fisheries and Aquatic Sciences, 65: 1991–2005.

Reeves, S. A. 2003. A simulation study of the implications of age-reading errors for stock assessment and management advice. ICES Journal of Marine Science, 60: 314–328.

Rehberg-Haas, S., Hammer, C., Hillgruber, N., Hüssy, K., and Temming, A. 2012. Otolith microstructure analysis to resolve seasonal patterns of hatching and settlement in western Baltic cod. ICES Journal of Marine Science, 69: 1347–1356.

Schaber, M., Hinrichsen, H-H., Neuenfeldt, S., and Voss, R. 2009. Hydroacoustic resolution of small-scale vertical distribution in Baltic cod *Gadus morhua*—Habitat choice and limits during spawning. Marine Ecology Progress Series, 377: 239–253.

Svedäng, H., and Hornborg, S. 2014. Fishing induces density-dependent growth. Nature Communications, 5: 4152.

Swain, D. P., and Benoit, H. P. 2015. Extreme increases in natural mortality prevent recovery of collapsed fish populations in a Northwest Atlantic ecosystem. Marine Ecology Progress Series, 519: 165–182.

Teschner, E. C., Kraus, G., Neuenfeldt, S., Voss, R., Hinrichsen, H. H., and Köster, F. W. 2010. Impact of hypoxia on consumption of Baltic cod in a multispecies stock assessment context. Journal of Applied Ichthyology, 26: 836–842.

Thurow, F. 1974. Changes in population parameters of cod in the Baltic. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 166: 85–93.

Walters, C., and Maguire, J. J. 1996. Lessons for stock assessment from the northern cod collapse. Reviews in Fish Biology and Fisheries, 6: 125–137.

Zemeckis, D. R., Hoffman, W. S., Dean, M. J., Armstrong, M. P., and Cadrin, S. X. 2014. Spawning site fidelity by Atlantic cod (*Gadus morhua*) in the Gulf of Maine: Implications for population structure and rebuilding. ICES Journal of Marine Science. doi:10.1093/icesjms/fsu117.

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