Dynamics of the eastern Baltic cod (*Gadus morhua*) stock in the 20th century under variable climate and anthropogenic forcing

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Ph.D. thesis
2008

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Preface

This Ph.D. study was carried out in the National Institute of Aquatic Resources in the Technical University of Denmark (DTU Aqua) in collaboration with the University of Southern Denmark. The study was supported by the Danish Research School for Studies in Marine and Coastal Environment, Heritage and Sustainable Tourism (MAST), by the History of Marine Animal Populations project (HMAP) of the Census of Marine Life and by the Commission of the European Communities FP6 Specific Targeted Research Projects 022717 (UNCOVER) and 44133 (RECLAIM) as a contribution to the FP6 NoE 511106-2 (EUROCEANS). Contributions from participants of these projects are acknowledged here.

I would like to thank Henrik Gislason for his advice and encouragement both on scientific and administrative issues throughout my Ph.D. study and many thanks to Poul Holm for supporting this project. I am grateful to Brian MacKenzie for many fruitful discussions and for his efforts trying to teach me scientific writing. My warmest thanks to Fritz Köster for providing me the possibility to do my Ph.D. in the Danish fisheries institute and especially, for always finding time for me to give me advice and inspiration and for his lasting care for my progress.

This work would have not been possible without a cooperation of a number of people from fisheries research institutes around the Baltic, who helped me to orientate in historical materials and provided access to relevant literature and data. I appreciate very much the great help from the staff in the Institute for Baltic Sea Fisheries in Rostock, Leibniz Institute for Marine Sciences in Kiel, Sea Fisheries Institute in Hamburg, Sea Fisheries Institute in Gdynia, AtlantNIRO, Latvian Fish Resource Agency, Estonian Marine Institute and Swedish Board of Fisheries. Including just a few names here, I would especially like to thank Fritz Thurow, Ole Bagge †, Wolfgang Weber, Hildrun Müller, Krzysztof Radke, Ritma Gaumiga and Maris Plikshs. Special thanks to the people in the Leibniz Institute for Marine Sciences in Kiel for providing me a possibility for three months stay in their institute. I am grateful to Keith Brander, Karin Hüssy and Bo Poulsen for valuable comments on an earlier version of my thesis and thanks to Christina Frisk for kind help with the Danish summary. Thanks also to all the colleagues in DTU Aqua for their support and for inspiring working environment during my studies.

Being first educated as fisheries consultant and ship officer, my way to science has not been straightforward. I am obliged to Evald Ojaveer for making a turn in my education possible. Special thanks to Henn Ojaveer for introducing me the world of marine science, for believing in me enough to take the trouble teaching me things from the basics, and for being there for me till today trying to answer even my most foolish questions. I am grateful to the United Nations University Fisheries Training Programme in Marine Research Institute in Iceland for teaching me the principles of stock assessment that became useful at various steps of my Ph.D. study. I appreciate also having been part of the wonderful research team in the University of Tartu and the possibilities to get a feeling for different aspects of marine science from coastal fish ecology to economics of marine fisheries that has broadened my view of the field and helped to define my research interests, also in relation to this Ph.D. thesis. Thanks for still welcoming me to join the field works during my summer holidays to have a chance to touch some real fish for a change to historical documents.

Last, but not least I would like to thank my friends and family for their support during my studies.

Copenhagen, April 2008

Margit Eero

Contents

Summary

This thesis focuses on extending the time series of stock dynamics of the eastern Baltic cod (*Gadus morhua callarias*) back to the mid-1920s and identifying the causes for major stock fluctuations in the 20th century.

The time series of annual cod abundance in the eastern Baltic from International Council for the Exploration of the Sea (ICES) assessments is available from 1966 onwards. As a first step in this study, I have identified and compiled the available data that could potentially be used to estimate the historical dynamics of the cod stock in the Baltic before 1966. The compiled material includes research data and fisheries statistics from different countries bordering the Baltic Sea. The data were mainly extracted from international and national publications and reports; a smaller part was obtained as unpublished material from fisheries research institutes or archives.

The compiled fisheries statistics were used to generate an overview of the development of the international cod fishery in the Baltic that is a prerequisite for understanding the long term influence of fishing on the cod stock. The assessment of the eastern Baltic cod based on Virtual Population Analysis (VPA) was extended back to 1946, thereby adding 20 more years to the previously available time series. Several alternative approaches were used to extend the estimates of stock size and fishing mortality further back to the year 1925.

The extended time series put the recent substantial stock fluctuations into historical perspective. The largest recorded stock size in the late 1970s - early 1980s was found to be outstanding, also in a longer term perspective considering the stock dynamics back to 1925. Low stock levels similar to those in recent decades were estimated to have occurred earlier in the 20th century. Major trends in cod recruitment and stock size coincided with climatic variations, whereas the level of stock size at similar climatic

conditions was mainly determined by compensatory and cumulative effects of different human activities influencing the Baltic ecosystem and the cod stock. The record high cod stock in the late 1970s - early 1980s was shown to have corresponded to a favourable combination of the four key drivers: favourable climate enhancing hydrographic conditions allowing successful reproduction, low marine mammal predation, high productivity environment fuelled by nutrient loading and reduced fishing pressure. A similar situation has not occurred in other time periods of the 20th century. The cod biomass in the 1920s-1940s was likely restricted by high abundance of marine mammals and low ecosystem productivity; and in the 1950s-1960s by high fishing pressure. Periods of deteriorated hydrographic conditions occurred throughout the 20th century, being most pronounced in recent ca 20 years restricting cod recruitment.

Resumé (Summary in Danish)

Denne afhandling har til formål at udvide tidsserien for bestands størrelsen af torsk (*Gadus morhua callarias*) i den østlige Østersø tilbage til 1920'erne. Hensigten dermed er at identificere de væsentligste processer, som ligger til grund for kraftige bestandsfluktueringer i det 20. århundrede.

Tidsserien for udviklingen i torskebestanden i den østlige Østersø fra International Council for the Exploration of the Sea (ICES) er tilgængelig fra 1966 og frem. Som første skridt har jeg identificeret og indsamlet tilgængeligt data som potentielt kan benyttes til estimering af den historiske bestandsstørrelse af torsk i den østlige Østersø før 1966. Materialet inkluderer forskningsdata og fiskeristatistikker fra lande omkring Østersøen. Data stammer hovedsageligt fra internationale og nationale publikationer samt rapporter, dog stammer en mindre del fra upubliceret materiale fra forskningsinstitutioner eller arkiver.

De samlede fiskeristatistiske data blev benyttet til at skabe et overblik over udviklingen af det internationale torskefiskeri i Østersøen, hvilket er fundamentalt for forståelsen af langtidseffekten af fiskeri på torskebestanden. Bestandsvurderingen af torsk i den østlige Østersø baseret på Virtual Population Analysis (VPA) blev udvidet helt tilbage til 1946, hvorved der blev tilført yderligere 20 år til den eksisterende tidsserie. Alternative metoder blev brugt til at estimere bestandsstørrelsen og fiskeridødeligheden tilbage til 1925.

Den udvidede tidsserie sætter de nylige bestandsfluktueringer i historisk perspektiv. Den højest dokumenterede bestandsstørrelse i slutningen af 1970'erne til starten af 1980'erne blev vist at være en sjældenhed, også historisk set, ved udbygningen af data serien til 1925. Lave bestandsstørrelser som set over de seneste årtier blev estimeret til at være forekommet tidligere i det 20. århundrede. Tendenser i rekrutteringen og bestandsstørrelsen af torsk var sammenfaldende med klima variationer. Niveauet i bestandsstørrelsen under ens klima forhold blev hovedsageligt bestemt af

menneskeskabte kompensatoriske og kumulative effekter på Østersøens økosystem eller direkte på torskebestanden. Den rekord-høje torskebestand i slutningen af 1970'erne til starten af 1980'erne blev vist at være et samspil mellem fire grundlæggende faktorer: favorabelt klima ledende til gode hydrografiske forhold hvorved rekrutteringen øges, lav predation fra havpattedyr, høj produktivitet grundet næringsstoftilførsel til økosystemet samt reduceret fiskeri. En lignende situation er ikke tidligere forekommet i det 20. århundrede. Biomassen af torsk in 1920'erne til 1940'erne var begrænset af en høj havpattedyrsbestand og en lavere produktivitet i økosystemet, og i 1950'erne og 1960'erne af et højt fiskeritryk. Perioder med forringede hydrografiske forhold er forekommet gennem hele det 20. århundrede, dog har disse været mest udtalte de seneste 20 år, resulterende i formindsket rekruttering af torsk.

List of original publications

The dissertation is based on the following papers, which will be referred to in the text by their Roman numerals:

I Eero, M., MacKenzie, B., Karlsdóttir, H., Gaumiga, R. 2007. Development of international fisheries for cod (*Gadus morhua*) in the eastern Baltic Sea during 1880-1938. Fisheries Research, 87, 155-166.

II Eero, M., Köster, F.W., Plikshs, M., Thurow, F. 2007. Eastern Baltic cod (*Gadus morhua callarias*) stock dynamics: Extending the analytical assessment back to the mid-1940s. ICES Journal of Marine Science, 64, 1257–1271.

III Eero, M., Köster, F.W., MacKenzie, B.R. Reconstructing historical stock development of the eastern Baltic cod (*Gadus morhua*) before the beginning of intensive exploitation (Submitted).

IV Eero, M., MacKenzie, B.R., Köster, F.W., Gislason, H. The Baltic Sea bio-manipulation experiment of the 20th century–resolving impacts of fishing, eutrophication, marine mammals and climate on a cod population (Manuscript).

1. Introduction

Human populations interact closely with their surrounding nature, including marine ecosystems. Their actions on land and in the ocean measurably affect ecosystems and changes in ecosystems affect humans. The major anthropogenic use of marine ecosystems is related to harvesting. Man has harvested the aquatic environments since the earliest historical and archaeological records and fisheries have played a significant role in the history of mankind. For example, fishing for cod was involved in the early exploration of North America and the race for cod in Newfoundland in the 16th century has been compared to the gold fever (Kurlansky, 1997). The settlement and movements of human populations in the 17th-18th century were also suggested to have been related to cod fishery (Myers, 2001). The trade with fish was an important part of ancient economic activities (Barret et al., 2004; Hoffmann, 2002; Holm et al., 1996) and fish was the major trade article of e.g. the Hanseatic League (Cushing, 1982). Conflicts over fishing rights for particular stocks, e.g. “cod wars” between England and Iceland date back to the early 15th century and were still an issue in the 20th century (Smith, 1994; Pálsson, 1991). Therefore, the interaction between society and fish resources has been and continues to be an important issue for national governments and for hundreds of millions of people (Hilborn et al., 2003).

Marine resources were long viewed as an inexhaustible source of protein for human use. In the 20th century, the effects of human activities on marine ecosystems were increasingly recognized (Smith, 1994; Pikitch et al., 2004). In recent decades marine fisheries have declined world wide, with large socio-economic impacts on fishing communities. The United Nations’ Food and Agricultural Organisation (FAO) (2006) estimated that currently 25 percent of the world’s fish resources are overexploited, depleted or recovering from depletion and 52 percent are fully exploited with no room for further expansion. A well-known example of fish stock collapse partly due to intensive fishing during just a few decades in the 20th century is the Newfoundland cod, the stock that had previously been harvested for 500 years (Hilborn et al., 2003). In addition to influence on single stocks, the effects of fishing on entire ecosystems have been recognized (e.g., Parsons, 1992; Tegner and Dayton, 1999; Pauly et al., 2002).

Concern of overfishing tends to set the focus on fishing as a cause of declines in stock abundances (e.g., Rothschild and Shannon, 2004). However, not all changes in marine fish populations are due to fishing. In many fish stocks, changes in climate and other natural fluctuations play an important role in population dynamics (Cushing, 1982; Beamish, 1995; Bakun, 1996). For example, the recent declines in cod stocks in several areas are suggested to be due to a combination of both human activities and environmental changes (e.g., Serchuk et al., 1994; Drinkwater, 2002; Brander, 2005). Differentiating between the effects of human activities and natural variability on fish stocks is a central dilemma for fisheries science. Separating the effects of different factors is often difficult, especially as the time series of stock developments from international assessments performed in North-East Atlantic areas by ICES (International Council for Exploration of the Sea) generally cover only recent 3-4 decades. This also implies that the perception of the present status of fish stocks often is short-sighted. Pauly (1995) has pointed out that each generation of marine scientists tends to accept as a baseline the stock-size and ecosystem structure that occurred at the beginning of their career, and uses this to evaluate subsequent changes, often assuming that inadequate data exist for earlier periods. This was termed the 'shifting baselines syndrome'.

Today, the need for a historical perspective in order to understand and manage marine ecosystems has become increasingly recognized. An example of this is the criticism in the Science Plan of the European Science Foundation Marine Board concerning the current practice of shortsighted time-series and a proposal to take into account the information of past historical evidence in future research in rebuilding marine ecosystems (Holm, 2003). Fisheries management measures have often been ineffective and there is need for more holistic management, considering ecosystem aspects and treating humans as components of the ecosystem they inhabit and use (e.g., Pikitch et al., 2004). Accordingly, an ecosystem approach to the management of human activities was defined in the 1992 Rio Declaration and reiterated at the 2002 World Summit on Sustainable Development in Johannesburg. The overall objective of ecosystem-based fishery management is to restore marine ecosystems and fisheries to a healthy level and sustain them. However, a prerequisite for restoration is a general understanding of the impacts of human activities on fish stocks and marine ecosystems. Furthermore, in order to take ecosystem considerations into account in managing fisheries, understanding the roles of different ecosystem parameters in fish stock dynamics is essential. A long-term historical perspective is needed for disentangling the relative impacts of different factors on fish populations that is important for sustainable management of fisheries and ecosystems (Southward, 1995; Holm, 2003; Pitcher, 2001).

The task of bringing a long-term historical perspective into ecosystem management may however go beyond the competence of marine biology and needs interdisciplinary approaches. Environmental history is a relatively recently developed field of research that combines the approaches of maritime history and ecological science. This area of study puts a special focus on the place of mankind in the historical development of ecosystems, through integrated analyses of ecosystems and human societies (Holm et al., 2001; Poulsen, 2007; Starkey et al., 2008; Poulsen, 2008). This PhD study contributes to the field of environmental history by drawing on both ecology and history and combining the ecosystem fluctuations with developments in human societies. Ecological knowledge and historical data are combined to interpret historical variations and improve the understanding of ecological processes.

A global inter-disciplinary research program, the History of Marine Animal Populations (HMAP), was established within the Census of Marine Life (CoML) in order to encourage the integration of natural sciences (e.g., biology, ecology), history and social sciences to understand the magnitude, causes and consequences of long-term changes in marine animal populations and ecosystems (Holm, 2003; Ojaveer and MacKenzie, 2007). This Ph.D. project is a contribution to the Baltic activities within HMAP. The main questions of interest for the HMAP are: (i) How have the diversity, distribution, and abundance of marine animal populations varied over the last 2000 years? (ii) Which factors have forced or influenced changes in the diversity, distribution, and abundance of marine animal populations? (iii) What has been the anthropogenic and biological significance of changes in marine animal populations? (iv) By what processes have marine ecosystems interacted with human societies? (Holm, 2003; Ojaveer and MacKenzie, 2007). These general underlying questions gave a motivation also for this Ph.D. study.

2. Motivation and objectives of the study

The time series of stock dynamics and fishing mortality of the eastern Baltic cod are available from ICES assessments since 1966 (ICES, 2007a). The spawning stock biomass is at present below 100 thousand tonnes, which is the lowest level observed since 1966. The highest spawning stock biomass, up to 700 thousand tonnes, was recorded in the late 1970s - early 1980s. This relatively short time series of stock dynamics showing pronounced changes makes it difficult to evaluate whether the high stock size in the late 1970s - early 1980s was extraordinary in a longer time scale or is rather the present low stock level unusual in a longer historical perspective.

Human activities have led to several major changes in the Baltic ecosystem in the 20th century. Intensive hunting in the early decades of the 20th century drastically reduced the abundance of marine mammals (Harding and Härkönen, 1999) that are the top- predators in the ecosystem. Furthermore, as a consequence of the increased use of fertilizers and intensified industrialization a major increase in nutrient input to the Baltic occurred after the Second World War, enhancing the productivity of the ecosystem (Elmgren, 1989). These major changes in the upper and lower trophic level are expected to have influenced the cod population in the Baltic Sea. However, their relative importance is difficult to quantify as the changes in the ecosystem occurred before the beginning of the time series of cod stock dynamics available from ICES assessments (Fig. 1). Therefore, it is also difficult to predict what impact a reversal of these changes might have. The cod stock was intensively exploited already in the 1960s which makes it also difficult to evaluate the relative influence of fishing on the population dynamics.

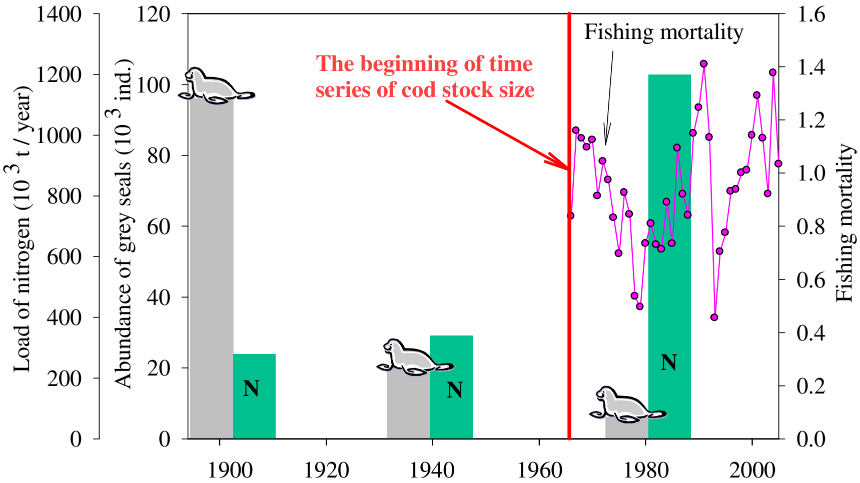

Fig. 1. A scheme showing major changes in the abundance of grey seals (Harding and Härkönen, 1999) and in nitrogen loading (Jansson and Dahlberg, 1999) comparing 1900, 1940 and 1980; and the time series of cod fishing mortality since 1966 (ICES, 2007a).

The management of the Baltic ecosystem is amongst others aiming at reduction in nutrient load as well as recovery of cod stocks and populations of marine mammals. In order to improve the basis for scientific advice for management of the Baltic Sea and for developing future ecosystem scenarios, knowledge of relative impacts of human-induced ecosystem changes compared to natural variability is important.

The major objectives for this Ph.D. study were:

i) Reconstructing a time series of stock size of the eastern Baltic cod back to the early decades of the 20th century.

ii) Reconstructing the historical development of cod fishery in the Baltic and a time series of exploitation intensity.

iii) Evaluating the influence of fishing and other human-induced ecosystem changes on cod population dynamics in comparison with the impact of climatic variability.

By improving the knowledge of anthropogenic and natural impacts on dynamics of a commercially and ecologically important fish species in the Baltic, this Ph.D. study contributes to the development of sustainable management of the Baltic ecosystem consistent with the general goals of organizations like Helsinki Commission (HELCOM) and ICES and with the European Marine Strategy and European Maritime Policy.

3. Cod in the Baltic Sea

This section gives an overview of general characteristics of the Baltic Sea and its specific hydrography. Furthermore, it provides an introduction to selected aspects of cod ecology in the Baltic and describes briefly the major human impacts on the Baltic environment in the 20th century that are relevant for this thesis.

3.1. General information on the Baltic Sea and its hydrographic characteristics

The Baltic Sea (Fig. 2) is a semi-enclosed water-body and among the largest brackish sea areas in the world. The Baltic Sea covers 415, 266 square kilometers, while its catchment area - at 1.7 million km^2 - extends over an area about four times as large as the sea itself. The catchment area is inhabited by more than 85 million people, and due to its special geographical and oceanographic characteristics, the Baltic Sea is highly sensitive to the environmental impacts of human activities. The Baltic Sea is only connected to the world's oceans by the narrow and shallow waters of the Sound and the Belt Sea and the water residence time in the Baltic is about 25–30 years (Voipio, 1981).

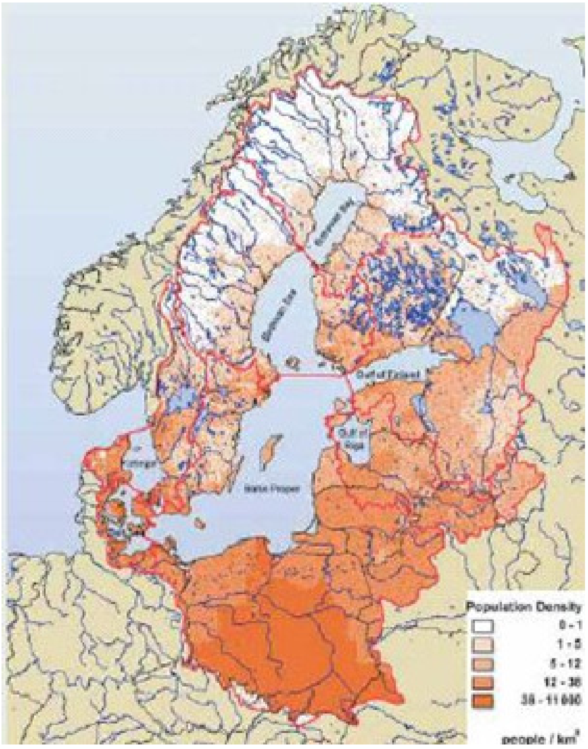

Fig. 2. Demographic map of the Baltic Sea region (http://www.helcom.fi)

The Baltic Sea is characterized by strong salinity gradients. Due to restricted connection to oceanic waters, salinity of the surface waters in the Baltic area declines from around 20 psu (parts per thousand) in the Kattegat to 1–2 psu in the northernmost areas compared to 35 psu in the open oceans. Salinity in the Baltic is controlled by occasional intrusions of saline water from the North Sea and by freshwater input from rivers (Schinke and Matthäus, 1998). The central Baltic Sea is permanently vertically stratified as a strong salinity gradient at 60-80 m depth prevents vertical mixing of the water. The water column consists of an upper layer with salinities of about 6-8 psu and a more saline deeper layer with salinities of about 10-14 psu (e.g., Matthäus, 2006). In spring, a steep temperature gradient develops at 25-30 m depths that further restricts vertical circulation of the water until late autumn. The horizontal deep water mixing is restricted by bottom topography with several sub-basins separated by under-water sills (Matthäus, 2006). Without renewal of the deep water, the oxygen conditions in the deeper layers deteriorate due to bacterial decomposition of organic matter. Oxygen depletion sometimes leads to development of hypoxic regions, characterized by the formation of hydrogen sulphide (Matthäus and Franck, 1992). The only mechanism by which the central Baltic deep water is renewed is the intrusion of saline oxygenated water from the North Sea (Schinke and Matthäus, 1998).

Frequent weak inflows (10 - 20 km^3) have little impact on the deep and bottom waters, as they are generally insufficient to displace the bottom water or significantly change oceanographic conditions in the Baltic deep basins. This can only be done by strong influxes of larger volumes (100- 250 km^3) of saline and oxygen-rich water (Matthäus and Franck, 1992), the events called major Baltic inflows (Dickson, 1971, 1973). The mechanisms of the occurrence of major Baltic inflows are complex and have been of interest for researchers far back in history. Already in the early decades of the 19th century, Catteau-Calleville (1815) thought that the winds, especially from south and south-west are responsible for the transport of salt water into the Baltic. Since then the processes and related preconditions have gradually been described by a number of researchers (Matthäus, 2006 and references therein). Contemporary investigations suggest that both meteorological and oceanographical conditions are necessary for the occurrence of major Baltic inflows (Matthäus and Franck, 1992; Matthäus and Schinke, 1994). The major inflow events are found to be characterized by high pressure over the Baltic region with easterly winds followed by a prolonged period with strong zonal wind and pressure fields over the North Atlantic and Europe. Variations in river runoff to the Baltic are considered to impact on the inflow activity as well (Schinke and Matthäus, 1998). The occurrence of major inflows is difficult to predict with few attempts in this direction being made (e.g., Hänninen et al., 2000).

The major Baltic inflow events are recorded back to the late 1800s. Until the 1980s, the major inflows were relatively frequent (Fig. 3). The longest periods without an inflow event before the late 1970s lasted only for three to four years (1927/1930, 1955/1960) (Matthäus, 2006). However, corresponding to reduced inflow activity in these periods, salinity declined in the 1920s-early 1930s and in the 1950s both in Gotland Deep (Fonselius et al., 1984) and in Bornholm Basin (Fonselius, 1962). Low oxygen values (below 1 ml/l) and the appearance of hydrogen sulphide in Gotland Deep in these periods were also recorded (Karasiova and Voss, 2004). The longest period without a major inflow event was the ten year period from 1983 until 1993 and only a few major inflows have occurred since then (Matthäus, 2006). Consequently, salinity and oxygen concentrations in the deep Baltic basins have declined (Matthäus and Nausch, 2003).

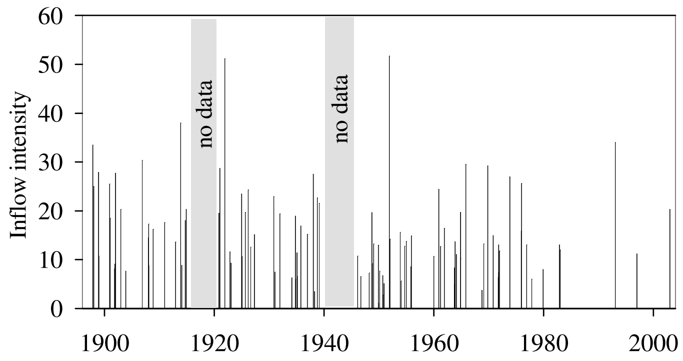

Fig. 3. Intensity of major Baltic inflows (Matthäus, 2006).

3.3. Selected aspects of cod ecology

Biodiversity in the Baltic Sea is relatively low as few marine and freshwater species have adapted to the brackish water conditions in the Baltic. Marine species, including cod invaded the Baltic Sea some 8000 years ago after the opening of the connection to the North Sea (Ojaveer and Lehtonen, 2001). The main problem for these species in adapting to the Baltic environment has been low salinity. Today the eastern Baltic cod is genetically highly divergent from the cod in the North Sea (Nielsen et al., 2001). There are considered to be two cod populations in the Baltic, eastern and western. The eastern Baltic cod is found east of Bornholm Island (ICES Subdivisions 25-32, Fig. 4) and has different biological traits (growth, maturation, genetics, migration behaviour) from those west of Bornholm (Bagge at al., 1994; Nielsen et al., 2001; Aro, 2002). At low population densities, the distribution of the eastern Baltic cod stock is narrowed to the southern Baltic but it extends north-eastwards and into the bays when the stock becomes more abundant (Aro and Sjöblom, 1982; Ojaveer et al., 1985; Bagge et al., 1994; Ojaveer et al., 1999).

Cod distribution in the Baltic varies also seasonally due to spawning and feeding migrations. The most important spawning grounds for the stock are the deep basins in the southern and central areas of the Baltic (Bagge et al., 1994), i.e. Bornholm Basin, Gdansk

Deep and Gotland Basin (Fig. 4). During the feeding period cod is distributed over large areas and can perform intensive migrations (Bagge, 1981; Aro, 1989). The feeding generally takes place in the more shallow waters (Aro, 1989). The Baltic cod has a rather late and prolonged spawning period compared to other North Atlantic cod stocks (Brander, 1994). In the eggs surveys conducted since the beginning of the last century, cod eggs have been found from March to October (Kändler, 1949). The main spawning period in 1970s-1980s was in April-June, and shifted to late July in the 1990s (Wieland et al., 2000).

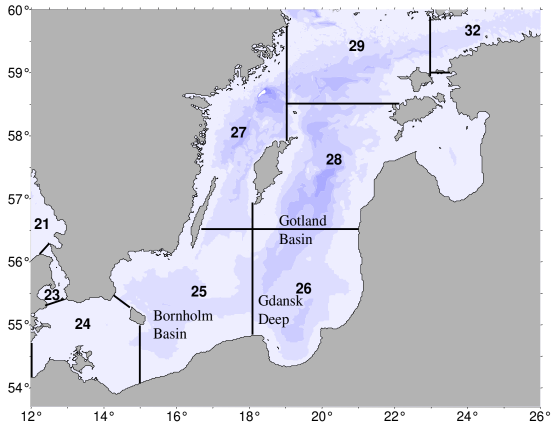

Fig. 4. Location of ICES Subdivisions and the main deep basins in the central Baltic, i.e spawning areas of the eastern Baltic cod.

The eastern Baltic cod has developed adaptations in egg characteristics to survive in a low salinity environment. The eggs of the eastern Baltic cod reach neutral buoyancy at salinities of around 12–14 psu. Ambient salinity in the Baltic is insufficient to keep cod eggs floating in the surface layer. Therefore, unlike other cod populations, cod eggs in the eastern Baltic are neutrally buoyant in the deeper water layers (Nissling and Vallin, 1996; Wieland and Jarre-Teichmann, 1997). Experimental studies revealed a minimum salinity of 11 psu required for activation of spermatozoa and thus successful fertilization of Baltic cod (Westin and Nissling, 1991), while at least 2 ml l $^{-1}$

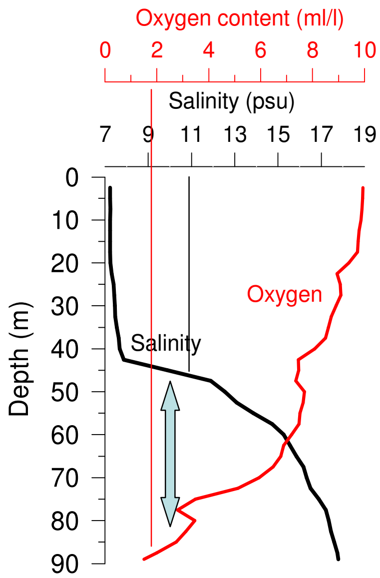

Fig. 5. General oxygen and salinity profiles in Bornholm Basin indicating cod reproductive habitat.

oxygen is needed for successful egg development (Nissling, 1994; Wieland et al., 1994). These limiting factors define a relatively narrow layer of water for successful development of cod eggs in the Baltic (Fig. 5, Plikshs et al., 1993; MacKenzie et al., 2000).

The salinity and oxygen conditions in the deep basins are largely determined by the frequency and intensity of major Baltic inflows. Additionally, the temperature of the inflowing water influencing oxygen solubility (Hinrichsen et al., 2002b) and oxygen consumption rates by biological processes (MacKenzie et al., 1996) influence the conditions for cod reproduction. The effect of a major intrusion of saline oxygenated water is usually sufficient to support better environmental conditions a maximum of two spawning seasons (Aro, 2000).

The recruitment of the eastern Baltic cod is related to the salinity and oxygen levels in the deep basins (e.g., Köster et al., 2005). Low oxygen concentration not only impacts on egg survival, but experimental studies demonstrated that low oxygen concentration at egg incubation impacts also on larval activity and the start of the vertical migration into upper water layers (Rohlf, 1999). Salinity has additionally an indirect impact on survival of cod larvae via its effect on the abundance of zooplankton *Pseudocalanus sp*. (Möllmann et al., 2000), the major prey for the first feeding cod larvae (Voss et al., 2003; Hinrichsen et al., 2002a).

Cod is the major top predator fish species in the southern and central Baltic (Sparholt, 1994). At relatively low numbers of marine mammals, adult cod has at present basically no natural enemies in the Baltic Sea. Cannibalism on juvenile cod however occurs, especially at higher population abundances (Neuenfeldt and Köster, 2000). Cod eggs are substantially preyed upon by sprat and herring (Köster and Schnack, 1994) though the impact is variable in time and space (Köster and Möllmann, 2000). Due to changes in predator-prey overlap, predation pressure on cod eggs appears to be higher in the periods of the absence of major Baltic inflows (Köster and Möllmann, 2000).

In conclusion, the major Baltic inflows favour cod recruitment through several processes while cumulative negative effects occur at stagnation periods.

3.4. Major human impacts on the Baltic Sea environment in the 20th century

The environmental situation in the Baltic Sea has drastically changed in the 20th century with increased pressure by human activities.

The first major anthropogenic impact on the Baltic ecosystem and the cod population can be considered to be the removal of the natural top-predators. Sealing has historically been of major importance for the local economies of coastal settlements. During the period 1300 AD to 1800 AD the Baltic was the most important producer of seal oil in Europe. At the end of the 19th century, seals successively lost their economic value as cheaper alternatives to seal oil became available and seals started to be seen as competitors for the fishermen. Consequently, their numbers were drastically reduced by intensive hunting (Harding and Härkönen, 1999 and references therein). By the 1940s the numbers of grey seals (*Halichoerus grypus*) and ringed seals (*Phoca hispida*) were reduced about five and eight times respectively, compared to their abundances in the early 1900s (Harding and Härkönen, 1999). In the 1970s, the numbers of seals declined further perhaps related to reduced fertility due to toxic contaminants (e.g., Olsson et al., 1992).

Since about the 1940s, accelerated industrialization and exploitation of natural resources has resulted in deterioration and degradation of the Baltic Sea. Until about the 1940s, the Baltic was an oligotrophic sea with low biological production and clear water (Jansson and Dahlberg, 1999). Since then, major developments in human activities resulted in substantial increase in nutrient load to the Baltic, the most important sources being agriculture, air emissions from the use of fossil fuel (industry and transport), and urban and industrial sewage (Jansson and Dahlberg, 1999). Increased nutrient load can be expected to have increased the primary productivity of the Baltic ecosystem and has been suggested to have increased also fish production (e.g., Elmgren, 1989). Continuous increase in nutrients has resulted in eutrophication of the Baltic Sea environment, characterized by increased intensity and duration of algal blooms and increased sedimentation of organic matter resulting in higher oxygen consumption. This has led to increased frequency and severity of oxygen deficiency in the bottom waters since about the 1960s (e.g., Fonselius, 1969; Elmgren, 2001), deteriorating e.g. spawning conditions for the eastern Baltic cod. The influence of eutrophication on oxygen conditions in the bottom waters becomes especially pronounced in the periods of lack of oxygen-rich water inflows from the North Sea into the Baltic.

At present, the most serious human-induced pressures on the Baltic environment are considered to be eutrophication and toxic contaminants (Elmgren, 2001), overfishing and alien (i.e. foreign) species (Leppäkoski et al., 2002). During the past two or three decades overfishing and the failure to maintain sustainable fisheries have become increasingly pronounced. Contamination and alien species are not considered to have had a major impact on the historical dynamics of the cod stock, and are therefore not further discussed here.

4. Background and overview of data and methods

Constructing the historical development of fisheries and fish stocks are interlinked processes. The availability of data for estimating cod stock size in the Baltic is closely related to the importance of the species for the fisheries in different areas and time periods, as this largely defined the priorities for historical scientific investigations. Therefore, in order to understand the limitations and possibilities for constructing the historical stock dynamics an overview of the developments in the fisheries and in fisheries research is necessary. In turn, the information on stock size is required in order to estimate the level of fishing intensity and its influence on the stock. Due to close linkages between these issues, this section includes an overview of the material compiled for this thesis, a review of developments in the cod fisheries and cod-related scientific investigations and a description of the methodology used to construct the historical stock dynamics.

4.1. Data compilation

A major task for this Ph.D. project was to identify and compile the information that could potentially be used to construct the history of cod stock development and its exploitation back to the early decades of the 20th century. In addition to extending the time series, this work also helps to identify where additional effort could be invested in future studies or which issues are likely to remain unknown as the necessary information can probably not be recovered or has not been recorded.

The Baltic Sea is one of the best investigated marine ecosystems and all bordering countries have a long tradition in marine science. However, until recent decades the research activities have not been internationally coordinated. This implies that the data are patchy in space and time, scattered across countries and the data collection procedures have not been homogeneous and systematic across countries. Many of the collected research materials are not published in internationally accessible journals, but in national reports in local languages. Other materials are lying around in research institutes waiting to be worked up and digitalised. The lack of synthesis of historical materials in previous times is related to the large number of countries (nine), cultures and languages, while the geopolitical situation (wars, dictatorships etc.) prevented scientific contacts and free access to data was denied. The HMAP project that developed since 2000 is the first coordinated attempt to recover and interpret the historical materials on the Baltic-wide scale (MacKenzie et al., 2002a; Baltic-HMAP, 2001).

Fisheries statistics

Fish landings for the total Baltic area since the beginning of the 20th century are available in the *ICES Bulletin Statistique*. These data are however not spatially disaggregated and data for all countries are not included in all years. For example landings from some eastern Baltic countries were not included in ICES statistics before the Second World War. A major effort in this Ph.D. project has been to compile the complete fisheries statistics for the five major cod-fishing countries (Denmark, Germany, Latvia, Poland, Sweden) for the period since the start of the time series until the Second World War (Paper I). The extent of fisheries data in different countries reflects various economic, cultural and political developments. Consequently, large amount of fisheries statistics are available for the west coast of the Baltic Sea since the late 19th or early 20th century (Ojaveer et al., 2007), while the corresponding information for the eastern Baltic Sea region was scarce until the 1920s. This is because the eastern countries developed national fisheries systems, corresponding institutions and statistics first in the 1920s. During the late 19th and early 20th century the Russian Empire was less interested in the fisheries in the Baltic Sea as its fish resources were mostly used locally, therefore no statistics of fisheries were collected (Lajus et al., 2007).

The fisheries data were extracted mainly from national official statistical reports, which are available in national libraries, however not in easily accessible digital form. A smaller part of the fisheries data utilised in this project was generated during archival research conducted by the HMAP project and a fraction of it was produced as a part of this Ph.D. study. The fisheries data compiled and digitalised during this Ph.D. project included area disaggregated landings (by harbour, county or sea area) of all recorded fish species, fish prices and effort (numbers of fishermen, boats, fishing gear).

The complete fisheries statistics for the period before the Second World War was compiled for the five countries from the following sources:

Denmark: 1888-1924 *Fiskeriberetning* published by the Danish Ministry of Agriculture
(later the Ministry of Fisheries)
1925-1938 statistical materials of the Danish Directorate of Fisheries
stored in the Danish National Archive

Germany: 1909-1925 *Deutsche Seefischerei*
1926-1938 *Jahresbericht über die Deutsche Fischerei*

Latvia: 1924-1938 *Bulletin statistique des peches maritimes de Lettonie*.
Poland: 1922-1937 *Rybolowstwo Morskie na Polskim Baltyku*, Sea Fisheries Office Publishing; *Prace Morskiego Instytutu Rybackiego.*
Sweden: 1914-1938 *FISKE* by the Royal Statistics Central Bureau

The HMAP project had previously compiled parts of the Swedish and Danish fisheries statistics, and made them available in the HMAP database (Awebro, 2002; Bager et al., 2002). The database facilities created within the HMAP allow the vast amount of fisheries statistics compiled and digitalised during this Ph.D. project to be made internationally accessible in the future. The fisheries data are utilised in this project only with respect to cod, whereas the complete spatially disaggregated statistics of five countries for all species covering several decades can potentially provide material for several other investigations regarding both ecological and socio-economic aspects.

Research data

Research data related to the eastern Baltic cod were assembled for the period from the 1920s to 1970s. For the time period from the 1940s to 1970s, the compiled data included age and length compositions of both commercial and research catches, individual weight at age/length and relative abundance indices from commercial landings and research surveys. For the 1920s-1930s, additionally data on egg abundance from ichthyoplankton surveys were compiled.

Majority of the data were extracted from international and national journals and institute reports. For example, in the period after the Second World War and up to the 1980s, several countries regularly reported their fisheries research data in the series *Annales Biologiques* and *Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer* published by ICES. Some countries published the respective data in their institute report series. A valuable sources of material for this study were for example the report series of the Polish fisheries institute *Prace Morskiego Instytutu Rybackiego w Gdyni* and the various reports of the institute of fisheries and oceanography of the former Soviet Union (VNIRO). Valuable data and background information were obtained also from several German publication series, e.g., *Berichte der Deutchen Wissenschaftlichen Kommission für Meeresforschung*, *Deutsche Fischerei Zeitung* and *Zeitschrift für Deutsche Fischerei*. A small part of the material utilized in this study was provided as unpublished raw data by the fisheries institutes. It was in several cases experienced that the historical data that had not been worked up and published at the time when they were collected could not be utilised as the data had either not been preserved or sufficiently documented to make use of them several decades later. Currently, the necessary input data for estimating fish stock abundances are collected internationally and stored in databases, which was not the case with the data in the time period covered in this study. Therefore, it is largely due to the common practise in this period to provide original data in a relatively disaggregated form in publications that the recovery of sufficient data for reconstructing historical stock size was possible.

The international data for estimating stock dynamics of the eastern Baltic cod has been compiled by ICES back to 1966 (ICES, 2007a). The spatially and temporarily disaggregated time series extend back to 1974 (ICES, 2006). However, the data especially for the earlier decades in these time series have been lacking sufficient documentation. This makes it difficult to evaluate the quality and limitations of the datasets and comparability with earlier data series. For this reason, the coverage and compilation procedures of the age structured catch and weight data for the eastern Baltic cod until the 1990s were also reviewed and documented during this Ph.D. project, as a contribution to the former Study Group for Multispecies Assessment in the Baltic (ICES, 2006).

4.2. Development of cod fishery

Fish resources in the Baltic have been exploited for centuries. Archaeological records show that fishing was conducted along the Baltic coast well before the Middle Ages (Makowiecki and van Neer, 1996; Enghoff, 1999). The cod fishery in the Baltic also has a long history. Archaeological studies have found cod bones on Bornholm and in other coastal areas along the Baltic that originated from the Stone Age period 7000 – 3900 BC (Enghoff et al., 2007) and the 6th-7th and 11th centuries AD (Enghoff, 1999). The quantities of cod captured in these ancient times are not known. However, archival research of the written records documenting the cod fishery in the Baltic in the period from the 16th to the 19th century showed that cod was locally economically important in this period (MacKenzie et al., 2007).

Cod fishery has not had the same historical traditions and it has not been similarly valued for human consumption in all areas in the Baltic. For example, cod was considered inedible along the coast of the current Estonia and Latvia until the end of 19th century due to its specific smell and the demand in the market was low. Cod fishing in these areas really started in 1915 when the German military established large salting and smoking facilities for cod and flatfish and provided fishermen with the right gears and knowledge for cod fishing (Schneider, 1928). Also in the Finnish waters cod was not fished much at the beginning of the 20th century due to lack of demand (Sandman, 1906) and special events were organized to inform consumers and fishermen about the qualities of cod (Anon., 1908). In contrast, the Swedish pioneer naturalist Linnaeus claimed in the 1740s that cod from the southern part of the Baltic Sea was the best in the world when it came to flavour and consistency (Sandahl, 2003).

In the early decades of the 20th century cod was generally among the five most important species in the Baltic fisheries both in terms of quantity and economic value (Paper I), flatfish and clupeids (herring and sprat) being the most important species in the 1920s-1930s (Fig. 6). The value of cod in relation to other species went through major changes in the 20th century. Until recent decades, cod has been cheaper or at the same economic value as herring (Paper I, *Fiskeriberetning, FISKE*). For comparison, in the recent years according to the statistics of the Danish Directorate of Fisheries and the Swedish Board of Fisheries the value of Baltic cod is about 6 times higher compared to the price of herring. Before the 1930s, the value of cod was relatively low partly due to poor infrastructure for cod processing and it was difficult to dispose the catches. On Bornholm Island for example the first filleting factory was built in 1937 while in the 1890s and in the early decades of the 20th century cod was transported alive to the markets in Copenhagen or in Germany and Poland (Rasmussen, 1993). The periods of lack of markets and cheap prices implied that large quantities of cod were put back in the sea (Poulsen, 1931).

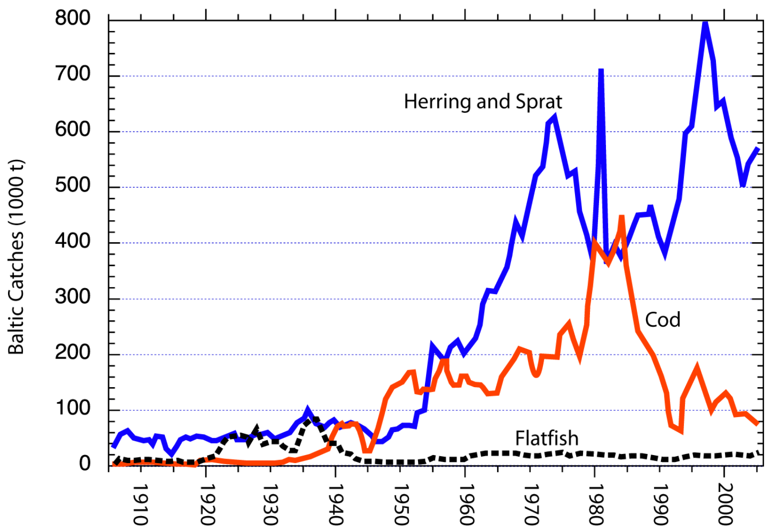

Fig. 6. Landings of cod, flatfish and herring and sprat in the Baltic Sea (Hammer et al., 2008).

In the first half of the 20th century, substantial changes occurred in the cod fishery in the Baltic in relation to technological developments. These included:

i) motorization of vessels,

ii) introduction of trawls and consequently

iii) moving the fishery from the coastal areas out to the open sea.

Although fishing technology has developed continuously since then (e.g. fish finding equipment etc.), the changes in the first half of the 20th century probably had the largest influence on cod fishing in the Baltic Sea.

Technological developments in the Baltic occurred relatively late compared to neighbouring areas. The first purpose-built steam trawlers appeared in the North Sea in the 1880s, while in the Baltic the leading countries only started to install engines in fishing boats in the 1900s (Paper I; Bager et al., 2007). Thereafter, the number of motorized vessels increased rapidly during the 1920s-1930s in all areas of the Baltic (Paper I, Fig. 7), the vessels became larger and the engines more powerful. For example the average horse power (HP) of the vessels in the Latvian and Polish fleets in the mid-1920s was less than 10 (Paper I), whereas in the 1950s -1960s cod was trawled by vessels with engines of 80-150 HP (Lablaika et al., 1991). In the 1940s few vessels were larger than 35 BRT, while in the 1950s increasing number of cutters of 60-100 BRT with engines of 150-200 HP were employed in the Baltic (Jensen, 1959a).

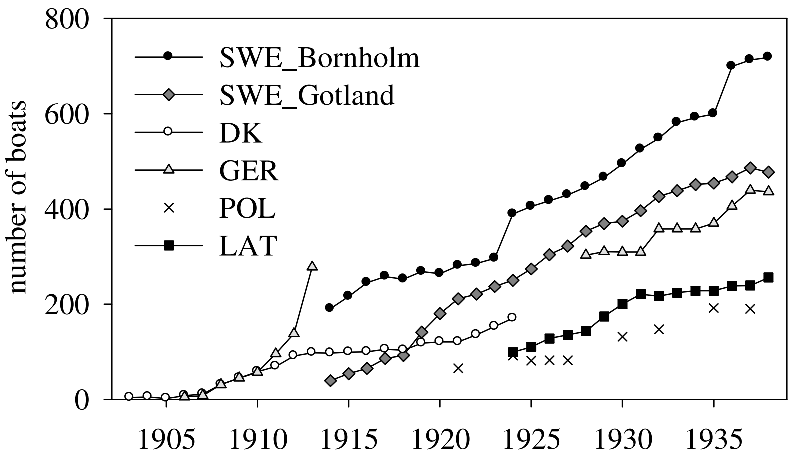

Fig. 7. Numbers of motorized boats in Sweden (SWE) in Bornholm and Gotland areas; in Denmark (DK) in the areas east of Bornholm; and in Germany (GER), Latvia (LAT) and Poland (POL) (based on data from Paper I).

Until about the 1920s-1930s, cod was mainly caught by hand-lines (Fig. 8) and long-lines (Fischer and Henking, 1905; Hessle, 1947; Jensen, 1954). For example, on Bornholm the cod fishery using hand-lines was practiced mainly by elderly fishermen and young boys who were not able to participate in more demanding fishing operations (Rasmussen, 1993). The cod fishery by hook and line in the early 1900s took place very close to the shore (Fig. 9).

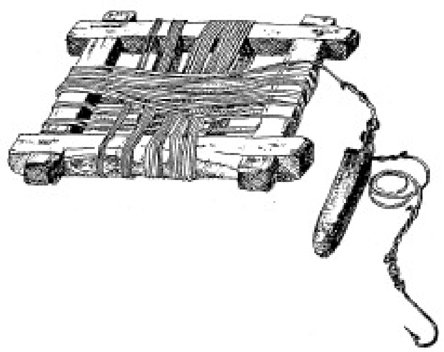

Fig. 8. Typical cod fishing gear on Bornholm in the late 19th century (Rasmussen, 1993)

The trawl fishery was introduced in the southern Baltic in the 1920s. These developments in the Baltic were slower compared to the neighbouring areas partly due to the rocky bottom, especially near Bornholm that hindered bottom trawling and due to lack of practical knowledge of trawl fishing (Bager et al., 2007). At first, the trawls were mainly used to catch flatfish that gave much higher landings in the Baltic in the 1920s-1930s compared to cod (Fig. 6). Cod was in this period only lightly exploited (Paper III). Only when flatfish catches declined in the 1930s and cod became more abundant in trawl catches were trawls adjusted to catch cod instead (Hessle, 1947; Sahlin, 1959). As the boats became larger and the engines more powerful, cod fishery gradually moved to the more offshore areas. A major turning point for the cod fishery in the Baltic was the Second World War when the German steamer fleet moved into the Baltic and the Baltic cod was intensively exploited likely for the first time in history (Paper III). Fishing by German steamers expanded to the areas were commercial trawling had not taken place before, i.e. near Gotland, where the catch rates were the highest (Meyer, 1952a). By the Second World War, the gradual moving of the cod fishery from coastal areas out to the open sea had been completed (Fig. 9).

After the Second World War, the cod fishery developed rapidly reaching a plateau by the second half of the 1950s (Lablaika et al., 1991). In the early 1950s, cod formed the largest part of Baltic fish landings (Fig. 6) and intensive cod fishing in this period is indicated by the rapid increase in fishing mortality (Paper II). During a ca 20-year period, the eastern Baltic cod fishery had changed from coastal, low intensity hook and line fishery to a fully developed trawl fishery exploiting all areas of the Baltic and exerting a high fishing mortality on the stock (Paper II, III).

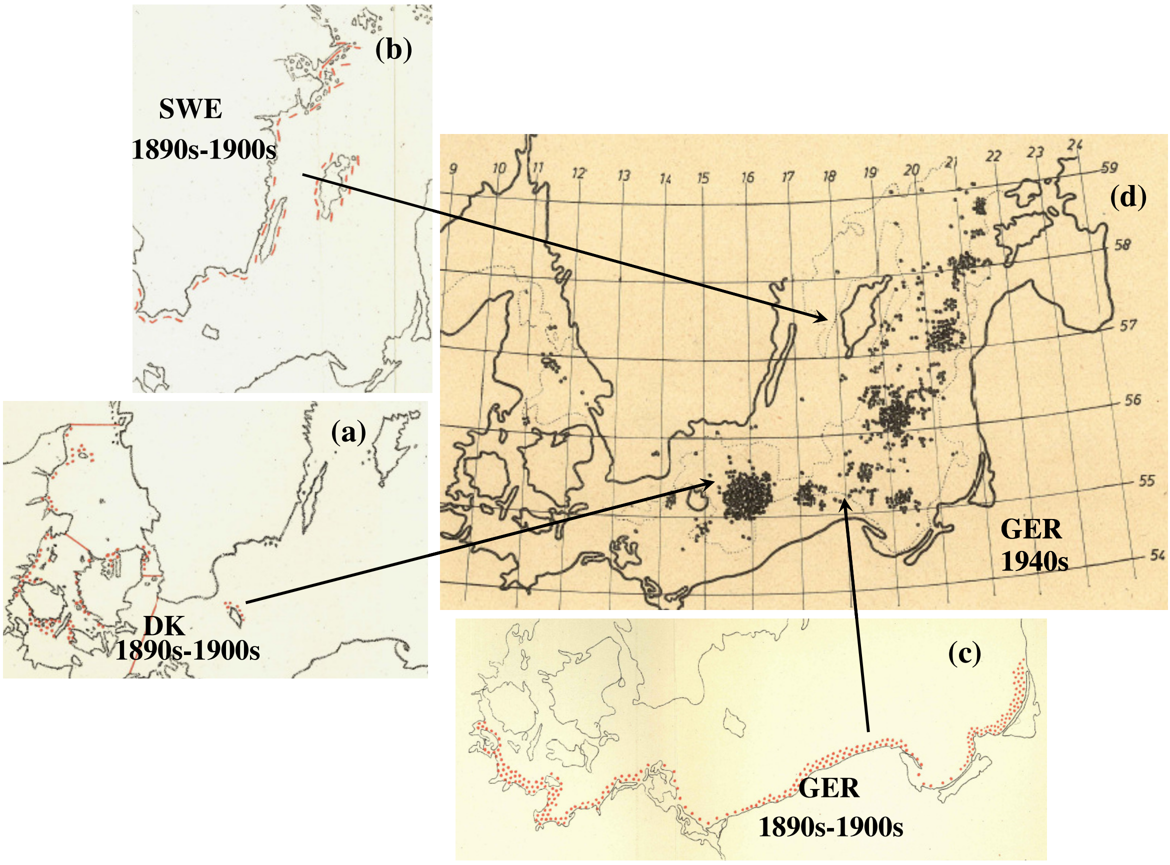

Fig. 9. (a) Danish (DK, Otterström, 1904), (b) Swedish (SWE, Trybom and Wollebæk, 1904) and (c) German (GER, Fischer and Henking, 1905) cod fishing areas in the Baltic in the 1890s-1900s compared to (d) German cod fishing areas during the Second World War (Meyer, 1952a).

4.3. Development of scientific investigations on the eastern Baltic cod

Research activities on Baltic fish and fisheries have a long history, dating back to the 18th century in Sweden (Sandahl, 2003). The first larger scale scientific expeditions related to fish and fisheries in the Baltic were conducted in the 1850s by the Baltic German naturalist Karl Ernst von Baer who laid the foundation of fish biology and fisheries science in the Russian Empire (Lajus et al., 2007). The fish investigations were mainly focussed on herring that had shown decline in landings and these expeditions have been suggested as the earliest large-scale scientific studies in the world addressing overfishing of marine fisheries (Lajus et al., 2007).

In order to coordinate investigations in marine fisheries and oceanography, the International Council for the Exploration of the Sea (ICES) was established in 1902. This organization had a crucial role in the further development of fisheries research in the Baltic Sea. In 1910 the First International Baltic Sea Fisheries Congress was organized to discuss the fisheries for salmon, sea trout, flounder, eel, herring and sprat in the Baltic (Ojaveer, 2002). The priorities of ICES member countries in marine problems in the early 1900s were largely related to the salmon and herring fisheries and the protection of undersized plaice (Ojaveer, 2002). Apparently, cod was not in the priority list for early fish investigations in the Baltic likely due to its relatively low importance for the fishery.

The first documented research materials on cod are from German surveys with RV "Poseidon" that started in 1903. The purpose of the first trips was to study fish eggs and larvae. In 1925 the investigations were expanded to the spawning stock. In this period flatfish were still much more important for the fisheries and therefore cod was given relatively less attention (Kändler, 1944). A few other studies before the 1940s were dealing with cod, e.g. Swedish investigations on growth, spawning and distribution (Hessle, 1923) and Danish investigations on cod biology, reproduction and growth (Poulsen, 1931; Jensen, 1959a). The first extensive scientific investigation of commercial catches of cod was conducted by Altnöder (1939), though only briefly documented. The first well-documented large-scale investigations on commercial cod fisheries in the Baltic are from the years of the Second World War where the Baltic cod provided the most important fish supply for the German steamer fleet. The research was first of all related to economic interests, i.e. catch rates in different areas, catch compositions and quality of the fish (Meyer, 1952 a, b, c). The chaos during the war and in the years after implied that a lot of valuable scientific information likely got lost, e.g. the materials from extensive cod investigations on the Estonian coast and in the Gulf of Riga during the war (Meyer, 1952b). Also, the materials collected on the Baltic cod before the war but not published at that time likely got lost during the war. Consequently, the scientific information on cod before the 1940s is relatively scarce.

After the Second World War, fish became an important food resource in the former east-block countries and fishery was part of the socialist planned economy. The analyses of the status of fish stocks and predicting future fishing possibilities were prioritized, leading to rapid development of applied fisheries science in these countries (Ojaveer et al., 2000). Therefore, the data for analysing the status of the cod stock were collected in the eastern countries well before the development of international assessments. However, the data were at this time not compiled for estimating the absolute stock size.

Research related to the status of fish stocks was not of equally high priority in all the countries. Large part of cod-related research activities focussed on e.g. distribution and migration in order to distinguish between different stocks. Accordingly, major research effort was put into tagging studies that started already before the Second World War (Aro, 2002). Little effort was made at this time to understand the long-term dynamics of fish populations; as the research related to stock dynamics mainly focussed on predicting short-term future catches. This is a general characteristic for fisheries science that the research focus first in recent decades has shifted from the immediate need to predict catches to the longer-term need to understand the population dynamics and related ecological mechanisms (Smith, 1994).

Although, the first research activities on fish in the Baltic were among the earliest in the world, long term changes in fish abundances in the Baltic Sea are much less well documented than in other areas. Analytical assessments of fish stocks in the Baltic Sea are shorter than available for example for the North Sea, North-East Arctic and Greenland (Buch et al., 1994; Pope and Macer, 1996; Hylen, 2002). This is partly due to different research priorities implying that the necessary data were simply not collected. Additionally, the geopolitical situation hampered data accessibility between the countries implying that the available materials have not been compiled. The first attempt to compile the relevant information for estimating cod stock size in the Baltic before the 1970s was made by Thurow (1999) and is carried further in this Ph.D. study (Paper II, III). The study also contributes significantly to understanding the causes of long-term changes in this stock (Paper IV).

4.4. Methodology used to construct the historical stock size

The historical, economic and geopolitical situation affected priorities for data collection and consequently historical data availability. This largely determines the opportunities and limitations for estimating eastern Baltic cod stock size at different time periods. The earlier preliminary calculations of the biomass of eastern Baltic cod before the 1970s (Thurow, 1999) were based on i) catch curve analyses using pooled age compositions from research and commercial catches and ii) catch per unit of effort data. The mortalities from catch curve analyses for the 1920s-1930s were in these investigations largely based on data from young fish surveys by eel-tog catching mainly 0 and 1-year old cod (Thurow, 1997a) that can hardly represent the mortality and consequently the biomass of an adult population reliably. The biomasses from the analyses of catch rates before the 1940s suggested unrealistic mortalities and were considered as unreliable by the author (Thurow, 1999). Therefore, the perception of cod biomass in the Baltic, especially before the 1940s needs to be evaluated by alternative data and analyses that was a major task for this Ph.D. study.

The previous knowledge of historical stock dynamics of the eastern Baltic cod was improved by recovering more extensive data material than previously considered and by more comprehensive evaluation of the data sets and methods in terms of being reasonably representative and appropriate for estimating historical stock size. The methods applied in this study to estimate the dynamics of the eastern Baltic cod stock before 1966 (Papers II, III) are briefly described below.

The period 1946-1965:

Virtual Population Analysis

Virtual Population Analysis (VPA) forms the basis of the standard methods used nowadays for estimating the size of fish stocks. The theory of this method developed in the 1960s (Gulland, 1965) and VPA became a standard tool in the 1970s (Ulltang, 2002). The method relies on the age structure of the catches and calculates the number of fish alive for each cohort (year-class). The analysis is based on a simple relationship for each cohort (Hilborn and Walters, 1992):

$$\begin{array}{c}\text{Number alive at}\\ \text{beginning of}\\ \text{next year}\end{array} = \begin{array}{c}\text{Number alive at}\\ \text{beginning of}\\ \text{this year}\end{array} - \begin{array}{c}\text{Catch this}\\ \text{year}\end{array} - \begin{array}{c}\text{Natural}\\ \text{mortality}\\ \text{this year}\end{array}$$

In the north-east Atlantic area, a VPA based method called Extended Survivors Analysis (XSA; Shepherd, 1999) is the standard analytical method for assessing demersal stocks, including cod in the Baltic Sea. The data on age composition of the catches compiled in this Ph.D. project allowed the analytical assessment of the eastern Baltic cod to be extended backwards until 1946, i.e. for 20 more years than what is currently available from ICES (Paper II). The analysis provides stock numbers and fishing mortalities by age-groups. Additionally, the total stock biomass and spawning stock biomass were estimated using compiled information on individual weight at age and assumptions on proportion mature by age (Paper II).

The period 1925-1944:

In the period before the mid-1940s the data were more scarce compared to the later decades inevitably leading to larger uncertainties in the stock estimates. Therefore, several independent analyses were conducted in order to evaluate the consistency in the results.

For the period before the Second World War, data on the age-structure of the catches were unavailable and standard stock assessment methods could therefore not be applied. In data poor situations and for estimating historical dynamics of fish populations, simpler methods have to be used. A method that is very often applied in these situations is e.g. surplus production model (e.g., Rose, 2004). In the case of the Baltic cod, this method was however not considered applicable, due to lack of a time series of relative abundance index that would be sufficiently long and show large contrasts that is needed in order to fit the model reliably (Haddon, 2001). Also, surplus production models are based on the assumption that population changes are largely driven by fishing, while Baltic cod was only very little exploited before the 1940s (Paper III). Therefore, four alternative approaches were used in this study for estimating the stock size in 1925-1944.

Linearized catch curve analyses

A method commonly applied in temperate waters for estimating total mortality is linearized catch curve analysis (Beverton and Holt, 1956; Ricker, 1975). The method uses information on age structure of the catches and tracks the reduction in numbers of a year-class with age. In situations where age information is lacking, e.g. in tropical waters, length distributions can be used instead by inferring the age structure from the information on growth. The method is called length-converted catch curve analysis (Sparre and Venema, 1998). The available length composition data for the eastern Baltic cod allowed this approach to be utilized for estimating total mortality in the early 1940s (Paper III).

Egg production method

For the 1920s-1930s, a simplification of the egg production method (Parker, 1980; Lasker, 1985) was applied. The egg production method has frequently been used to estimate the spawning stock size of pelagic species. For the eastern Baltic cod, a significant relationship between potential and realized egg production has previously been demonstrated (Kraus et al., 2002), suggesting the possibility to estimate the spawning stock biomass on the basis of egg production. Estimating potential egg production however requires information on maturity, fecundity etc., that were not available for the historical period. Therefore, a simplified approximation was utilized, assuming similar egg abundances to reflect similar spawning stock biomasses (Paper III).

Analyses of catch rates from research surveys

Relative abundance indices from research surveys were utilized to produce an estimation of absolute level of stock size, assuming catch per unit of effort to be proportional to the stock size (Paper III). This is a general assumption used in many standard stock assessment methods (e.g., Hilborn and Walters, 1992).

Analyses of spatial distribution of landings

An alternative method was applied for estimating the biomass in the 1920s-1940s using the knowledge of spatial distribution of cod in the Baltic at different stock sizes. Increased cod landings in the northern Baltic and in the gulfs can be used as an indicator of increased distribution area and stock abundance (Aro and Sjöblom, 1982; Ojaveer et al., 1985; Ojaveer et al., 1999). Accordingly, similar amounts of landings in the northern Baltic and in the Gulf of Riga in the 1920s-1940s compared to the landings in recent period were assumed to indicate similar levels of stock size (Paper III).

The estimates produced in this study to prolong the time series of cod stock dynamics are based on poorer and less representative data than available for the assessment working groups in ICES in recent decades (Paper II, III). Therefore, the exact values of the historical biomass estimates, especially before the 1940s should be treated with caution. However, it is important to realize that the purpose and perspectives of constructing historical developments of fish stocks differ from those of the regular stock assessments conducted by ICES.

Contemporary assessments are used to provide advice on total allowable catches by predicting future year-class strength and stock size at a certain level of fishing. To make this prediction, a high precision in the annual stock estimates is required, especially in the latest years. In contrast to regular stock assessments, the purpose of reconstructing historical developments of fish stocks is generally to examine broad temporal trends instead of details in annual variability (Pope and Macer, 1996; Rose, 2004). Information on long-term population trends helps to improve the understanding of ecological processes influencing stock dynamics and the magnitude of different human influences on marine ecosystems and fish stocks. This is one of the main objectives also in this Ph.D. study and the historical stock estimates were used to identify major fluctuations in stock size at different time periods under variable environmental conditions and anthropogenic influences in order to evaluate their relative impacts. Therefore, although the historical stock estimates are based on less representative data compared to the later period, this is not expected to seriously affect the outcome of the study.

The major uncertainties related to each of the analyses are discussed in the papers (Paper II, III), and are therefore not addressed here in details. Concerning the time period 1946-1965, the uncertainties in the stock estimates were shown to be mainly related to poor data coverage for Subdivision 25. The data coverage for the subpopulations in SDs 26 and 28 was considered to be similar to the later period. The problem of uncertainties in the stock estimates before the mid-1940s was tackled by i) using multiple datasets and different approaches that were independent of each other and thereby allowed evaluation of the consistency of the results, ii) discussing the uncertainties, providing the best possible evaluation of the direction of potential bias in the results, iii) treating the results with suitable caution while drawing conclusions, iv) providing additional qualitative evidence to support the conclusions. The multiple proxies of stock size were consistent, which increases the confidence in the results (Paper III).

The multiple methods applied in parallel with relatively similar outcome (Paper III) may be useful for exploring the possibilities for reconstructing cod stock size even further back in time. Generally, the data material for reconstructing the cod biomass in earlier decades is even scarcer than for the period covered by this thesis. However, if the necessary data for one of the methods applied in this thesis would be available for the earlier period, this could potentially be used to provide a proxy for the stock size as in this study the different methods were validated by multiple approaches. From the types of information used in this thesis, the spatial distribution of landings is likely the most promising for potentially estimating the stock size in earlier periods as a lot of respective information for the 16^{th}-17^{th} century has already been recovered through archival research (MacKenzie et al., 2007a).

5. Cod stock dynamics under variable climate and human impacts

5.1. Relative impacts of human activities on cod stock dynamics

Understanding the anthropogenic impacts on fish population dynamics and ecosystems is of central importance for sustainable management of marine resources. Separating the effects of human activities and resolving their interactions with natural variability is however often difficult as natural variations, e.g. changes in climate, have additional major impacts on fish populations and ecosystems. The difficulties of separating the effects of different factors are in many cases also related to the shortness of available time series (e.g., MacKenzie et al., 2002b; Jennings and Blanchard, 2004) and to co-varying driving forces. An example of this is the cod in the Baltic Sea, where the impacts of fishing and other anthropogenic influences on population dynamics are presently not well understood.

The stock dynamics of the eastern Baltic cod is available from ICES assessments from 1966 onwards. The spawning stock biomass since 1966 has varied between approximately 100 000 and 700 000 tonnes. The highest stock size was recorded in the late 1970s - early 1980s and in recent years the stock has been at the lowest level observed since 1966 (ICES, 2007a; Fig. 10). The stock in the early decades of the 20th century is previously believed to have been at a very low level, largely based on low landings and preliminary biomass estimations by Thurow (1999), which are however associated with large uncertainties. Nevertheless, in the absence of other investigations, the current understanding of the impacts of major human-induced changes in the Baltic ecosystem in the 20th century is based on the perception of a very low cod stock size before the 1940s.

This Ph.D. study extends the time series of stock development of the eastern Baltic cod back to 1925, i.e. by app. 40 years further back in time than the ICES assessments (Fig. 10). The results of this reconstruction of historical population dynamics contradict the previous view that the cod stock size in the Baltic was very low in the early decades of the 20th century. The cod stock was estimated to have varied in a similar range in the 1920s-1940s as in the 1950s-1970s and from the mid-1980s to the present (Fig. 10). This estimate is based on more extensive data and more comprehensive analyses than previously considered and the results therefore represent an important advance in the state of knowledge of historical stock dynamics of the eastern Baltic cod (Paper III).

The improved knowledge of cod population dynamics puts the influence of human-induced ecosystem changes, i.e. reduction in marine mammal predators and increase in nutrient concentration into a new perspective. The impacts of these changes in the upper and lower trophic level on fish populations in the Baltic Sea have previously been discussed (e.g., Nehring et al., 1989; Hansson and Rudstam, 1990; Thurow, 1997b) and recently investigated by a mass-balance ecosystem model (Österblom et al., 2007). These earlier studies were based on the opinion that the cod stock was very low until it started to increase in the 1940s, suggesting this to be the effect of reduced marine mammal predation and increased nutrient loading (Thurow, 1997b; Österblom et al., 2007). The record high cod abundance in the late 1970s - early 1980s has been suggested to be due to a combination of favourable hydrographic conditions and increased nutrient input (e.g., Bagge and Thurow, 1994; Österblom et al., 2007). However, none of these analyses has simultaneously considered the historical developments in all four key factors, i.e. climate, fishing, eutrophication and marine mammals, as potentially influencing long-term cod stock dynamic, at a sufficiently high time resolution.

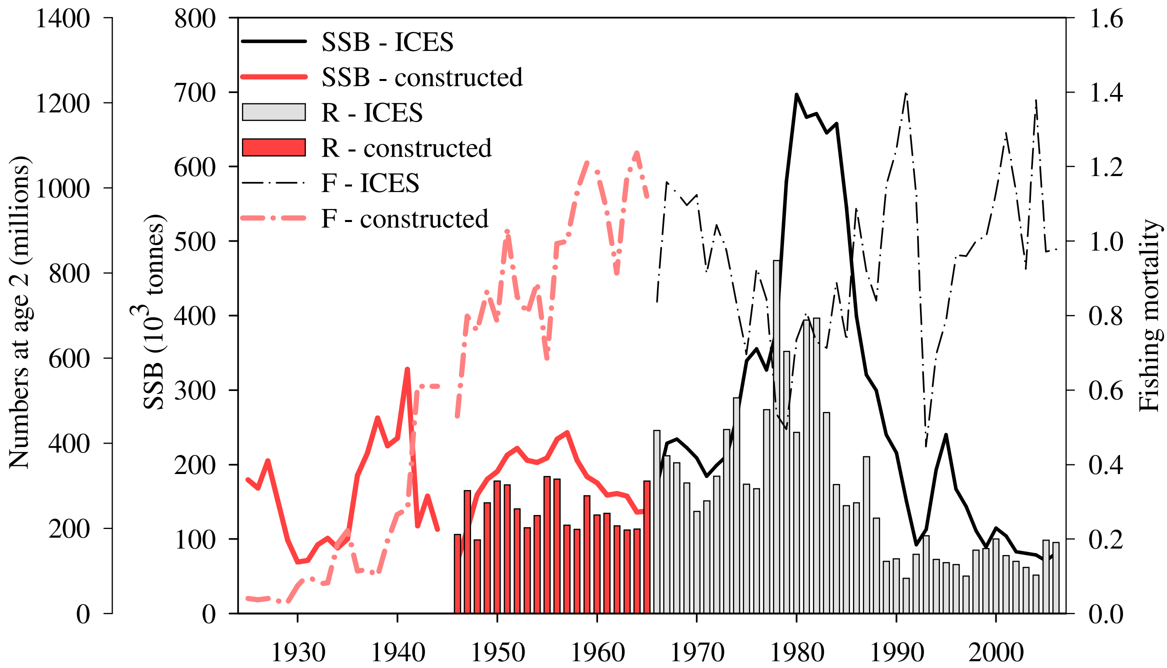

Fig. 10. Spawning stock biomass (SSB), recruitment (age 2) and fishing mortality of the eastern Baltic cod (SD 25-32) as available from ICES assessments from 1966 onwards (ICES, 2007a) and the constructed estimates back to 1925 (based on Papers II, III, IV).

This Ph.D. study, reconstructing the cod stock dynamics in the period when major changes in human perturbations on the Baltic ecosystem occurred, reveals the cumulative and compensatory effects of different factors at different time periods (Paper IV, Fig. 11). Major reductions in marine mammal abundance occurred during the period from the 1900s to 1940s, when the number of grey seals was reduced by about four to five times and the number of ringed seals by more than eight times (Harding and Härkönen, 1999).

The increase in nutrient loading started thereafter, i.e. after the Second World War (Elmgren, 1989), when the abundance of marine mammals was already reduced substantially; during the 1940s-1960s their numbers were stable (Harding and Härkönen, 1999). The expected positive impacts of these two factors on the cod stock were counteracted by substantial increases in fishing mortality in the period from the late 1930s to 1950s (Paper II, III). The increased nutrient load may have enhanced the cod biomass up to the mid-1950s, partly compensating for the increase in fishing mortality, while no major positive impact of the continued increase of nutrients during the 1950s-1980s was detected (Paper IV).

Thus, this study did not confirm that increased nutrient concentrations could explain the record high cod stock in the late 1970s - early 1980s. Hydrographic conditions had been similarly favourable earlier in the 20th century and can not by themselves have been responsible for the substantial stock increase either. The stock in the time period in the late 1970s - early 1980s experienced a combination of four major factors favouring the cod stock, i.e. favourable climate enhancing reproductive success, low marine mammal predation, high ecosystem productivity and reduced fishing pressure. A similar combination has not occurred earlier in the 20th century, and probably explains the record high stock level in the late 1970s - early 1980s (Paper IV). In the 1920s-1940s the cod stock was likely limited by low ecosystem productivity and high abundance of predators, i.e. marine mammals, and in the 1950s-1960s by high fishing pressure (Fig. 11). The low stock level in recent decades is considered to be due to a combination of high fishing pressure and reduced recruitment success (Bagge et al., 1994; Köster et al., 2003) that is related to poor salinity and oxygen conditions. The period corresponding to the stock in the late 1970s - early 1980s clearly stands out as representing milder pressures on the cod stock, compared to the other time periods in the 20th century (Fig. 11).

In the present study, the mainly qualitative analyses of relative effects of different forcing factors on cod stock dynamics are based on constructing and interpreting the historically observed patterns. Acting mechanisms could be further investigated e.g. by ecosystem modelling exercises. As an example, the increase in nutrients in the 1940s-1950s was suggested to have contributed to the enhancement of cod SSB in this period. The magnitude of the likely increase in cod production and/or individual growth as a response to increase in primary production and subsequent higher trophic levels in the Baltic ecosystem could be subject for future analyses.

This study highlights some of the important issues that should be considered in future modelling exercises not only in order to improve the understanding of ecosystem functioning but also to simulate the consequences of future management scenarios. The investigations presented here demonstrate the importance of looking at relevant ecosystem drivers in parallel and at a relatively high time resolution in order to improve understanding of the relative impacts of single factors on fish populations.

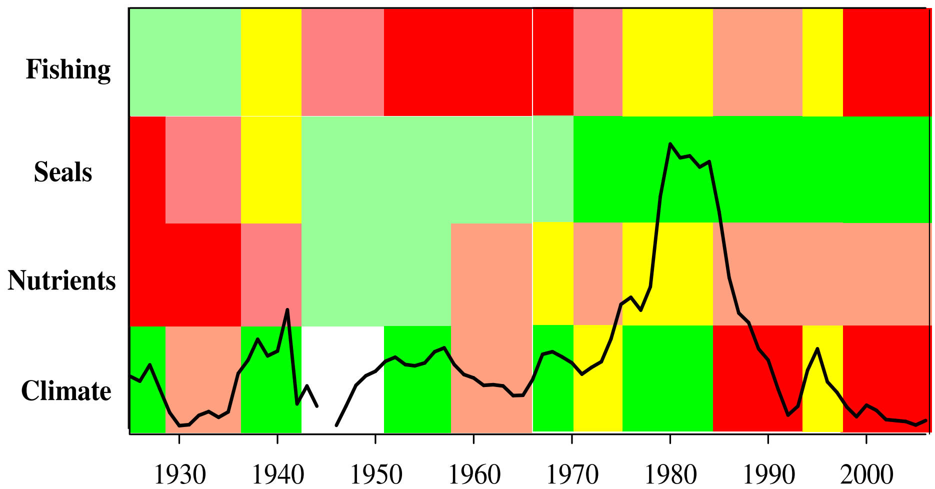

Fig. 11. Major changes in the impact of climate, nutrients, seal abundance and fishing on the spawning stock biomass of eastern Baltic cod (represented by the line) in 1925-2006. The years on the x-axis refer to the cod spawning stock biomass. The colours represent schematically the changes in different factors corresponding to major fluctuations in the cod biomass. The colour scale from red to green denotes restricting and favouring influence of the changes in forcing factors on the cod stock, respectively (Paper IV).

5.2. Can the historical reference level of the cod biomass be identified?

A general goal for rebuilding depleted fish stocks is to restore the pristine state of the ecosystem or the “virgin biomass” of fish populations. However, a stable pristine state or a constant level of “virgin biomass” has been demonstrated not to exist for several populations showing large scale fluctuations in pre-industrialised time period (e.g., Baumgartner et al., 1998; Finney et al., 2000). Also, it is difficult to define the pristine state of an ecosystem that is continuously evolving and changing over time (Holm, 2003). These issues are relevant also for the Baltic Sea in relation to defining the target levels for recovering fish populations or restoring the historical state of the ecosystem.

The spawning stock biomass of eastern Baltic cod has fluctuated between less than 100 000 and up to 700 000 tonnes in the period since 1925. The stock levels at different time periods reflect the developmental stages of the Baltic ecosystem partly related to developments in human society that have modified the Baltic environment, e.g. hunting, developments in fisheries, agriculture and industry etc. Human impacts on the Baltic ecosystem were considerably lower in the 1920s compared to later decades. Nevertheless, cod biomass in the Baltic in the earlier decades was lower compared to the record high stock size in the late 1970s - early 1980s (Paper III). The eastern Baltic cod thereby provides a contrasting example to many other marine fish stocks that were much larger in pre-industrialized time periods compared to their present levels (e.g., Myers and Worm, 2003; Rosenberg et al., 2005).

It is presently unknown whether similar high cod stock levels as observed in the Baltic in the late 1970s - early 1980s have ever occurred earlier in the past. In previous centuries, the Baltic environment was probably rather unfavourable for cod as the Baltic was oligotrophic and contained large abundances of marine mammals. There are also some indications that the salinity, particularly in the 1500s-1600s, might have been lower than at present (Emeis et al., 2003; Bock et al., 2005). In general, the conditions in the past centuries with respect to presence of cod predators, low ecosystem productivity and low fishing pressure can be expected to have been more similar to the conditions in the early decades of the 20th century compared to later developments. As the cod stock size in the 1920s was estimated to be lower than in the late 1970s - early 1980s, earlier occurrence of cod biomasses as high as observed in the late 1970s - early 1980s may be considered relatively unlikely. However, there are indications that cod was relatively abundant in the Baltic in some periods during the 16th -19th century (MacKenzie et al., 2007a). Continued investigations on the stock size in previous centuries could reveal whether similar levels of cod biomass as observed in the late 1970s - early 1980s have ever occurred before in the Baltic that would help to further elaborate on the necessary preconditions.

In the 20th century, different human impacts modified the level of cod stock size significantly; however major trends coincided with climatic variations related to the intensity of major Baltic inflows that influence cod recruitment through various processes. Major fluctuations in cod stock size corresponding to the trends in climate variability occurred also in the early decades of the 20th century when the human impacts on the stock were much lower compared to later developments (Paper IV).

It is well known that besides the environmental variables self-regulating internal forces, such as density dependence can affect individual survival (e.g., Bjørnstad et al., 1999; McCann et al., 2003; Cianelli et al., 2004). Understanding their joint effect is however complex (e.g., Cianelli et al., 2004). In the eastern Baltic cod, analyses of data for the 1970s-1990s have shown cannibalism to increase at higher stock abundances (Neuenfeldt and Köster, 2000) and it is suggested to be an important self-regulatory mechanism in the central Baltic stock (Sparholt, 1995). In the earlier decades of the 20th century when the productivity of the Baltic ecosystem was lower, the carrying capacity for cod can be expected to have been lower compared to e.g. the 1970s-1980s. Cod stomach analyses from the early 1940s showed that cannibalism in this period occurred in all the areas in the Baltic (Meyer, 1952c) indicating the operation of self- regulatory mechanisms also in this period.

Hydrographic conditions influencing cod recruitment in the Baltic have shown cyclic variations in the 20th century. Longer periods with constantly favourable climatic conditions have not been observed, which makes it difficult to detect potential oscillations in the cod stock driven by density dependency. Favourable climate enhances cod recruitment and subsequently the stock size; at high stock sizes self-regulatory mechanisms are expected to intensify. If this is followed by deterioration of climate conditions contributing to reduced recruitment, separating the effects of environment and density dependency is difficult. Therefore, historic oscillations in cod biomass in the Baltic may also partly be related to self-regulatory mechanisms besides the climate variations.

Density dependent processes have been argued to influence the growth and size at maturity of fish populations (e.g., Cardinale and Modin, 1999; Cook et al., 1999; Lorenzen and Engberg, 2002). The evidence for density-dependent growth is however not convincing where the studies have not considered alternative explanations for the growth changes, e.g. changes in prey abundance (Brander, 2007). The eastern Baltic cod shows significant negative relationship between weight-at-age and stock abundance using data from recent decades (Brander, 2007); this has however been ascribed to predator-prey relationships between cod and sprat and herring, rather than to density-dependence (Gislason, 1999; Brander, 2007). Food availability has also been shown to influence the relative fecundity of eastern Baltic cod (Kraus et al., 2002). Historical information on cod prey abundance is scarce and its possible influence on cod population dynamics before the 1970s could therefore not be evaluated. However, the available growth information from the mid-1940s onwards indicates that the growth in the period from the mid-1940s to mid-1970s was stable (Paper II). In the time period before the mid-1940s, potential changes in growth and in reproduction parameters such as size at maturity and fecundity could have modified the spawning stock biomass estimates from some of the analyses (Paper III). However, as multiple analyses using different data and assumptions resulted in consistent estimates, these changes are not expected to affect the results seriously.

6. Implications for fisheries management

Major historical changes in the management of the eastern Baltic cod

Up to the second half of the 20th century, the cod fishery in the Baltic was not internationally regulated. The need for international measures to protect the Baltic cod stock was first realized in the 1950s. In 1957, a special scientific meeting on measures for improving the stocks of demersal fish in the Baltic was held. It suggested a minimum landing size of 30 cm for cod and a mesh-size of 80 mm in the cod-end of demersal trawls (Jensen, 1959b). In some countries technical measures in cod fishery were in place already earlier, whereas for example, in Poland, which was one of the main cod fishing countries in the Baltic in the 1950s, technical measures were first introduced in 1963. Consequently, a substantial reduction in the proportion of young cod in the catches was observed (Kosior, 1975). Total allowable catches to limit the fishery removals of cod, herring and sprat in the Baltic were first implemented in 1977.

Since the late 1990s, the eastern Baltic cod stock has been managed according to the so-called precautionary approach that is based on reference levels for biomass and fishing mortality. These reference points are predefined limits that should be avoided to ensure that the stock and its exploitation are within safe biological limits (ICES, 2000). The limit for spawning stock biomass (Blim) is defined as a level below which the probability of recruitment failure is high or the dynamics of the stock are unknown. For the eastern Baltic cod this minimum level of spawning stock biomass has currently been set to 160 000 tonnes (ICES, 2007b). Recently, a management plan for the eastern Baltic cod stock has been adopted with a target fishing mortality at 0.3 to ensure a low probability of the spawning stock biomass falling below 160 000 t (ICES, 2008).

Management reference points

The basis for the biomass reference point is the stock-recruitment relationship over a period of time. However, identifying the level of spawning stock below which recruitment is restricted by spawning stock size is not trivial, as stock-recruitment relationships are often noisy and affected by measurement errors (Hilborn and Walters

1992). In addition to the influence of spawning stock size, recruitment can also be strongly influenced by environmental variability, as is the case for the eastern Baltic cod. Differences in the estimate for Blim for this stock considering different time periods with variable environmental conditions have recently been intensively discussed (ICES, 2007a, b).

The currently defined biomass reference point is based on the data from 1976 onwards. The earlier information back to 1966 is excluded as these data are considered to be of poor quality (ICES, 2007b). This Ph.D. study has generated stock and recruitment data-points for an additional 20 years and documented more specifically the uncertainties in the historical data compared to the more recent. For Subdivisions 26 and 28 the data coverage for the period from the mid-1940s to the mid-1970s was found similar to the following years (Paper II). The extended time series covers the period where variations in climate also occurred and can potentially improve the basis for exploring the dependency of biomass reference point on environmental conditions.

The data currently used for estimating biomass reference points include the period of relatively high stock productivity in the late 1970s in terms of the recruitment produced per unit of spawner biomass followed by lower productivity in the more recent decades. The reconstruction of stock developments further back in time puts these productivity changes into a longer-term historical perspective. The high stock productivity in the 1970s does not appear to be historically outstanding as similar numbers of recruits per spawning stock biomass were produced in several periods during the late 1940s-early 1970s. In the recent period since the 1980s the stock productivity appears to have changed to a lower level compared to the previous period, especially in the eastern areas (Fig. 12).

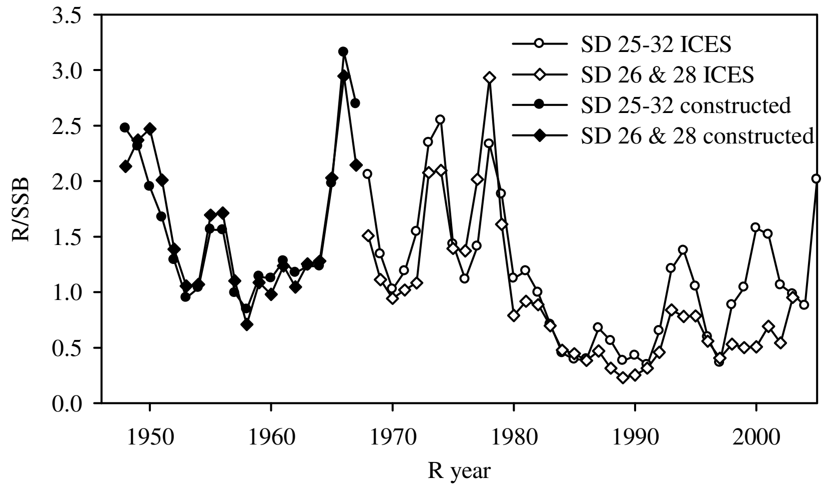

Fig. 12. Recruitment (age 2) produced per unit of spawning stock biomass (SSB) for the total stock (SD 25-32) and separately for SDs 26 and 28 (based on data from Paper II and ICES, 2006, 2007a).

Evaluation of management measures

The constructed long term stock development can contribute to the evaluation of the historical performance of the management measures applied on this stock. For example, one of the goals of sustainable fisheries management is a rational selection pattern to protect small fish and thereby enhance the spawning stock.

Stricter regulations and technical measures to protect small cod in the Baltic have gradually been implemented in the second half of the 20th century; major positive effect on young cod survival is however not obvious. Although, the proportion of young fish in the reported landings has been lower in recent years than e.g. in the 1950s, the effect is counteracted by discarding (Fig. 13). Information on discards for the 1950s is not available; however high-grading, i.e. selectively discarding smaller individuals was unlikely to take place (Paper II). Assuming no discarding for the early period, the fishing mortality in the 1950s when no international protection measures were yet enforced was estimated at a relatively similar level as in recent years where the data includes discards (ICES, 2007a; Paper II).

At present the level of fishing mortality on eastern Baltic cod is relatively high (around 1.0) and the desired reduction in fishing pressure has not been achieved (ICES, 2007a). It is interesting to note that after the cod fishery had fully developed by the 1950s and fishing mortality reached high levels, a substantial reduction in fishing pressure occurred in the period where no catch limits on the stock were yet implemented, i.e. during the first half of the 1970s (Fig. 10). The decline in cod fishing effort in this period was partly related to the development of more profitable fishing possibilities for other species, i.e. the pelagic fishery for sprat and herring (Lablaika et al., 1991). Hilborn (2007) discusses the potential success of two fisheries management strategies, one attempting to manage the fisheries by increased level of regulations, and the other by changing fishermen's incentives. Baltic cod provides a good example of the second case, where the changed economic incentives are likely to have reduced fishing mortality, whereas the long-term effect of stringent management measures in a situation where the cod fishery has been highly profitable is less obvious.

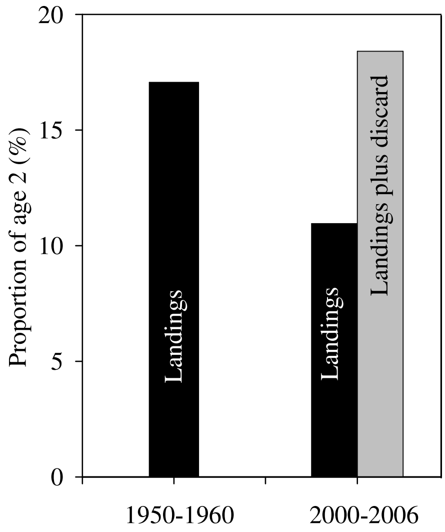

Fig. 13. Proportion of cod at age 2 in landings and in total catches (incl. discard) (based on data from Paper II and ICES, 2007a).

Future scenarios

At the present state of the Baltic ecosystem, it is difficult to predict whether high cod abundances as observed in the late 1970s - early 1980s can ever be reached again. According to the present understanding of future hydrographic conditions, declines in salinity due to increase in precipitation in the 2000s are to be expected due to climate change, which indicates a pessimistic outlook for eastern Baltic cod (MacKenzie et al., 2007b). Due to the strong influence of hydrographic conditions on the recruitment of eastern Baltic cod, such changes are important to take into account in defining realistic target levels for rebuilding the population. However, even at the present low level of recruitment, a reduction in fishing mortality is expected to result in a substantial recovery of the stock compared to its present level (ICES, 2008). The cod stock has historically responded significantly to human-controlled changes, including a reduction in fishing pressure (Paper IV), which demonstrates the potential for enhancing the cod biomass in the Baltic by management measures.

In addition to recovery of the cod stock, rebuilding the seal populations and reducing eutrophication are part of the goals for ecosystem management in the Baltic Sea. Some research effort has been made to analyse fisheries management scenarios in the Baltic at different levels of marine mammal abundances and ecosystem productivity (e.g., Hansson et al., 2007). The results of this Ph.D. study, providing the time series of cod stock dynamics in the time periods of different level of marine mammal abundance, nutrient load and fishing effort and at variable climate provide valuable information for validating the results from exercises simulating future management scenarios.

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Cover picture: Drechsel, C.F. 1890. Oversigt over vores saltvandsfiskerier i Nordsøen og farvandene indenfor Skagen. København, p. 51.

Paper I

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Fisheries Research 87 (2007) 155–166

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Review

Development of international fisheries for the eastern Baltic cod (*Gadus morhua*) from the late 1880s until 1938

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Received 3 July 2006; received in revised form 16 February 2007; accepted 22 February 2007

Abstract

The paper provides an overview of eastern Baltic cod (*Gadus morhua*) fisheries from the end of the 1880s until 1938, in order to improve the knowledge of long-term stock dynamics. The data compiled and included in the study comprise catches and economic values of exploited fish species, time series of indicators of fishing effort and qualitative information on developments in fishing technology. This information has been assembled for different countries and locations in the Baltic Sea. We first summarize the multi-decadal development of national cod fisheries and their relative importance during the first decades of the 20th century. We then assess whether these data can be used to estimate the relative roles of fishing and ecosystem changes on variations in catches. We conclude that the assembled data reveal biologically meaningful variations in the state of the cod stock and that some of the variations in the catches of different countries (e.g. decline in the late 1920s; increase in the late 1930s) were caused by factors other than fishery developments. These factors probably include ecosystem-induced variations in cod population dynamics and need further investigation.

Keywords: Baltic sea; Cod fishery; Exploitation; Historical development; Late 19th century; 20th century

Contents

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0165-7836/$ – see front matter
doi:10.1016/j.fishres.2007.02.015

1. Introduction

The information on stock development of eastern Baltic cod (ICES Subdivisions 25-32) is currently available from 1966 onwards (ICES, 2005a), while the biomass in earlier years is unknown. Scientific investigations since the later decades of the 20th century have demonstrated that cod recruitment and stock development in the Baltic are influenced by several factors, including exploitation, hydrographic conditions (e.g. Kosior and Netzel, 1989; Lablaika et al., 1989; Köster et al., 2005), the food supply for larvae and early juveniles (Hinrichsen et al., 2002), predation on cod eggs by clupeids (Köster and Möllmann, 2000) and cannibalism on juveniles (Sparholt, 1994; Uzars and Plikshs, 2000). In addition, several major long-term changes in the Baltic ecosystem (i.e. eutrophication, removal of large populations of marine mammal predators), which likely affect cod population dynamics (Thurow, 1997; MacKenzie et al., 2002a) have occurred prior to the start of the available time series of cod biomass. Therefore, longer time series of stock dynamics are needed in order to better understand the causes of long-term variations in stock abundance and the role of human impacts on the Baltic ecosystem.

Previous studies in other areas using data from the 19th and earlier centuries have shown that fishing was the dominant factor responsible for century-scale declines of cod populations near Newfoundland (Rose, 2004) and on the Scotian Shelf, eastern Canada (Rosenberg et al., 2005). In the Baltic; however, it is presently unclear whether fishing had a similarly large role on the long-term development of the local cod stock (MacKenzie et al., 2002a,b). Available documentation indicates that cod has been intensively exploited only since the 1950s (Bagge et al., 1994). Earlier landings were <50,000 tonnes/year (Fig. 1; Bagge et al., 1994; Sparholt, 1994; Thurow, 1997) which is not only much lower than during the more recent decades, but also relatively lower than cod landings in other geographic areas (Øiestad, 1994; Daan et al., 1994; Rose, 2004) during the same time period. The reasons for low cod landings in the Baltic are unclear and could possibly be an undeveloped fishery, low local demand for cod, changes in carrying capacity or possibly a temporarily low stock size (MacKenzie et al., 2002a).

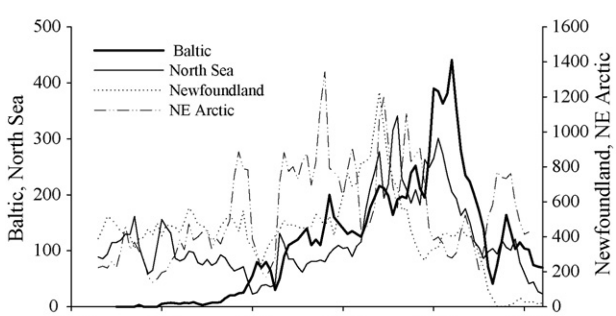

Fig. 1. Cod landings (th. tonnes) in the Baltic (Sparholt, 1994; ICES, 2005a) compared with the North Sea (Daan et al., 1994; ICES, 2005b), Newfoundland (Rose, 2004) and Northeast Arctic (Hylen, 2002) areas.

Fisheries statistics for most of the countries exploiting the cod stock in the Baltic have been systematically recorded since the early decades of the 20th century. These data are the main source of information available related to Baltic cod in the first half of the 20th century and could potentially be used for investigating historical stock developments and the relative roles of fishing and ecosystem-related factors on stock variations. In this paper we present catch, effort and economic data and provide an overview of fishing technology and gear developments and importance of the cod fishery in relation to other species for the time period from the 1880s until 1938. Our main objective is to evaluate whether observed variations in cod catches in 1880s–1938 can be attributed to developments in effort and fishing technology. Identification of time periods when variations in cod catches must be due to other factors affecting, e.g. productivity of the stock would facilitate future investigations on causes of relative trends in stock dynamics and historical impact of fishing on cod population.

2. Materials and methods

The geographic focus of this study is the area in the Baltic north-east of Bornholm Island (Fig. 2). Cod in this area have dif-

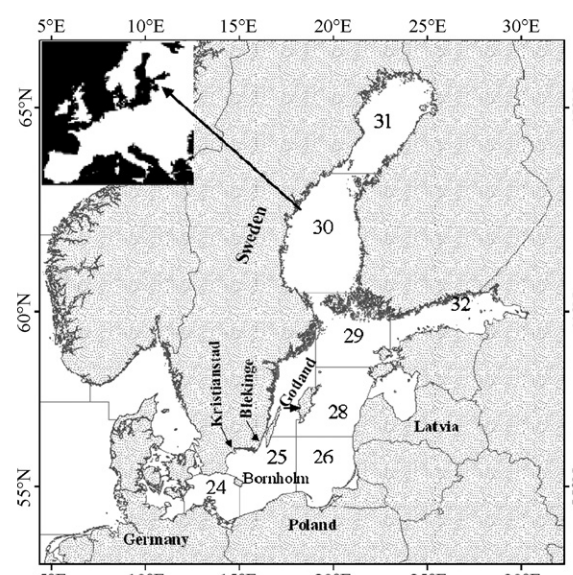

Fig. 2. Map of the Baltic Sea with names of selected localities that are mentioned in the paper. Numbers refer to ICES Subdivisions.

ferent biological traits from those west of Bornholm (Bagge et al., 1994; Nielsen et al., 2001; Aro, 2002) and are therefore considered a separate population for assessment purposes (ICES, 2005a).

The data used in this study are mainly compiled from official fisheries statistical reports of different countries available in national libraries. The fish landings corresponding to these reports are also published in the Bulletin Statistique des Peches Maritimes by the ICES, but not for all years for all countries and on a spatially disaggregated basis. The published statistics in this study is supplemented by a few datasets obtained through archival research.

The landings and revenue data are included for all species (marine and migratory fish and coastal species of freshwater origin) as recorded in available statistics for Baltic fisheries. These data enable to quantify how cod landings and their economic value varied relative to other targeted species. Data for effort indicators, if not specified, represent the total fishery in given areas for a given country, and are not usually available for individual species. Further details for data sources and treatments for each country are given below.

2.1. Denmark

Time series of systematic annual fisheries statistics since 1888 are available in the report series Fiskeriberetning published by the Danish Ministry of Agriculture (later the Ministry of Fisheries). The landings (Bager et al., 2002) and value of all the recorded fish species are given by harbour for the years 1888–1924. Data by harbour from 1925 until 1938 were obtained from the statistical materials of the Danish Directorate of Fisheries stored in the Danish National Archive. The data referring to Christiansø and the harbours located on the east coast of Bornholm Island were included as the cod landed in these ports were assumed to have been caught in the waters east of Bornholm.

Landings of herring in 1888–1915 are recorded in units of Ol corresponding to 80 individuals (Rasmussen, 1975). In order to calculate relative dynamics of the share of cod in total fish landings, herring catches have been converted to weight units by assuming an individual weight of 50 g. This assumption affects the absolute estimate of the share of cod in fish landings in 1888–1915, but its relative dynamics during these years should be reliably represented if mean weight of herring in the catches in 1888–1915 was unchanged. However, the share of cod in landings in 1888–1915 may not be directly comparable with the period 1916–1938, when herring landings were reported by weight. The cod catches in 1888–1903 are partly recorded in numbers of individuals, partly in kg. The value of catch is available separately for both and catches in numbers were converted into weight units using the data on price/kg.

The numbers of boats until 1924 and the entire time series of the numbers of fishermen are available by harbour and are presented in the paper for the areas east of Bornholm. The numbers of boats since 1924 and the entire time series of numbers of various fishing gears in the Baltic include the area west of Bornholm, which corresponds approximately to ICES Subdivision 24 (Fig. 2).

2.2. Germany

The earliest data concerning the value of German fish catches are available since 1892 in the series Mitteilungen des Deutsche Seefischerei Vereins. Systematic spatially disaggregated fisheries statistics are available in the series Deutsche Seefischerei for the years 1909–1925 and in the Jahresbericht über die Deutsche Fischerei for 1926–1938. The spatial segregation of the value of catches in the years 1892–1907 is slightly different from the later time period; therefore the time series of revenues in these two time periods may not be directly comparable. The price data are from 1922 onwards available only as an average for the whole Baltic and Belt Sea region.

The numbers of boats and fishermen in the time periods 1906–1913 and 1928–1938 are not directly comparable due to territorial changes of Germany as a consequence of the Versailles Treaty of 1919.

2.3. Latvia

Systematic Latvian fisheries statistics in 1924–1938 are published in the series Bulletin statistique des peches maritimes de Lettonie. In this study only the statistics for the harbours along the open coast of the Baltic, which is the main Latvian cod fishing area, were used (i.e. excluding the Gulf of Riga).

2.4. Poland

Polish fisheries statistics in 1922–1937 were compiled from publications by the Sea Fisheries Office (Anon., 1928, 1933a, 1936), Laszczynski et al. (1964), Hryniewicki (1925) and Borowik (1930). The data on fish prices (in Shillings) reported in the Bulletin Statistique des Peches Maritimes by the ICES were used to calculate the share of cod in the total value of Polish fish landings in 1936 and 1937. The exchange rate in 1935 was applied to convert the prices in Shillings into Polish currency in 1936–1937.

2.5. Sweden

Systematically recorded official fisheries statistics by counties since 1914 are published in the series FISKE by the Royal Statistics Central Bureau (Awebro, 2002). In this study the data are presented for Blekinge and Kristianstad counties (Fig. 2), where fisherman landed fish caught mainly in the Bornholm Basin, which was the main Swedish cod fishing area in the southern Baltic. Additionally, data are presented for Gotland, which was one of the next most important cod fishing areas, but had different technological developments.

Swedish landings and effort data before 1914 were compiled from several archival sources by the History of Marine Animal Populations (HMAP) program of the global Census of Marine Life (CoML) project (Awebro, 2002; Ojaveer et al., this volume). The present study includes data for Blekinge county for the years

1889–1910; this area has the longest time series and historically had highest cod landings in the Swedish Baltic fishery. Annual catch data are included for cod, herring (*Clupea harengus membras*), flounder (*Platichthys flesus*) and eel (*Anguilla anguilla*); these were also the most abundant species in the catches. Fish landings and their value on Gotland in 1887–1913 are presented by Hessle (1922).

2.6. Evaluation of the impact of effort developments on relative catch fluctuations

National fishing effort data in the Baltic before the 1940s are mainly limited to total numbers of boats, fishermen and fishing gear, regardless of the species that was targeted. Very few effort data are specific to the cod fishery and these do not give an estimate of the actual fishing intensity (e.g., number of days per year, etc.). Moreover, fishing technology went through major developments (e.g. motorization of vessels, increase in horse power, gear developments) and the fishery expanded spatially from coastal to offshore areas. These changes likely had considerable impact on exploitation intensity and catchability (Bagge et al., 1994). Therefore, it is difficult to construct quantitative time series representing effort in cod fisheries during this period. This prevents quantitative analysis of the relationship between cod catches and effort and construction of catch per unit of effort time series that are traditionally used as indices of relative stock dynamics.

The present study focuses on identifying the time periods when major effort developments (e.g. motorization of vessels, implementation of trawls) occurred in the cod fishery, not on absolute measure for fishing effort. Possible deviations in the dynamics of cod-directed fishing effort from the general developments are addressed by evaluating the economic incentives for changing the allocation of effort into the cod fishery over time. The dynamics of cod price in relation to other economically most important species and information on the economic importance of cod in the fishery of different countries are used as indicators for these incentives. The economically most important species included in interpreting price developments are herring and salmon (*Salmo* spp.) in all countries and areas; eel in Germany, Poland and Sweden (Bornholm area); flatfish in Sweden (Gotland area), Denmark, Germany, Poland and Latvia and sprat (*Sprattus sprattus*) in Germany, Poland and Latvia. The time series of prices of different species were standardized by subtracting the mean and dividing by standard deviation.

Based on these relative effort indicators, we discuss whether observed relative fluctuations in cod catches could be due to simultaneous developments in fishing intensity. Our main interest is the identification of major multi-annual and decadal trends in catch data for several countries, rather than variability between single years.

3. Results

Dynamics of national cod landings, their value and indicators of fishing effort.

3.1. Cod landings

Danish and Swedish cod landings both in Bornholm Basin and in the Gotland area declined in the early 1900s compared to their relatively higher levels in the end of the 19th century (Fig. 3). The reduction in Danish landings was followed by six-fold increase in the end of the first decade of the 1900s. Danish, German and Swedish landings near Bornholm area peaked during World War I, while Swedish landings near Gotland peaked somewhat later in the early 1920s. Danish, Latvian and Swedish landings (in both areas) were relatively high in the mid-1920s followed by a declining trend towards the early 1930s. German landings also increased in the 1920s. In the end of the 1930s increase in cod landings occurred in all countries and areas (Fig. 3) and also in landings by different fishing gears as indicated in Swedish data (Fig. 4). The total cod landings of the analysed countries increased by six-fold between 1931 and 1938 (Fig. 5).

3.2. Share of cod in total fish landings and revenues

The dynamics of the share of cod in total fish catches and in revenues have in all countries and areas mostly followed similar dynamics as those of the cod landings. One exception is the Swedish fishery near Gotland in the early 1900s, when the share of cod in catch revenues increased while the catches were low. Additionally, the share of cod in German Baltic fish catches and catch value declined during the second half of the 1920s-early 1930s and cod importance in catch volumes was relatively lower in the early 1930s also in Polish fisheries. These fluctuations are not seen in German and Polish cod landings, but they are similar to respective developments in the other countries in this time period (Fig. 3).

The share of cod in Swedish fish landings in Bornholm Basin before World War I was very low (under 5%), whereas on Gotland cod formed over 30% of the catch volumes in the 1890s and gave nearly 30% of revenues in the early 1900s. However, fewer species may be included in the statistics before 1914, which may contribute to the relatively higher importance of cod in Gotland fisheries in this time period. In Denmark cod importance in the Baltic catch revenues before World War I was 10–25% and in Germany it was ∼15% in the periods of peaks in landings and <10% when cod catches were at low levels (Fig. 3).

In the mid-1920s cod generated ca. 15% of the catch revenue in German fisheries and in Swedish fisheries in Bornholm Basin, while providing 20–30% of catch volumes. The share of cod in landings near Gotland was somewhat lower. Cod had relatively little importance (<10%) both in catches and revenues in Danish and Polish fisheries while it was much more important in Latvia, where it gave 20–30% of revenues and over 30% of catch volumes (Fig. 3).

In the early 1930s the share of cod both in landings and revenues dropped in all countries and areas, reaching especially low levels (<5%) in Denmark and in Swedish fisheries on Gotland. In the end of the 1930s cod importance in fish catches increased in all analysed time series, reaching highest levels in Swedish

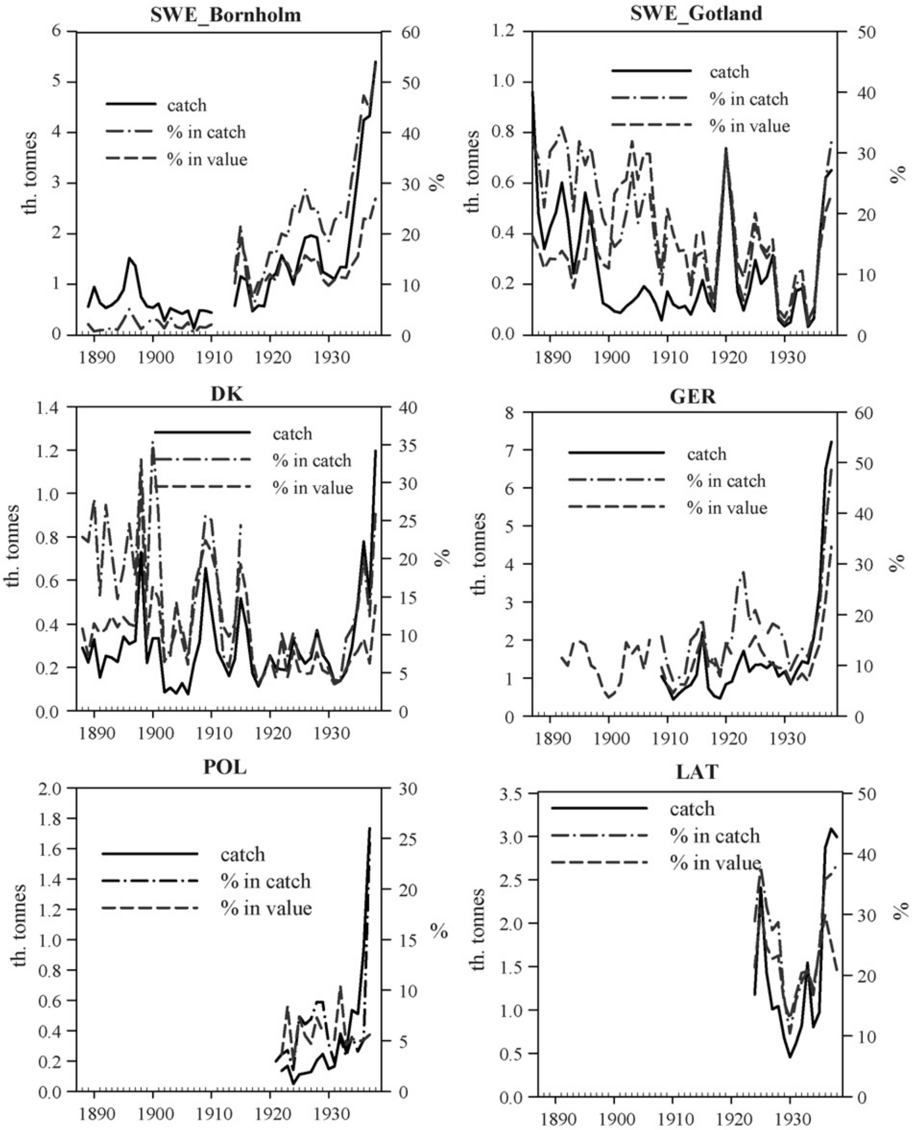

Fig. 3. Cod catches (th. tonnes), share (%) of cod in total fish catches and in their value in Sweden (Bornholm and Gotland areas), Denmark, Germany, Poland and Latvia. (Share of cod in Danish catches in 1988–1915 may not be directly comparable with later years, see Section 2).

fisheries in Bornholm Basin and in Germany, where cod formed up to 50% of the catches. Similarly, contribution of cod to catch revenues increased in all countries and areas, except in Poland. In the end of the 1930s cod had the highest (>30%) economical importance in German and the lowest (<15%) in Danish fisheries (Fig. 3).

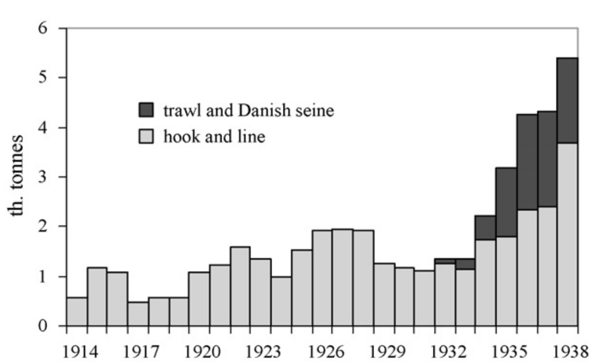

Fig. 4. Swedish cod catches (th. tonnes) by hook and line and by trawl and Danish seine in Bornholm Basin.

3.3. Fish prices

In the early 1900s, ca. eight-fold increase in cod prices was observed in the Swedish fisheries on Gotland and cod became relatively more valuable also in the Danish fisheries on Bornholm. The prices of fish generally increased during the World War I, while relatively higher cod prices in relation to other species in these years is indicated in German and Swedish data for Bornholm area. In the late 1920s–early 1930s, cod price increased compared to the mid-1920s in all countries besides Sweden, where it remained stable. However, relatively higher cod price in relation to other species in the early 1930s is indicated also in the Swedish data. In the late 1930s cod prices dropped in all countries and areas, also in relation to other species (Fig. 6).

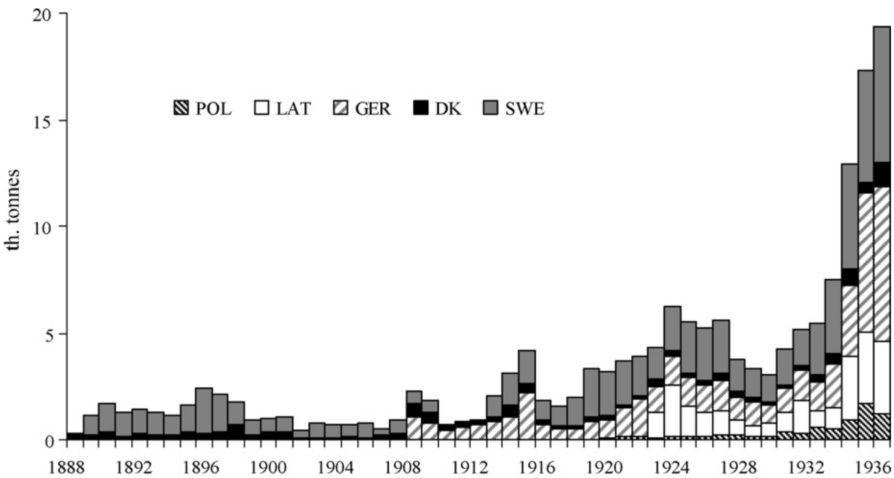

Fig. 5. Swedish, Danish, German, Polish and Latvian cod landings (th. tonnes) in the Baltic in the fishing areas located east of Bornholm.

3.4. *Effort*

In the first decade of the 1900s, the number of participants in cod fisheries in Sweden in Blekinge county was ca. 30% higher than in the 1880s. The number of cod fishermen in the Danish time series fluctuated without a trend during 1888–1910, apart from relatively lower numbers in a few years at the turn of the century. During the 1920s–1930s, the total numbers of professional fishermen increased in Poland and in Swedish fisheries on Gotland, whereas in Latvia they declined by half during the 1920s. In Denmark numbers of fishermen increased sharply in the early 1920s and stabilized thereafter. Part-time fishermen declined in numbers by ca. 30% on Gotland over the 1920s–1930s, but increased in Denmark throughout the whole time period since the 1890s until the end 1930s and in Poland in the 1920s. In other areas their numbers do not indicate major trends (Fig. 7).

The motorization of fishing vessels progressed steadily in Swedish fisheries in both areas after the 1910s and in Germany during the periods before World War I and in the 1920s–1930s

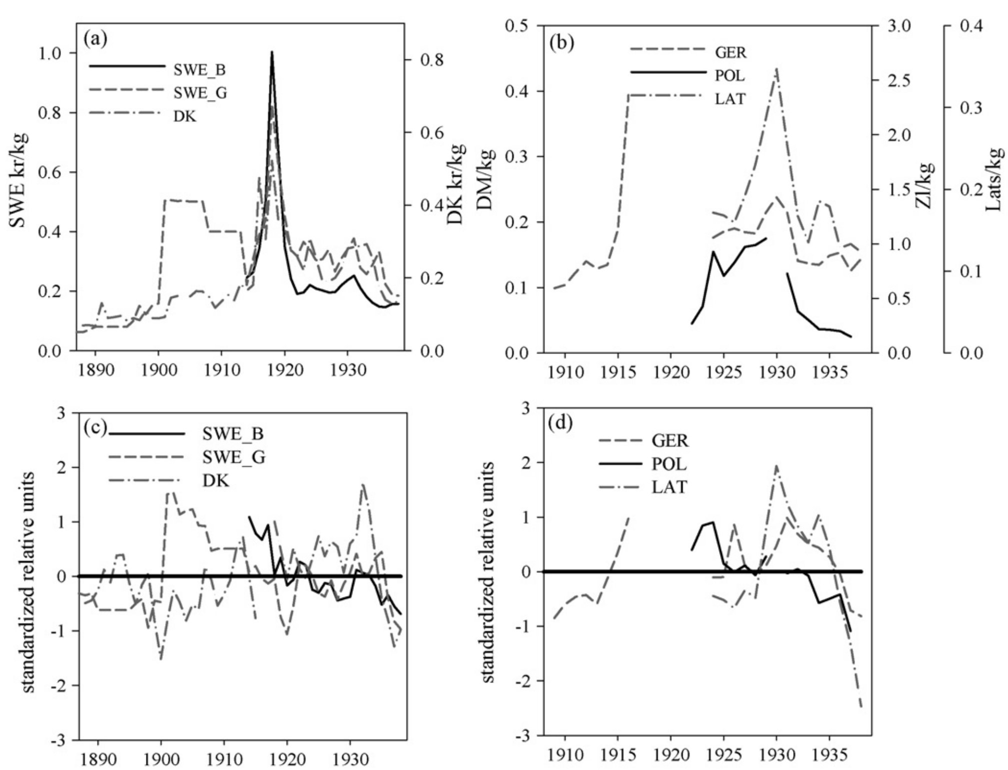

Fig. 6. Prices of cod in national monetary units in (a) Sweden (kr/kg, in Bornholm and Gotland areas) and Denmark (kr/kg; herring in 1888–1915 kr/80 ind.) and (b) in Germany (DM/kg), Poland (Zl/kg) and Latvia (Lats/kg). Panels (c) and (d) show the dynamics of standardized cod price in relation to the average of the other economically most important fish species in each country, which is indicated by 0-line (see Section 2 for species included in average price for individual countries).

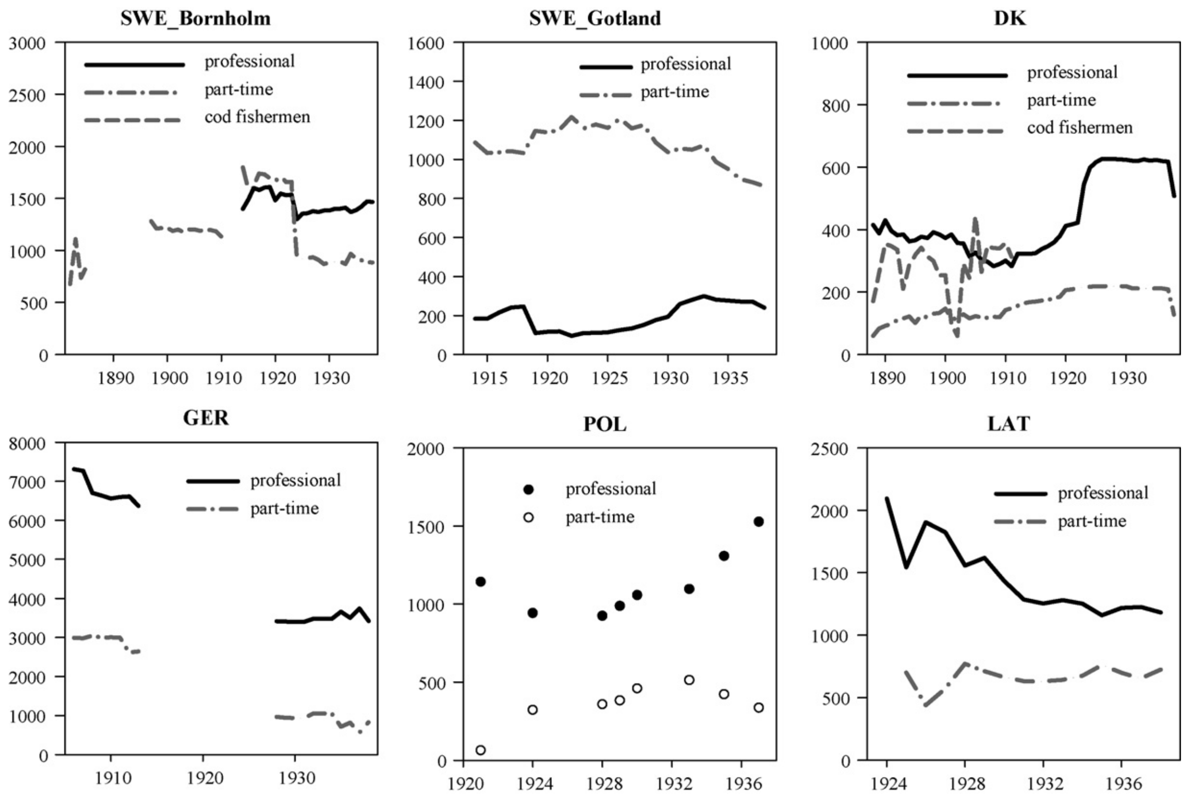

Fig. 7. Numbers of professional and part-time fishermen in Sweden (Bornholm and Gotland areas), Denmark, Poland, Latvia and Germany (data for the two time periods 1906–1913 and 1928–1938 are not comparable, see Section 2). Numbers of participants on cod fisheries are included for Denmark and Sweden (Blekinge county, Ojaveer et al., this volume).

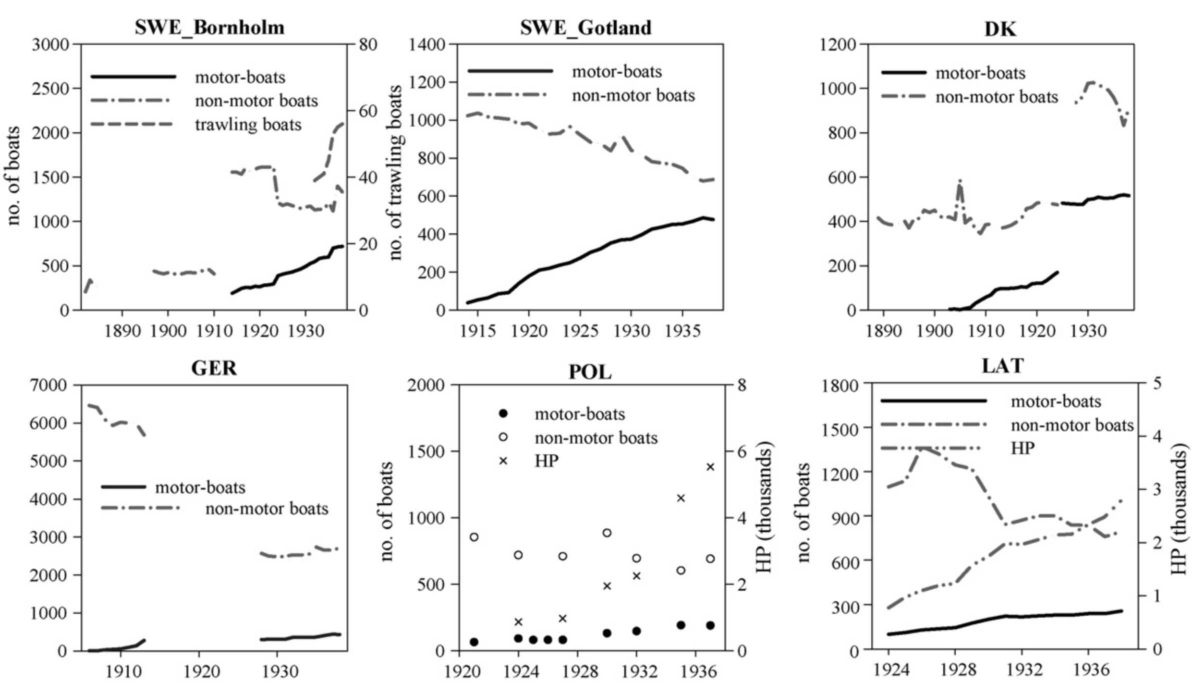

Fig. 8. Numbers of motorized and non-motorized boats in Sweden in Bornholm (before 1914 in cod fisheries in Blekinge country; Ojaveer et al., this volume) and Gotland areas, Denmark (in 1989–1924 in the areas east of Bornholm, in 1925–1938 including SD 24), Germany (data for the time periods 1906–1913 and 1928–1938 are not comparable, see Section 2), Poland and Latvia. The total horse power (HP) of the Polish and Latvian fleets and the number of motorboats participating in trawl fisheries (all species) in Sweden in Bornholm area are also indicated.

Table 1
Numbers of hooks and lines, trawls and seines in the Baltic fisheries in various areas and time periods

Hooks		Hooks and lines							Trawls and seines		
Year	SWE[a]	Year	DK[b]	POL[c]	LAT[c]	SWE[d]	SWE[e]	SWE[f]	Year	DK[g]	SWE[h]
1889	15,371	1912	4,940						1912	57	
1890		1913	3,870						1913	63	
1891		1914	4,895						1914	64	
1892		1915	5,970			14,260			1915	73	
1893		1916	4,780			14,316			1916	35	
1894		1917	4,645			14,400			1917	98	
1895		1918	5,450			15,610			1918	81	
1896		1919	5,860			15,600			1919	96	
1897	15,530	1920	5,790			18,000			1920	93	
1898	14,780	1921	7,690			15,658			1921	108	
1899	14,882	1922	7,525			15,676			1922	127	
1900	14,710	1923	7,195			15,676			1923	265	
1901	14,280	1924	7,810	9,380					1924	534	
1902	14,480	1925	10,070	9,300	38,154		21,527		1925	668	
1903	14,460	1926	16,865	8,490	43,740		20,916		1926	708	
1904	14,243	1927	9,955	10,150	26,161		20,823		1927	720	
1905	14,763	1928	14,472	9,376	47,298		21,076		1928	717	
1906	14,504	1929	11,780		35,141		21,206		1929	740	
1907	15,094	1930	11,757	9,846	29,419		21,396		1930	753	
1908	11,988	1931	11,680		54,453				1931	771	
1909	15,259	1932	10,670	9,177	34,080			21,514	1932	782	144
1910	14,650	1933	10,370		41,358			20,957	1933	785	133
		1934	9,663		51,212			19,307	1934	757	140
		1935	9,885	8,335	28,489			19,854	1935	741	147
		1936	9,940		37,236			21,502	1936	758	169
		1937	10,100		33,388			21,857	1937	724	174
		1938	9,993		57,889			20,463	1938	706	178

[a] Hooks in cod fisheries in Blekinge county (Ojaveer et al., this volume).
[b] Longlines with 100 hooks in the total Baltic area (incl. SD 24)
[c] Hooks (in hundreds).
[d] Hooks (in hundreds) in Blekinge county.
[e] Longlines in Bornholm Basin, number of hooks per line not specified.
[f] Codlines with 100 hooks in the east and south coast of Sweden.
[g] Trawls and seines in the total Baltic area (incl. SD 24).
[h] Trawls in Bornhom Basin.

(Fig. 8). An increasing number of boats participated in Swedish trawl fisheries in the 1930s. In Denmark the number of motorized boats increased relatively faster in the first decade of the 1900s compared to the relative rate of development in the following time period. The motorization process in Poland did not show major progress in the 1920s, but accelerated in the 1930s with a sharp increase in engine power of the fleet. The most rapid developments in motorization and increase in engine power in the Latvian fleet occurred in the late 1920s. Numbers of row- and sailboats declined on Gotland throughout the 1910s–1930s, in Latvia in the 1920s and in Germany in the period 1906–1913. Declining tendency in non-motorized boats in the 1930s can be observed also in Denmark (Fig. 8).

Data on numbers of the main fishing gear employed in cod fisheries are fragmentary (Table 1). The numbers of hooks and lines deployed in the southern Baltic by Sweden were relatively stable during the first decade of the 1900s, in the 1910s and in the 1920s–1930s, while the numbers of trawls increased in the 1930s. The number of hooks and trawls and seines increased sharply in the Danish total Baltic fisheries in the 1920s and stabilized in the 1930s, with slight reduction in the numbers of hooks. The numbers of hooks in Poland and Latvia in the 1920s–1930s were relatively stable (Table 1).

4. Discussion

4.1. Quality of the catch data

In this study we investigate trends and variations in fish landings during a time period when data collection procedures were not as comprehensive as today. It is therefore important to consider whether these trends can be attributed to data artifacts, including how the data have been collected. The majority of the data we have used were extracted from published official fisheries statistical reports, where the data collection procedures are generally not described. In Denmark, local inspectors provided the background material for the Danish Fishing Reports; the data collection was re-structured in the beginning of the 20th century (Bager et al., 2002, supporting document). Swedish statistical reports became more regular and standardized during the 1880s as the agricultural societies in several counties appointed inspectors to collect information on fishing activities. However, because official publications on fisheries statistics were first started in 1914, data for earlier years could be less systematic (e.g., some smaller harbours may not have been covered in all years).

Although the true absolute catches may have been higher than those given in official statistics, e.g. due to misreporting in order to reduce income taxes (Bager et al., this volume), several indicators suggest that the main trends in cod landings are nevertheless reliably presented by the given data. Similar fluctuations were observed in several countries during the same periods and these were species specific, while parallel developments in catches of all species would be expected in case of some general changes in the catch statistics. Also, during the analysed time period no quantitative restrictions of fish catches were applied in the Baltic and quota-related incentives for misreporting were therefore not present.

4.2. Relative economic importance of the cod fishery

Cod has generally been among the top five economically most important species in the Baltic fisheries during the analysed time period in terms of catch revenues. The other important species were herring, salmon, eel, and flatfishes; sprat was important in some countries and at certain time periods. Therefore, price information of these species gives an indication of the economic incentives for changing the relative effort allocated to cod fishery. The actual price for cod during the periods of relatively higher cod catches was generally the lowest among these species, while salmon and eel were by far the most valuable fishes (data not shown).

The presented data indicate that the economic importance of cod in fisheries of different countries and areas reflects developments of cod catches and they generally follow similar trends, except when cod importance has been strongly affected by price fluctuations (Figs. 3 and 6). In many cases the price of cod followed a supply-demand relationship: cod prices were relatively high at lower supply and vice versa. This observation is important background information for evaluating the economic incentives for participating in cod fisheries and their possible influence on catch fluctuations. For example, when a decline in catch of a fish species is observed while it is economically relatively important for the fishery and catch reduction is followed by an increase in price, the cause for the decline in catches is not likely reduced interest for exploiting this particular species. In this example, even if quantitative effort data were not available, it is likely that a decline in effort could not have caused the decline in catches. Similarly, an increase in the catch of a species that has at a time relatively little economic importance for the fishery cannot easily be explained by increased economic incentives, especially if the increase in catch has been accompanied by a reduction in price.

4.3. Major developments in fishing technology and effort in 1880–1938

Technological developments in the Baltic fisheries have generally been different and occurred much later compared to, e.g. North Sea, where trawl fishery by steamers developed already in the 19th century (e.g. Haines, 1998).

Cod in the Baltic was mainly caught by hand-lines and long-lines until the 1920s–1930s (Henking and Fischer, 1905; Hessle, 1947; Jensen, 1954). Anchored nets were also used in some areas, but they had generally little importance (Hessle, 1947; Hessle, 1922). The cod fishery operated very close to the coast (Henking and Fischer, 1905): on Bornholm for example cod were caught only 1–1.5 mile from the shore (Andersen, 1985). Cod fishing became first more intensive and moved further offshore as boats became motorized (Andersen, 1985). Motorization of the vessels, increase in vessel size and possible increase in the number of fishing days and moving to open sea areas are considered to be the major factors that intensified the cod fishery.

The motorization process in the Baltic fisheries only started in the 20th century and varied considerably between countries and areas. Denmark was the leading country in motorizing its fishing vessels (Thurow, 1993), with rapid developments already during the first decade of the 20th century (Fig. 8). Developments in the German fishery were slower compared to Scandinavian countries. This is due to little interest in motorizing vessels in the eastern Baltic areas before World War I as fishing grounds were close to shore and catches were sufficient (Meyer, 1947). On Gotland technological developments were delayed and prevented by its isolation and poor harbour conditions, which were unsuitable for large and heavy boats (Hessle, 1922).

Motorization process was accompanied by an increase in the horsepower of the engines and the introduction of trawls in the southern Baltic in the 1920s–1930s and the movement of the fishery further offshore. At first, when the trawls were introduced in Sweden, Denmark and Germany in the 1920s they were relatively small and adopted to catch flatfish. In the mid 1930s, after flatfish had lost their importance in fisheries, cod became more abundant in trawl catches (Jensen, 1954) and trawls became bigger and better adopted to catch cod (Hessle, 1947; Sahlin, 1959). In the 1930 the pair-trawl was introduced in German fisheries, which could catch cod, herring and sprat (Thurow, 1974; Meyer, 1947). The Polish offshore cod fishery was performed by trawls since 1931 (Laszezynski, 1955). However, in Latvia trawls were introduced only in the 1940s (Pesse, 1999; Lablaika et al., 1991).

4.4. Dynamics of cod catches in relation to developments in fishing effort and technology

In the late 1890s and early 1900s declines were observed in Swedish and Danish cod catches and also in the share of cod in German catch revenues (Fig. 3). Cod also disappeared from the Russian and German coasts at the turn of the century (DFT, 1903). This period has been described as a stagnation and general crisis for fisheries on Bornholm (Andersen, 1985; Rasmussen, 1993). However, the share of cod in total fish landings also declined in all time series which indicates that the observed decline in cod catches was not only caused by an overall decline in fishing intensity. The number of fishermen participating in the cod fishery from Bornholm was also relatively lower especially in 2 years during this time period of low cod catches (Fig. 7), but this change can hardly explain the reduction in catches as they remained low for several years longer. Moreover, despite an eight-fold increase in cod price on Gotland and the highest economic importance of cod in fish catches in the time series, the catches remained low in the early 1900s compared to previous decade (Figs. 3 and 6). Danish cod prices also increased in the early 1900s (Fig. 8a). These price fluctuations show that the decline in cod catches was not likely due to reduced interest in cod fishing. Furthermore, the decline in cod catches motivated fishermen on Bornholm to discuss the benefits of introducing North Sea cod into the Baltic in order to increase the catches; however this idea was not implemented in practice (Bøggild, 1983).

The increase in Danish cod landings in the end of the first decade of the 1900s corresponds to the time period when the overall economic value of fisheries increased and fisheries were undergoing technological developments (Andersen, 1985). The latter included the rapid motorization of the Danish fishing vessels (Fig. 8). A corresponding increase in cod catches is not evident in Swedish data. Therefore, technological changes could have contributed to the increased Danish cod catches in these years. However, the share of cod in total fish catches also increased (Fig. 3).

Cod landings during World War I peaked in the southern Baltic in all available time series. The dynamics of fish catches in these years is difficult to interpret due to several factors having opposite effects on the fishery. Prices of all fish species increased considerably during the war and improved conditions for catch disposal could have favored the fishery. On the other hand, many fishermen were not able to fish during the war due to mine restrictions, the lack of gear, etc. (e.g. Anon., 1933b). Therefore, the reasons for increased cod catches remain unclear. The share of cod increased in catches during World War I in all the available time series, which suggests that a general intensification of fishing activities may not be the only explanation for increased cod catches during this period, and that change in the relative abundance of this species may have occurred. However, increase in cod price relative to other species may have provided an incentive for intensified cod fishery in Sweden and Germany (Fig. 6).

In the time period from the mid-1920s until the end of the 1930s continuous motorization of vessels occurred in all countries for which data are available and bottom trawls were introduced in the southern Baltic (Thurow, 1993). The development of more powerful engines was accompanied by an increase in trawl size. Higher daily cod catches by vessels with more powerful engines in these years have also been documented (Altnöder, 1941). Based on these developments, an overall increasing trend in cod catches in the 1920s and 1930s could be expected. However, cod landings in the second half of the 1920s and early 1930s actually declined in all national time series, except Germany and Poland (Fig. 3). German and Polish cod landings probably remained stable because of relatively faster increase in the efficiency of their fishing fleets compared to other nations due to development of the sprat fishery in these countries during this time period (Kändler, 1949; Dixon, 1937; Altnöder, 1940). Despite of stable cod landings, the share of cod in catches by Germany and Poland declined in the late 1920s–early 1930s as in other countries (Fig. 3). Complaints of Polish fishermen over low cod catches in the 1930s compared to those in 1880s and 1890s have also been documented (Sparholt, 1994). The decline in the share of cod in total fish catches in the late 1920s–early 1930s in all countries indicate that reduced cod landings in this period cannot be explained by a general reduction in fishing activities, which could have occurred in relation to the global economic crisis. Furthermore, the relative increase of cod prices in this period indicates that reduced interest especially in cod fisheries was also unlikely.

Fishery developments contributed to an increase in cod landings in the late 1930s, but this also appears to be partly related to ecological factors. The trawl fishery was undergoing rapid development and market conditions, which had been poor in the Baltic area until the end of the 1930s (Otterlind, 1984; Kändler, 1949), were improving. However, cod landings increased even in fisheries whose gears had not changed over long periods of time. For example, cod landings in the late 1930s increased in hook and line fisheries in Latvian waters and in Swedish fisheries both near Gotland (Fig. 3) and in the Bornholm Basin (Fig. 4) even though the number of lines was stable (Table 1). Moreover, increased cod supply induced fishermen to adjust their trawls to make them more suitable for catching cod (Hessle, 1947; Sahlin, 1959). However, after nearly all the vessels became equipped with new trawls by the mid-1930s, there was a continuous increase in catch per boat (Hessle, 1947; Jensen, 1954). No other species showed a similar increase in this time period, and as a result, the share of cod in fish catches increased in all analysed countries. The improved supply of cod ultimately led to improved market conditions for cod. For example, the first filleting factory on Bornholm was built in 1937 when infrastructure for transport and distribution of cod became saturated with the increased landings of cod (Rasmussen, 1993). Cod prices relative to other species declined in all countries, which show that distinctive economic incentives did not exist specifically for the cod fishery.

Comparing the Baltic cod landings for the period before the 1940s with those in other areas, e.g. North Sea, it is obvious that the Baltic cod fishery was much less important. After World War II this situation changed and Baltic landings increased up to ca. 400,000 tonnes in the 1980s and the Baltic cod fishery became as productive as that in the North Sea and some other regions. However, also before the 1940s during the period of very low total cod catches we have identified time periods when landings differed by several-fold (Fig. 5). Our results show that fluctuations in catches in some of these earlier time periods were not caused by changes in fishing intensity and therefore suggest that variations in stock size of Baltic cod occurred prior to the start of existing time series of biomass. Consequently, our results indicate that in these time periods catch variations can be used as an index for relative stock variations and in investigations of factors causing these variations (e.g. hydrographic conditions and food availability).

5. Conclusions

The cod fishery in the Baltic underwent major developments in the first half of the 20th century. The intensity of the cod fishery was influenced by continuous motorization, increased engine power and tonnage of the vessels, and introduction of more effective fishing gear.

Cod catches in the eastern Baltic were relatively high in the 1880s compared to the turn of the century. Peaks in total catches were observed again in the end of the first decade of the 1900s and during World War I. Relatively higher catches in the mid-1920s were followed by a decline towards the early 1930s and catches increased again in the end of the 1930s. Available effort and economic indicators suggest that it is unlikely that declines in cod catches in the late 19th century and in the early 1930s were due to reduced fishing intensity. Furthermore, fishery developments and technological improvements cannot by themselves fully explain the increased cod catches in the late 1930s. We conclude that these catch fluctuations are related to variations in stock biomass (i.e. changes in production, survival, distribution). The causes of these fluctuations are unknown and require further study.

Acknowledgements

This work is a contribution to the History of Marine Animal Populations project of the Census of Marine Life, a Danish climate change project (CONWOY) and the MarBEF Network of Excellence 'Marine Biodiversity and Ecosystem Functioning' which is funded by the Sustainable Development, Global Change and Ecosystems Programme of the European Community's Sixth Framework Programme (contract no. GOCE-CT-2003-505446). This publication is contribution number MPS-07011 of MarBEF. The study was partly financed by the research school MAST in the University of Southern Denmark. We thank Fritz Köster, Poul Holm and Maibritt Bager for discussions and advice.

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Paper II

Eastern Baltic cod (*Gadus morhua callarias*) stock dynamics: extending the analytical assessment back to the mid-1940s

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Eero, M., Köster, F. W., Plikshs, M., and Thurow, F. 2007. Eastern Baltic cod (*Gadus morhua callarias*) stock dynamics: extending the analytical assessment back to the mid-1940s. – ICES Journal of Marine Science, 64: 1257–1271.

The status of the eastern Baltic cod (*Gadus morhua callarias*) stock has been assessed annually by ICES since 1966. To understand better the causes of stock fluctuations and to evaluate human impact on the stock relative to natural variability, longer time-series than currently available are needed. To achieve this, data back to the mid-1940s were compiled to extend the analytical assessment. Estimates are provided of stock development and its exploitation for a 20-year period before the start of the current assessment. The quality of the data and the credibility of the historical estimates are discussed. Considerable fluctuations in cod biomass and recruitment in the pre-assessment years were identified. Stock size was estimated to be relatively low after the Second World War, then increased during the first half of the 1950s, but did not reach the high levels of abundance subsequently observed in the early 1980s, and then declined towards the mid-1960s. Fishing mortality was low after the Second World War but increased rapidly in the second half of the 1950s, reaching the high levels observed since the 1980s.

Keywords: Baltic cod, exploitation, historical assessment, stock development.

Received 19 February 2007; accepted 24 June 2007; advance access publication 2 August 2007.

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Introduction

A historical perspective is important to evaluate the state of marine ecosystems and to set achievable goals for their management (Southward, 1995; Jackson *et al.*, 2001; MacKenzie *et al.*, 2002; Holm, 2003). Marine ecosystems change over time, and it is often difficult to separate the impacts of anthropogenic activities, such as fishing, from natural environmental change. Without a long-term perspective, fisheries management runs the risk of using the recent past to evaluate the present, a situation referred to as the "shifting baseline syndrome" (Pauly, 1995). For this reason, there have been several studies of long-term changes in fish populations in the North Atlantic. These include analyses of landings data to reconstruct cod stock abundance on the Newfoundland and Scotian shelves going back several centuries (Rose, 2004; Rosenberg *et al.*, 2005), and investigations of commercial and survey catch per unit effort (cpue) for demersal fish in the North Sea and British coastal waters during the 20th century (Daan *et al.*, 1994; Rijnsdorp *et al.*, 1996; Rogers and Ellis, 2000). Others have extended the assessments provided by ICES using historical catch-at-age data to generate stock estimates back to the early decades of the 20th century, e.g. North Sea gadoid stocks (Pope and Macer, 1996), Greenland cod (Buch *et al.*, 1994), northeast Arctic cod (Hylen, 2002), and Norwegian spring-spawning herring (Toresen and Østvedt, 2000).

International working groups conducting assessments of fish stocks in the ICES areas were first established in the 1960s, and regular estimates of stock abundances drawn from virtual population analysis (VPA) became available in the early 1970s (Ulltang, 2002). Therefore, time-series of fish stock trends in the Northeast Atlantic from the annual assessments are generally relatively short and mainly cover the last 3–4 decades (ICES 2006a, b, c). The eastern Baltic cod stock [ICES Subdivisions (SDs) 25–32] has been assessed annually since 1973 (Weber, 1989), and the current time-series of stock dynamics starts in 1966 (ICES, 2006a).

Eastern Baltic cod are considered to be a different stock from those in the western Baltic (ICES SDs 22–24) (Bagge *et al.*, 1994), and occupy a separate assessment unit. However, the Baltic Sea is characterized by a heterogeneous topographic and oceanographic environment that influences the reproductive success of cod as well as species interactions in different areas in the central Baltic (Köster *et al.*, 2001). Therefore, area-disaggregated multispecies assessments have been applied in the Baltic (Köster *et al.*, 2001) generating separate estimates for subpopulations in SDs 25, 26, and 28 (ICES, 2006d). These SDs correspond roughly to the central Baltic basins where cod spawn (i.e. Bornholm Basin in SD 25, Gdańsk Deep in SD 26, and Gotland Basin in SD 28) (Bagge *et al.*, 1994).

The first attempt to estimate the biomass of Baltic cod before 1966 was made by Thurow (1999), using catch curve analyses. This work is carried further here, where we identify the available historical data sources and compile the relevant dataseries to extend the analytical assessment of eastern Baltic cod back to the mid-1940s. This period corresponds to the time when systematic scientific investigations on eastern Baltic cod began and relevant dataseries started to become available. An area-disaggregated approach was applied to obtain separate estimates for those subpopulations where data were suitable. The results of this study will contribute to a better understanding of the mechanisms behind the fluctuations in the eastern Baltic cod and hence also improve our knowledge about functioning of the Baltic ecosystem (MacKenzie *et al.*, 2002).

Material and methods

Assessment input data

Assessment input data for SDs 25–32 from 1966 on were obtained from ICES (2006a). Data by SD and quarter in the years 1974–2003 were available from the database compiled by the Study Group for Multispecies Assessment in the Baltic (ICES, 1997, 1999, 2006d), hereafter referred to as the MSVPA database. For the years 1946–1973, data were compiled from various sources, wherever possible separating SDs 25, 26, and 28 (Figure 1). Quarterly catch-at-age for the period 1946–1973 was only estimated for those countries and time periods where seasonal data on age distribution were available. In the following section, details concerning the data sources and calculation procedures are described.

Landings data

Baltic cod landings of the former USSR for the years 1946–1959 (VNIRO, 1968) were assumed to have been taken in SDs 26 and 28. This is a simplifying assumption because before economic zones were introduced in 1978 (Bagge and Thurow, 1994), fleets of the USSR also had the possibility to fish in SD 25. However, the Gotland Deep and areas next to the east coast of the Baltic are documented as the principal USSR fishing regions for cod (Dementjeva, 1959). Therefore, the landings data presented to ICES since 1960 were allocated to SDs 26 and 28 (Lablaika *et al.*, 1975; ICES, 2006a). Therefore, the proportion of landings taken in SD 25 before 1960 is likely to be relatively small. The quarterly distribution of Latvian cod landings in the years 1950–1955 (Lablaika and Uzars, 1967) was applied to total USSR landings

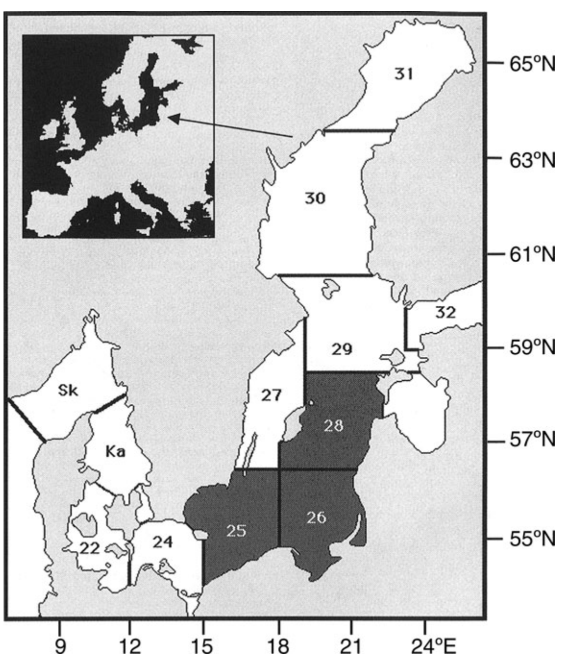

Figure 1. ICES SDs in the Baltic Sea indicating the areas included in analyses for separate SDs (shaded).

and the average quarterly shares in these years were applied to landings in 1946–1949. USSR landings by quarter for the years 1956–1974 are presented by VNIRO (1968) and in the national reports to the ICES Assessment Working Group.

Polish area-disaggregated landings for the years 1946–1960 were taken from Rutkowicz (1963). Since 1960, the data are available in ICES reports (ICES, 1974, 2006a). The quarterly distribution of the total Polish landings in the period 1965–1973 (Kosior, 1969, 1977) was applied to the landings in both SD 25 and 26.

Cod landings by the former Democratic Republic of Germany (GDR) in the years 1947–1962 were only available for the total Baltic Sea (Borrmann and Berner, 1984). Cod landings in SDs 25–32 were estimated by combining the total landings with estimates of the average share taken from the areas east of Bornholm (Berner, 1959, 1960, 1962; Berner and Anwand, 1962/1963). Cod landings reported by the Rostock fishing company (Berner, 1962) were assumed to have been taken in SDs 25–32 (H. Müller, pers. comm., Institute for Baltic Sea Fisheries in Rostock). GDR landings in SDs 25–32 for 1963 and 1964 were taken from ICES (1975). Landings in the period 1965–1971 were available aggregated for SDs 25–32, and are also presented separately for SD 25 (Berner and Borrmann, 1980); the difference was allocated to SD 26. On average, the landings in SD 26 amounted to ~10% of the landings reported from SDs 25–32, and a similar percentage of the total landings was allocated to SD 26 also in earlier years. From 1972 on, landings data by SDs are available in ICES (2006a). GDR landings in all SDs in the years 1967–1973 were split into quarters based on the average quarterly distribution of landings in the periods 1960–1962 (Borrmann and Berner, 1984) and 1974–1976 (MSVPA database).

The cod landings of the Federal Republic of Germany (FRG) in the Bornholm Basin (SD 25) from 1947 to 1958 were estimated by Kändler and Thurow (1959). From 1963 on, data by SDs are available from ICES (1974, 1979, 2006a). The average proportion of the FRG cod landings taken in the Bornholm Basin in the years 1947–1958 (Thurow, 1974) and the average proportions in 1958 and 1963 were used to estimate the FRG landings in SD 25 in 1946 and in the period 1959–1962, respectively. Landings in the years 1969–1973 were split into quarters based on the average quarterly shares of the landings in the period 1974–1978 (MSVPA database).

The Danish cod landings from the Baltic in the period 1946–1964 are aggregated for SDs 24–32 (Thurow, 1974), but from 1965 on, separate data for SD 24 and SDs 25–32 have been provided to ICES (1977, 2006a). The average share of SD 24 to the total landings in the period 1965–1969 (24%) was assumed to apply for the entire time period from 1946 to 1964, and the estimated landings from SD 24 were subtracted from the total landings to obtain rough estimates for SDs 25–32. No data were available to allow further disaggregation of these landings into SDs. However, most of the fishery likely took place in the Bornholm Basin and the landings from SDs 25–32 were assumed to have been taken in SD 25.

Swedish cod landings by county for 1946–1959 were extracted from the Swedish official fisheries statistics series FISKE, published annually by the Royal Statistics Central Bureau. The landings of each county were allocated to the SD corresponding to its location. Data by SD have been presented to ICES since 1960 (ICES, 1974, 1979, 2006a).

Finnish cod landings from the Baltic in the years 1953–1965, as reported in the ICES Bulletin Statistiques, were assumed to have been taken in SDs 29–32.

No information is available on the level of potential misreporting for any of the countries in the period before 1966, but no quantitative catch restrictions were imposed then, so misreporting was probably less significant than these days. Estimates of potential discarding are also not available for the study period, and discards in pre-assessment years were not included in the analyses. Discard estimates are available since 1996 in the current ICES assessments, and the average discard rates from the recent time period are applied back to 1966. In the MSVPA database, extrapolation of discard estimates to historical data was not applied.

Age composition data and calculation of catch-at-age

Data on the age composition of cod landings in the period 1946–1973 were compiled from various publications and from national data submitted to ICES (Table 1). In most of the earlier years, only percentage age distributions were available; average weights-at-age

Table 1. Availability of age composition data (by percentage or catch number) by country, SD, and time of year, 1946–1973, and the respective data sources.

Country	Years	Time	SD	Age distribution source	Weight-at-age	Weight-at-age source
USSR	1946–1957	First half year[a]	26–32	Dementjeva (1959)	1946–1950: mean for 1955–1957 averaged over first and second half year; 1951–1957: mean for 1955–1957 in first half year	Dementjeva (1958)
USSR	1958	First half year	26–32	Dementjeva and Tokareva (1958)	1958–59: mean for 1955–1957 averaged over first and second half years	Dementjeva (1958)
USSR	1959	First half year	26–32	Birjukov *et al.* (1960)	–	–
USSR	1951–1957	Second half year[a]	26–32	Lablaika and Vismanis (1957), Dementjeva (1958)	Mean for 1955–1957 in second half year	Dementjeva (1958)
USSR	1960–1973	Annual mean	26–32	Presented to ICES	–	–
Poland	1946–1954	Annual mean	26	Rutkowicz (1963)	Annual[d]; SD 26	Rutkowicz (1963)
Poland	1955–1959	Annual mean	26	Kosior (1974)	Annual; SD 26	Rutkowicz (1963)
Poland	1960–1964	Annual mean	26	Kosior (1975)	Mean for 1965–1974; SD 26	Kosior (1977)
Poland	1965–1970	Quarter 1[b]	26	Kosior (1975)	Mean for 1965–1974; SD 26	Kosior (1977)
Poland	1971–1973	Quarter 1[b]	26	Presented to ICES	–	–
Poland	1951–1952	Annual mean	25	Zhukowski (1957)	Mean for 1951–1952; SD 25	Zhukowski (1957)
Poland	1953–1954	Annual mean	25	Reimann (1962)	Mean for 1951–1952; SD 25	Zhukowski (1957)
Poland	1955–1956	Annual mean	25	Stanek (1962)	Mean for 1951–1952; SD 25	Zhukowski (1957)
Poland	1957–1959	Annual mean	25	Stanek (1965)	Mean for 1951–1952; SD 25	Zhukowski (1957)
Poland	1960–1964	Annual mean	25	Kosior (1975)	Mean for 1965–1974; SD 25	Kosior (1977)
Poland	1965–1970	Quarter 1[b]	25	Kosior (1975)	Mean for 1965–1974; SD 25	Kosior (1977)
Poland	1971–1973	Quarter 1[b]	25	Presented to ICES	–	–
German Democratic Republic	1967–1973	Quarters 1 and 2[b]	25[c]	Berner and Borrmann (1980)	Annual; SD 25	Berner and Borrmann (1980)
German Democratic Republic	1971–1973	Quarters 1 and 2[b]	26	Berner (unpublished)	Annual; SD 26	Berner (unpublished)
Federal Republic of Germany	1969–1973	Quarters 1 and 2[b]	25–28	Presented to ICES	–	–

Additionally, weight-at-age information for calculating the catch numbers, when only age distribution in percentages was available, is presented.
[a]The original data that refer to spawning and feeding season were applied for first and second halves of the year, respectively.
[b]Applied to annual landings of that country from those SDs.
[c]Average of the data for northern and southern Bornholm Basin.
[d]Weight-at-age for 1948 was used for 1946–1947; for other years, annual data were available.

Table 2. Origin of the age data applied to landings by country, SD, and year.

SD	Years	USSR	Poland	GDR, German Democratic Republic	FRG, Federal Republic of Germany	Sweden	Denmark	Finland
25	1946–1950	–	*Poland SD 26*[a]	*Poland SD 26*[a]	*Poland SD 26*[a]	*Poland SD 26*[a]	*Poland SD 26*[a]	–
	1951–1966	–	Poland SD 25	*Poland SD 25*	*Poland SD 25*	*Poland SD 25*	*Poland SD 25*	–
	1967–1968	–	Poland SD 25	GDR SD 25	*Poland/GDR*	*Poland/GDR*	*Poland/GDR*	–
	1969–1973	–	Poland SD 25	GDR SD 25	FRG SD 25–28[b]	*Poland/GDR / FRG*	*Poland/GDR / FRG*	–
26 and 28	1946–1959	USSR SD 26–32	Poland SD 26	*USSR/Poland*	–	*USSR/Poland*	–	–
26	1960–1968	USSR SD 26–32[b]	Poland SD 26	*USSR/Poland*	*USSR/Poland*	–	–	–
	1969–1970	USSR SD 26–32[b]	Poland SD 26	*USSR/Poland /FRG*	FRG SD 25–28[b]	–	–	–
	1971–1973	USSR SD 26–32[b]	Poland SD 26	GDR SD 26	FRG SD 25–28[b]	–	–	–
28	1960–1968	USSR SD 26–32[b]	–	–	–	*USSR*	–	–
	1969–1973	USSR SD 26–32[b]	–	*USSR/FRG*	FRG SD 25–28[b]	*USSR/FRG*	–	–
27	1946–1965	–	–	–	–	*SWE SD 25/SD 28–31*	–	–
29–31	1946–1965	–	–	–	–	*USSR SD 26–32*	–	–
25–32	1952–1965	–	–	–	–	–	–	*USSR SD 26–32*

Non-italicized entries refer to original data
[a]Average weight-at-age, 1951–1952 in SD 25 (Zhukowski, 1957) was applied in calculating catch numbers-at-age.
[b]Combined catch numbers for several SDs in the original data were split between SD according to the proportion of landings (t) taken in respective areas.

were therefore used to calculate the corresponding catch in numbers-at-age. The scheme for applying the available catch-at-age information to calculate catch in numbers-at-age by country and SD is shown in Table 2. When age compositions for several countries were available for a given year and SD, the datasets were averaged using landings within each SD as a weighting factor.

Weight-at-age

Time-series of weight-at-age in the catch were based on the information presented in Table 1. The scheme for compiling mean weight-at-age by SD is shown in Table 3. Annual data on weight-at-age were not available before 1967 in SD 25 and for the period 1960–1970 in SDs 26 and 28. In those years, the estimates were based on long-term means or data were borrowed from other years. In the time periods where several datasets of weight-at-age were available for a SD (either as annual values or as averages of several years), these were averaged, weighting by the catch numbers of the respective countries taken in a SD. Since 1976, weight-at-age by SD has been available from the MSVPA database. A time-series of weight-at-age for SDs 26 and 28 combined in the period 1960–2003 was calculated as an average of the two areas, weighted by catch numbers. In the assessment for the total stock in SDs 25–32, weight-at-age from 1946 to 1965 was calculated as a weighted average of the data for SD 25 and for SDs 26 and 28.

Weight-at-age in the stock was set equal to the weight in the catch of fish aged 3–8+. Weights of age 2 cod in the stock between 1946 and 1975 in all SDs were set equal to the values applied for the period 1976–1989 in the MSVPA database.

Biological parameters

Estimates of maturity ogives from the period 1976–1984 by SD were applied to the period 1946–1975, because no data were available for those years. For the area covering SDs 26 and 28, average maturity estimates for the two areas were applied. In the analyses for the total stock (SDs 25–32), the maturity values for the period 1966–1984 from ICES assessments were applied also for the earlier years. Natural mortality of all ages (2–8+) was assumed to be 0.2 for all years and SDs.

VPA runs

The Lowestoft version of eXtended Survivors Analysis (XSA; Darby and Flatman, 1994) was used to estimate stock sizes and fishing mortalities using the same settings as in the ICES assessments (ICES, 2006a). Three separate runs were performed including (i) total stock (SDs 25–32), (ii) SD 25, and (iii) SDs 26 and 28. The last two SDs were combined because no information was available to separate the landings between the two before 1960. In the run including the total stock, the ICES assessment input data were used from 1966 on. The runs for separate SDs use the input data from the MSVPA database starting from 1974.

In the run including the whole stock (SDs 25–32), the tuning fleets were used as in the current ICES assessment (ICES, 2006a). Area-disaggregated XSA runs were tuned with abundance indices from international bottom trawl surveys (Sparholt and

Table 3. Data included in the time-series of weight-at-age by SD, 1946–1975.

Years	SD 25	SD 26	SD 28	SDs 26 and 28
1946–1959	Poland SD 25; mean 1951–52	–	–	Poland SD 26; annual USSR SD 26–32; mean 1955–1957 Averaged over first and second half years
1960–1966	Poland SD 25; mean 1965–1974	Poland SD 26; mean 1965–1974 USSR SD 26–32; mean 1960–1975	USSR SD 26–32; mean 1960–1975	–
1967–1970	Poland SD 25; mean 1965–1974 GDR SD 25; annual	Poland SD 26; mean 1965–1974 USSR SD 26–32; mean 1960–1975	USSR SD 26–32; mean 1960–1975	–
1971–1974	Poland SD 25; mean 1965–1974 GDR SD 25; annual	Poland SD 26; mean 1965–1974 USSR SD 26–32; mean 1960–1975 GDR SD 26; annual	USSR SD 26–32; mean 1960–1975	
1975	Poland SD 25; mean 1965–1974 GDR SD 25; annual	Poland SD 26; mean 1965–1974 USSR SD 26–32; mean 1960–1975 GDR SD 26; annual	USSR SD 26–32; annual	–

Tomkiewicz, 2000) from 1983 to 2003, as made available by SD by the Multispecies Study Group in the Baltic. In the run covering SDs 26 and 28, time-series of abundance indices for both areas were included. Additionally, in the run for SDs 26 and 28, a commercial cpue time-series for the years 1954–1966 from a Latvian company fishing for cod (Lablaika *et al.*, 1991; Lablaika, unpublished) was included in tuning. The catches (t d^{-1}) were converted to numbers and distributed to age groups using USSR age composition and weight-at-age data for the respective years. Only the commercial cpue data until the mid-1960s were included in the tuning because shorter commerical cpue time-series are presumably less influenced by technological developments. To assess the sensitivity of the results to the availability of tuning data for the historical period, two additional XSA runs for SDs 26 and 28 were performed. One included the entire time-series of input data (1946–2003) tuned only with the survey data for the recent decades. Another was performed including all the input data only from the historical period (1946–1966) tuned with the commercial cpue index for the years 1954–1966.

Results

Spatial distribution of landings

In the 1950s, up to 70% of the cod landings in the Baltic were taken in SDs 26–32 (Figure 2). Thereafter, the importance of these areas to the Baltic cod fishery declined, and in the early 1970s, they contributed some 40% of cod landings (Figure 2b). In the decades following, the landings in SDs 26–32 were higher than in SD 25 only in the late-1970s and early 1980s, when the total Baltic landings were the highest on record (Figure 2a). Since the 1980s, the share of northeastern areas to cod landings has declined sharply, to 30% of the previous value (Figure 2b).

Age structure of landings

In SD 25, age distribution data are available for ~15–30% of the landings between the 1950s and the 1970s, and no age-specific information is available for earlier years. Availability of age composition data improves considerably in the early 1980s, when the coverage increases to 60–80% of the landings. In SDs 26 and 28, age-specific information covers from 70% to >90% of the landings in the period from 1946 to the 1980s, with somewhat reduced data availability around the 1990s (Figure 3). The

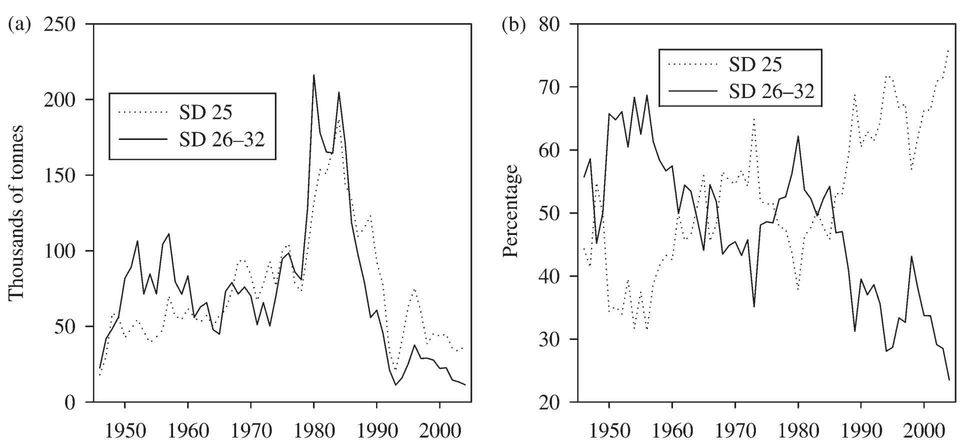

Figure 2. (a) Cod landings (as estimated in this study, see Material and methods) in SD 25 and in SDs 26–32, and (b) percentage of landings taken in the same SDs.

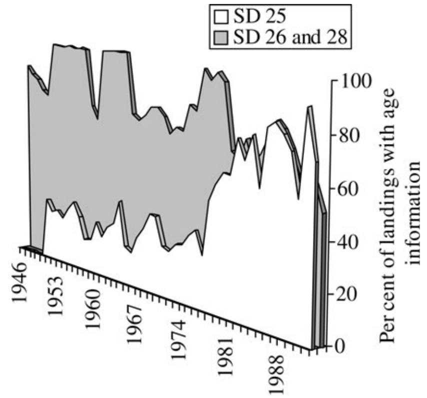

Figure 3. Approximate percentage of cod landings in SD 25 and SDs 26 and 28 for which age composition data are available from individual countries, SDs, and quarters, 1946–1992.

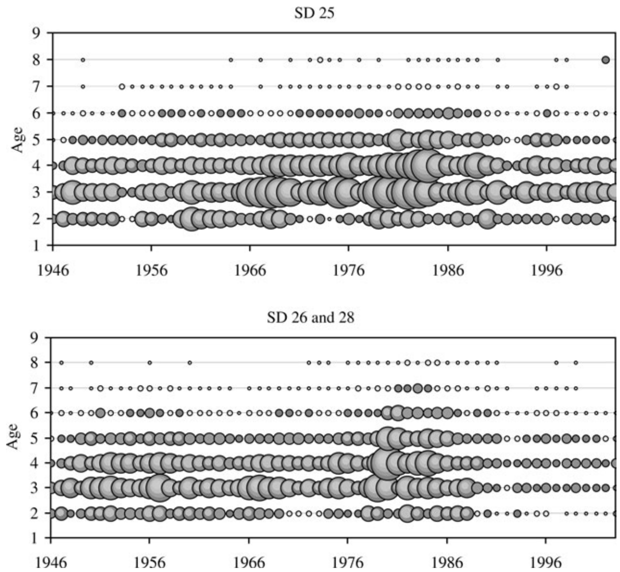

Figure 4. Relative age structure in the catch of cod from SD 25 and from SDs 26 and 28 combined.

availability of information on age structure of landings is estimated at the level of country, SD, and quarter. When only the annual mean age distributions were available, it was assumed that they represented the total annual catch of the country in that SD.

The consistency of the estimated catch-at-age in the historical pre-assessment time period relative to the more recent decades was compared by plotting and correlating numbers-at-age for the main age groups in the fishery (ages 3–7) against numbers-at-age of the same cohort in the following year. Larger residuals in the pre-assessment years compared with the later part of the time-series were not apparent, apart from a single outlier in SD 25 corresponding to the age group 7 in 1952 (results not shown). The ability to track year-class strength in SD 25 was less ($r^2 = 0.34–0.67$) than in SDs 26 and 28 ($r^2 = 0.71–0.76$).

Before 1960, the numbers-at-age caught in SD 25 were similar to the most recent time period, although more 2-year-old fish appear in the landings. In SDs 26 and 28, similar quantities of age 2–3 cod were caught during the 1950s and early 1980s, when total cod landings in the Baltic peaked. However, the catch of older age classes was considerably less in the early 1950s (Figure 4).

Stock dynamics from VPA analysis

The total (SDs 25–32) spawning-stock biomass (SSB) after the Second World War was only 70 000 t, but it increased to 200 000–240 000 t in the mid-1950s (Figure 5, Appendix Table A1). Subsequently, the SSB declined to 136 000 t in 1964, then recovered to 230 000 t in 1967.

Separate estimates for SD 25 indicate a relatively stable SSB at ~60 000–80 000 t in the late-1940s and early 1950s, followed by an increase in the late-1960s to 130 000 t by the mid-1970s. The subpopulation in SDs 26 and 28 varied more in the 1950s and 1960s, the SSB declining from ~140 000 t in the early 1950s to 70 000 t in 1964, then increasing to 110 000 t in 1969, where it remained until increasing noticeably in the late-1970s.

Since 1966, the available estimates of SSB in SDs 25–32 from the ICES assessment indicate a similar trend to our estimate for SDs 26 and 28. In SD 25, the trend in SSB is somewhat different and generally less variable (Figure 5, Appendix Table A1). The dynamics of total-stock biomass (TSB) between the 1940s and the 1970s is similar to the trends in SSB, a finding related to the maturity ogives having been assumed constant over time.

The trends in summed stock biomass and recruitment estimates from the assessments by SD agree with the results from the assessment for the total stock ($r^2 = 0.925$ and 0.927, respectively; years 1946–1975 included in the correlation).

Estimated numbers of 300–320 million cod aged 2 (SDs 25–32) indicate several relatively strong year classes in the early 1950s. This was followed by a period of lower recruitment between the late-1950s and the mid-1960s, ~200 million cod, then an increase to 310–430 million cod annually. A similar variability in recruitment is clear for SDs 26 and 28, but in SD 25, the numbers aged 2 were more stable, with low recruitment from the start of the time-series until the mid-1960s. Stronger year classes appeared in some years in the late-1960s, followed by lower values again in the early 1970s, similar to the pattern in SDs 26 and 28 (Figure 5, Appendix Table A1).

The average fishing mortality (F) exerted on the stock increased from a level of ~0.5 after the Second World War to 0.7 in the late-1940s, then to values >1.0 by the early 1960s (Figure 5). Thereafter, the fishing mortality declined to 0.5 by the late-1970s. A similar development of the estimates of F for the entire stock was derived for combined SDs 26 and 28. In SD 25, mortalities show unrealistically high values at the start of the time-series in some years and age groups, and the decline from the 1960s to 1970s is less pronounced. Fishing mortality on younger age groups (age 2 in both areas, age 3 in SDs 26 and 28) in the 1950s and 1960s was also generally higher than in the 1970s (see Appendix).

The results from the XSA runs covering the whole stock (SDs 25–32) and the run including SD 25 were tuned with abundance indices from the most recent decades (1991 and 1983 on, respectively). Tuning data for the earlier time period were included only for SDs 26 and 28. However, the XSA estimates for SDs 26 and 28 were insensitive to the availability of historical tuning information. The results from the three runs including (i) the entire time-series of input data (1946–2003), and tuning information for 1954–1966 and 1983–2003, (ii) the entire time-series of input data tuned only with abundance indices for 1983–2003,

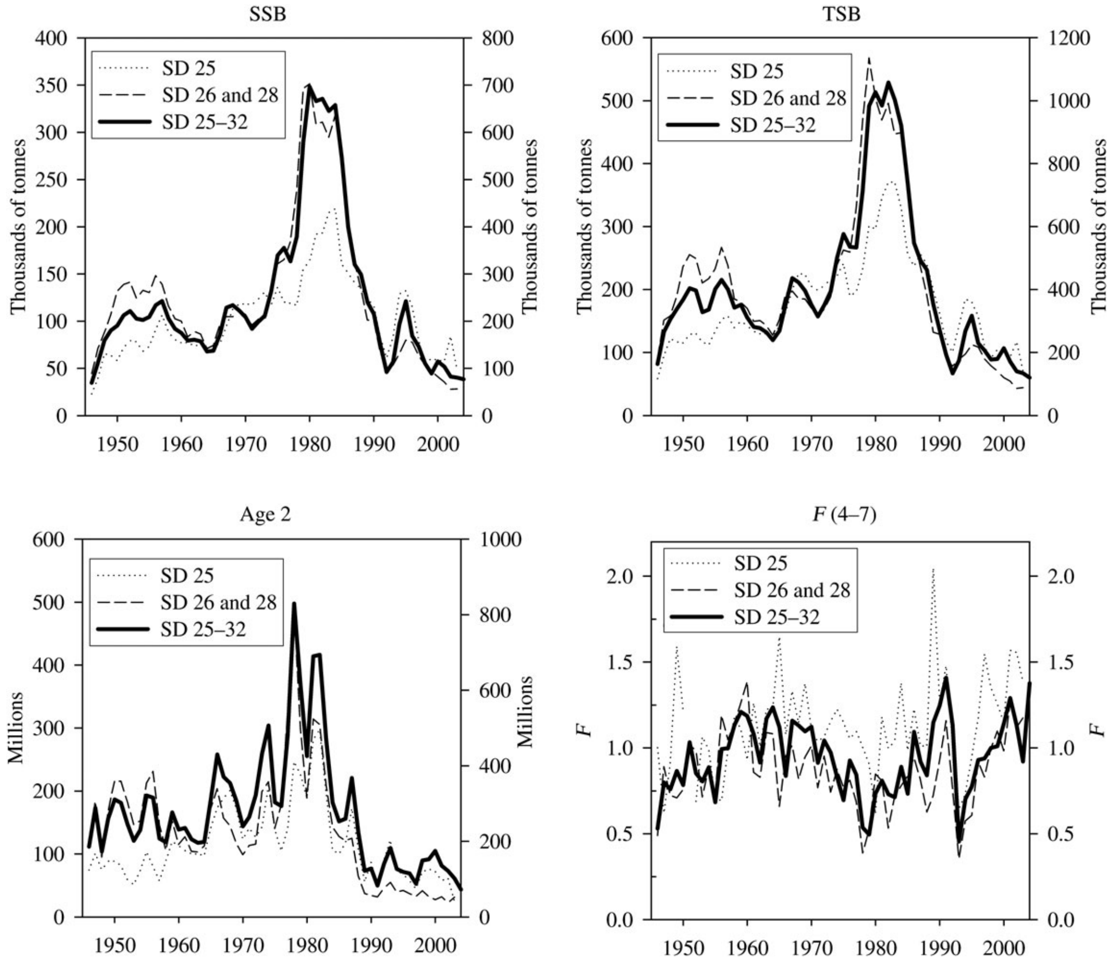

Figure 5. SSB ('000 t), TSB ('000 t), fishing mortality *F* (ages 4–7) and recruitment (age 2, millions) of cod in SDs 25–32 and separately for SD 25 and SDs 26 and 28. The left axis refers to the separate SDs, the right to the entire stock.

and (iii) only the historical portion of the input data (1946–1966) tuned with commercial cpue for 1954–1966 were similar.

Comparison of VPA estimates with cpue data

Time-series of cpue for the 1940s, 1950s, and 1960s were available for SDs 26 and 28. However, the dataseries are short and do not show a clear trend throughout all years. The available datasets are divided roughly into two time periods, covering the years from the late-1940s to the mid-1950s, and from the mid-1950s on. One of the longest cpue time-series covering the latter period was also included in XSA tuning. Generally, different cpue series for the same time period show similar trends. For the first time period, all dataseries indicate relatively higher cpue in the late-1940s and early 1950s and again in the mid-1950s, with lower values for some years in between. The time-series for the later period show relatively higher cpue in the mid-1950s than in the late-1950s and early 1960s, and there is again an increase in the mid-1960s. Apart from the late-1940s, similar trends can be observed in estimated cod biomass in SDs 26 and 28 (Figure 6a), although they do not correlate significantly.

Data from the former USSR young fish survey in the areas corresponding to SD 26 (Birjukov, 1970) indicate relatively strong year classes in the early 1950s and the mid-1960s, and fewer young cod in the late-1950s and early 1960s (Figure 6b). These results correspond to recruitment estimates from the VPA analysis for SDs 26 and 28, which indicate relatively poor recruitment in late-1950s and early 1960s (Figure 6b).

Discussion

Historical background on stock assessment and fisheries research

The analytical assessment of the eastern Baltic cod stock currently extends back to 1966, although the Baltic Fisheries Assessment Working Group (WGBFAS) considers the data before ~1970 to be uncertain and possibly of poor quality (ICES, 2006a). This study has demonstrated, however, that there is considerable relevant information available for earlier periods. The main problem with the data is the incomplete spatial coverage not only in pre-assessment years, but also in the first decade covered by the ICES assessment. Spatial differences in data availability result from differences in national sampling priorities related to basic differences in the importance of fish stocks as natural food resources in former eastern bloc and western countries. In countries to the east, fisheries investigations were state-controlled and financed, and research related to the status of fish stocks and prognoses on fishing potential was prioritized. Scientists were producing regular prognoses and recommendations for the exploitation of Baltic fish stocks already in the late 1940s

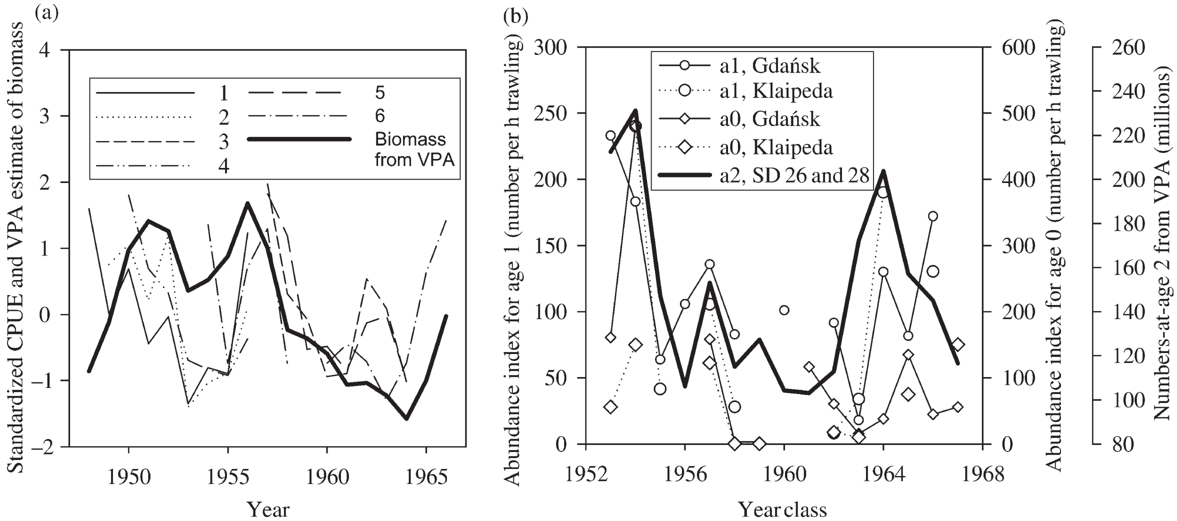

Figure 6. (a) Standardized time-series of cpue in the Gdańsk and Gotland areas (SDs 26 and 28) compared with stock biomass in SDs 26 and 28 derived from a VPA. 1—USSR, February–June, kg h^{-1} (Dementjeva, 1959); 2—USSR, February–June, kg h^{-1} (Dementjeva, 1959); 3—USSR, Gotland Basin, February–June, kg h^{-1} (Birjukov, 1970); 4—Poland, Gdańsk, kg h^{-1} (Rutkowicz, 1959); 5—USSR, Gdańsk, February–June, kg h^{-1} (Birjukov, 1970); 6—Latvia, annual mean, t d^{-1} (Lablaika *et al.*, 1991; Lablaika, unpublished). All cpue series are commercial except for time-series 2, which is based on research survey data. Time-series 6 was included in VPA tuning for SDs 26 and 28. (b) Time-series of cpue from young fish surveys (number per hour of 0- and 1-group cod) in the Gdańsk and Klaipeda areas (SD 26; Birjukov, 1970) contrasted with recruitment estimates (age 2) from VPA for SDs 26 and 28 (shifted in the figure to match the year classes).

(Ojaveer *et al.*, 2000), and those formed the basis of production plans in the centrally planned economies of the socialist countries. Therefore, applied fisheries research developed much earlier in those countries than did the international assessments of Baltic fish stocks performed by ICES.

In the west, focus on fish stocks assessments and related research was less of a priority. Before the 1970s, research surveys of eastern Baltic cod were conducted (Alander, 1949; Jensen, 1959a) and commercial catches were sampled (Jensen, 1959a), but either the sampling procedures were not systematic or designed to provide information related to stock abundance or the data were not analysed, summarized, or archived in a manner to allow them to be used here.

Differences in priorities in fisheries investigations among countries and differences in spatial distribution of their catches result in pronounced differences in the availability of catch composition data by area before the 1970s (Figure 3). To account for this, we followed an area-disaggregated approach, separating the estimates for SD 25 from SDs 26 and 28, where the availability of catch composition data remained at approximately the same level from the 1940s.

Quality of assessment input data

The historical catch data do not include discards that could potentially bias estimates. Since 1996, ca. 30% of the catch of 2-year-old cod and 8% of that of 3-year-olds have been discarded (on average), whereas the discarding percentage for older fish is negligible (ICES, 2006a). Before the 1970s, "highgrading" of landings as a consequence of catch restrictions was unlikely to have taken place. There could have been discarding of small cod below the minimum landing size, perhaps influencing our recruitment estimates. Further, recruitment estimates, particularly for SD 25, may be compromised by landings of young fish for industrial purposes, which are not included in cod landings in the Swedish statistics (Otterlind, 1974). Some discarding could have taken place also because of unfavourable market conditions. In the late-1940s, limited markets for cod <50 cm in Sweden have been documented (Alander, 1946), which resulted in a large proportion of the catch being returned to the sea. Because of this and other factors (e.g. poor documentation of landings in the first years after the war), landings information for the late-1940s should be considered less certain than subsequently.

Uncertainty related to allocating landings to SDs before the 1960s and 1970s concern mainly SD 25, for which our estimates of catch are based on several and in some cases rather rough assumptions. The landings of the GDR and the FRG in SDs 26 and 28 are also relatively uncertain, but because they constitute <5% of the total landings from those areas, their effect is here considered negligible.

Pronounced spatial differences exist in the availability of age distribution data. However, the estimated proportion of the landings covered by age information (Figure 3) should not be treated as exact because, for example, the annual mean age distributions were assumed representative of annual catches, although sampling may not have covered all quarters. The availability of age-specific data for SDs 26 and 28 in the pre-assessment years is similar to the situation later and considerably better than for SD 25 before the 1970s. Age-specific data coverage for SD 25 in the official ICES assessment improves a few years earlier than shown in this study, which uses the information in the MSVPA database. This is because the age distribution data from one country that has been included in ICES assessments since 1974 (excl. 1975; ICES, 1976) have not been archived well and could therefore not be included in the MSVPA database, which was compiled in the mid-1990s.

The sampling level in pre-assessment years does not appear to be particularly low. The Polish fisheries institute aged some 6000–7000 cod per year from the Baltic in the 1950s (Rutkowicz, 1959) and 2000–3000 in the period 1965–1974 (Kosior, 1977). In the early 1950s, the Latvian Department of the Fisheries Institute of the former USSR annually aged 1200–4500 cod (Prieditis, unpublished, Latvian State Archive). By comparison, Poland aged fewer than 1000 Baltic cod in 2003, and the countries of the former USSR aged ∼2500 cod from SDs 26 and 28 (ICES, 2004). The quality of age reading in the pre-assessment period is difficult to judge. Errors arising from age determination were considered important during the Assessment Working Group meeting in 1972, when large disagreements in age readings among countries were noted (Bagge *et al.*, 1994). Age discrepancies have since then been one of the major problems related to the assessment of the eastern Baltic cod stock, and have still not been resolved satisfactorily (ICES, 2006a). Here, pronounced differences in the ability to track differences in year-class strength in historical and more recent catch-at-age data could not be identified, suggesting that the problem has likely been of a similar magnitude over the years. Reeves (2003) analysed the effect of ageing errors on the assessment of the stock and stated that they had relatively little effect on historical trends of SSB and *F*. It is therefore unlikely that the general trends in our estimates are seriously affected by ageing errors, although recruitment estimates may be "smoothed" and show less interannual variation (Reeves, 2003).

The presence of relatively few older fish in the catches from the 1950s and 1960s and the high estimates of *F* then, similar to those noted more recently, may appear surprising. However, this is unlikely to be caused by errors in age determination in the earlier period because the length composition data indicated that there were relatively few large fish in the catch. For example, in SDs 26 and 28, the proportion of cod >60 cm in the landings was <10% during the 1950s and later, in the 1970s and early 1980s (Chrzan, 1954; Dementjeva, 1959; Kosior, 1976, 1980).

An annual rate of natural mortality (M) of 0.2 was used for the entire time-series for ages 2 and older, as in the current ICES assessment. Higher values of M (0.3–0.4) were suggested by Thurow (1974), and were applied by the Working Group before 1988 (ICES, 1988), because it was felt that eastern Baltic cod may suffer from poorer feeding and/or hydrographic conditions in the Baltic than in the North Sea (Thurow, 1974). However, there are no observed anomalies in the inflow of North Sea water into the Baltic that would have caused less favourable hydrographic conditions for cod before the 1970s compared with the later period (Schinke and Matthäus, 1998). Moreover, poorer feeding conditions would be reflected primarily in patterns of growth, and a significantly lower weight-at-age before the 1970s has not been observed (Appendix Figure A1). Therefore, assuming the same value of M in the pre-assessment years as in the current ICES assessment is probably reasonable. However, sensitivity of the results to this assumption was tested applying values of M of 0.4 in the period 1946–1965. This resulted in 20–30% lower fishing mortality and correspondingly greater estimates of SSB in this period.

Annual data on weight-at-age in SDs 26 and 28 were not available for the period 1960–1970, so we had to base our estimates on long-term means. Because annual estimates of weight-at-age in the 1950s and 1970s do not indicate notable changes in growth rate and because the stock in the 1960s was of a similar size as in the two adjacent decades, it is probably realistic to assume that growth in the 1960s was similar too. Weight-at-age declined when stock size increased dramatically in the late-1970s and early 1980s, which has been suggested to be attributable to a reduction in food availability (Baranova, 1989). Annual data on weight-at-age in SD 25 are not available before 1967, which might smooth the interannual variability both in TSB and SSB. However, and for comparison, the ICES assessment of the eastern Baltic cod stock is based on constant weights-at-age up to 1982 (ICES, 2006a). Another source of potential bias in the estimates of SSB is that maturity ogives are based on constant values for nearly 40 years. During the last two decades, the proportions of mature fish aged 2–4 have varied by 20–25%, with earliest maturation noted in the early 1990s (ICES, 2006a). The older age groups are mainly mature and indicate less variability between years. Applying constant maturity data might imply that distinctive developments in SSB were not captured by our analyses. However, the assumption of constant maturity is unlikely to affect the main patterns in abundance and SSB.

Stock dynamics

Area-disaggregated assessments can resolve the basin-specific dynamics of cod (Köster *et al.*, 2001). Cod migrate between SDs in the Baltic, as shown by various investigations summarized by Aro (2000), but the effect of migration is unlikely to have a major effect on area-disaggregated assessments (Köster *et al.*, 2001). Area-disaggregated multispecies analyses have revealed differences in trends in the cod stock in the three main basins (represented by SDs 25, 26, and 28, respectively) since the mid 1970s. The differences have been related primarily to differing reproductive success caused by varying hydrographic conditions (MacKenzie *et al.*, 2000).

Our estimates of cod biomass and recruitment before the 1970s reveal differences in population trajectories between SDs 25 and 26/28 (Figure 5). A relatively large population in SDs 26 and 28 in the first half of the 1950s followed by a reduction in the mid-1960s is supported by similar trends in cpue time-series (Figure 6a). Moreover, estimates of year-class strength correspond to available survey data, indicating relatively weaker year classes in the late-1950s and early 1960s (Figure 6b). A similar trend does not appear to take place in SD 25. However, the VPA estimates for SD 25 are probably less certain because of poor landings data and a scarcity of catch composition information before the 1970s.

The catch numbers-at-age in SD 25 during pre-assessment years are based only on Polish catch composition data, young age groups dominating the landings. In the 1950s and early 1960s, up to 30% of the Polish landings consisted of 2-year-old cod. A minimum landing size of 30 cm was introduced in the Polish fisheries after 1963 (Kosior, 1974), following which the proportion of young cod in the landings declined. The catch composition from Sweden and Denmark, which were the main countries fishing for cod in the Bornholm Basin, may have been different. Some 40% of Swedish cod landings from the southern Baltic in the late-1950s and early 1960s was of cod >50 cm (Otterlind, 1974), whereas cod of this size generally contributed <20% to the Polish landings then (Stanek, 1965). However, the estimates for Sweden do not include landings of industrial fisheries, which contained young cod and which varied between 2000 and 8000 t annually from the late-1950s to the 1970s (Otterlind, 1974). A minimum landing size of 30 cm was introduced by Sweden in 1957 (Otterlind, 1974). In Denmark, the minimum landing size was 33 cm from 1953 and 27.5 cm in earlier years. Corresponding restrictions in mesh size and minimum landing size in the cod fishery were introduced in parallel in several countries. The minimum mesh size in the Polish cod fishery was 80 mm and in the Swedish, 70 mm, although 75–80 mm was generally used in the latter (Otterlind, 1967). In Denmark, fishers used a mesh size of 80–90 mm when fishing for cod (Jensen, 1959a).

In conclusion, the total cod landings from SD 25 may have consisted of a larger proportion of older cod than shown by the Polish landings, so our value for *F* for the area may be an overestimate. Estimates of total mortality based on recaptures of tagged cod conducted in SD 25 in the late-1950s indicate very high levels (ca. 86%), but these investigations were experimental and suffered from various uncertainties (Jensen, 1958, 1959b). The relative uncertainty of our average estimates of *F* for SD 25 are also indicated by the variability among age groups up to the 1980s, whereas the estimates for SDs 26 and 28 over the entire time-series were more stable (Appendix Figure A2). *F* in SD 25 also appears unrealistically high in the 1940s (Figure 5). The trend of increasing fishing mortality in SD 25 from the 1950s to the 1960s, however, corresponds to the decline in the proportion of larger fish in Swedish landings during the same period (Otterlind, 1974).

In SDs 26 and 28, the estimated intense exploitation levels in pre-assessment years are based on more representative data and supported by more information than in SD 25. In those SDs, cod were caught mainly by former USSR and Polish fishing fleets. Cod was the most important species in the Polish Baltic fisheries, representing 60–85% of the landings in the years 1946–1960 (Anon., 1989). The corresponding share of cod in the landings of the former USSR varied between 25% and 40% during the same period (VNIRO, 1968). Although cod was at that time relatively cheap and may not have been valued by fishers, state plans had to be fulfilled. In the 1950s, the share of Baltic cod landings taken from SDs 26–32 was the largest in the time-series (Figure 2b), much larger than in the years with greatest cod stock on record (the late-1970s and early 1980s; Figure 5). These large temporal differences in spatial distribution of cod landings are unlikely to be caused by uncertainties in spatial allocation of the landings, but rather indicate relatively high fishing pressure in the northeastern areas of the central Baltic in the 1950s, with a high proportion of young cod in the catches (Figure 4, Appendix Figure A2).

The low stock size at a relatively low level of *F* after the Second World War may appear counter-intuitive. However, German North Sea steam trawlers aggressively targeted cod in the Baltic during the first years of the war (Meyer, 1952), and the cpue and the size of the cod in the landings decreased (Meyer, 1952). Sweden also fished cod intensively during the war, when fishers from the Swedish west coast moved to the Baltic, and very large quantities of small cod were taken with small-mesh trawls because of a food shortage (Alander, 1946). According to Alander (1946), the mean weight of cod in Swedish catches during the war years was only 100–200 g. Alander (1947) speculated too that recruitment in the last years of the war was relatively poor. Heavy fishing pressure during the war years, particularly on young fish, might therefore explain the estimated low stock levels after the war. However, uncertainties in recorded fish landings in those years may also contribute to the low estimate.

In the 1950s, heavy exploitation of the demersal fish stocks in the Baltic caused anxiety about their future, and international protective measures were urgently requested (Jensen, 1959c). As a result, a special meeting on measures to improve the stock of demersal fish in the Baltic was held in 1957 (Jensen, 1959c). Our estimates indicate a declining trend in fishing mortality from the early 1960s to the 1970s, which could partly be an effect of technical measures introduced to protect the stock. However, at the end of the 1950s and during the 1960s, herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) fisheries developed in the former USSR and Poland, and cod targeting declined (Lablaika *et al.*, 1991). Therefore, the development of alternative fishing possibilities may have contributed to the reduction in fishing pressure on cod.

Our estimates of fishing mortality for the total stock are affected by uncertain estimates for SD 25. If the true mortality of the subpopulation in Bornholm Basin was lower than estimated here, the absolute level of *F* for the whole stock would also likely have been lower. The scarcity of age data for cod combined with an overestimation of *F* in SD 25 may also explain the estimated low stock size and the low proportion of the total stock contained in this SD in the 1950s, compared with the later part of the time-series. Therefore, the SSB at the time of peak abundance in the 1950s may have been higher than estimated here, although probably not exceeding 350 000 t assuming similar proportions of SDs 26 and 28 cod in the total stock in these years as in later years. Our estimates of historical stock sizes from this analysis could be validated by other studies using alternative methods, e.g. production model analyses. Another method that could be used potentially to validate our reconstructed historical stock trends would be to compare them with egg production data from ichthyoplankton surveys. However, such analyses would require reliable vertical egg distribution models for the Gdańsk Deep and the Gotland Basin, to estimate the loss of egg production from the water column in periods of low salinity.

Trends in the cod stock in the Baltic depend largely on the strength of incoming year classes as well as fishing pressure (Bagge *et al.*, 1994). Early life stages of cod are affected by a number of processes, summarized by Köster *et al.* (2005). Because of the complexity of the mechanisms that can potentially influence cod population abundance, interpretation of the stock–recruitment relationship and stock development in relation to fishing mortality is not straightforward. Therefore, we chose not to include analyses of environmental and other factors in the present study. Such considerations could, however, provide a worthwhile subject for future investigation.

Summarizing, our analyses do not indicate problems in data availability and quality that preclude analytical stock assessment of cod in SDs 26 and 28 before 1966, i.e. before the first years of the ICES assessment. The first year in the current ICES assessment corresponds to an improvement of fisheries-specific data for SD 25. However, the age composition data for that area remain relatively poor up to the late 1970s. Our results have identified considerable fluctuations in the abundance of Baltic cod before the period covered by the ICES assessment. In the 1950s, the stock was already exposed to intensive exploitation at least in the Gdańsk and Gotland areas (SDs 26 and 28), and our results provide potentially important new knowledge on the eastern Baltic cod stock from both an ecological and management perspective.

Acknowledgements

Compiling the materials and reconstructing the time-series for this study involved the cooperation of a number of people from fisheries laboratories around the Baltic. We appreciate the help and advice of the staff in the Institute for Baltic Sea Fisheries in Rostock, the Sea Fisheries Institute in Gdynia, the Latvian Fish

Resource Agency, the Estonian Marine Institute, the Leibniz Institute for Marine Sciences in Kiel, and the Swedish Board of Fisheries. Special thanks are due to Hildrun Müller, Ritma Gaumiga, Krzysztof Radke, and Ole Bagge†. We thank Henrik Gislason and Brian MacKenzie for discussions and advice on the manuscript. ME also received support from the Danish Research School for Studies in Marine and Coastal Environment, Heritage and Sustainable Tourism (MAST), which is gratefully acknowledged. This analysis is a contribution of the EU FP6 European Network of Excellence for Ocean Ecosystems Analysis 511106-2 (EUR-OCEANS) to the EU FP6 Specific Targeted Research Project 022717 (UNCOVER) and the History of Marine Animal Populations (HMAP) project under the Census of Marine Life programme.

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Appendix

Input data on weight-at-age and estimates of biomass, spawning stock biomass, recruitment, and fishing mortality from the VPA analyses.

Table A1. Estimated TSB ('000 t), SSB ('000 t) and recruitment (age 2, millions) in SDs 25–32 and separately for SD 25 and SDs 26 and 28.

Year	TSB			SSB			Recruitment (age 2)		
	SD 25–32	SD 25	SD 26 and 28	SD 25–32	SD 25	SD 26 and 28	SD 25–32	SD 25	SD 26 and 28
1946	163.5	58.3	91.3	69.9	23.2	44.6	186.0	74.4	109.3
1947	265.9	94.5	151.2	112.6	39.7	71.0	288.5	101.1	183.6
1948	305.4	121.8	158.2	159.6	65.6	88.1	173.0	74.8	95.2
1949	338.4	116.8	190.0	180.5	63.7	107.2	260.3	88.2	168.2
1950	368.0	115.0	236.9	190.8	58.2	131.8	311.1	88.7	215.9
1951	403.6	128.7	255.5	212.5	72.2	138.9	302.0	81.7	215.2
1952	397.0	130.0	249.0	221.6	79.4	141.5	246.1	59.3	182.7
1953	327.8	116.3	210.3	205.6	78.3	124.1	201.5	51.1	146.6
1954	336.2	112.3	217.3	202.5	68.2	132.8	230.2	73.7	152.4
1955	401.8	133.9	232.8	209.1	73.3	130.3	321.6	103.5	212.4
1956	430.4	152.6	267.0	234.1	91.1	148.3	315.6	80.3	231.2
1957	399.5	157.5	237.9	242.8	106.6	139.2	207.4	57.6	147.0
1958	342.3	139.0	185.1	205.9	88.5	116.1	197.9	88.5	106.1
1959	351.6	149.8	179.5	183.8	80.4	102.6	276.9	119.8	153.0
1960	310.9	142.5	169.7	175.2	77.1	99.9	231.6	113.0	115.0
1961	281.4	133.4	149.4	159.2	77.4	83.4	235.4	105.1	127.3
1962	277.2	129.6	150.6	161.0	74.0	89.2	205.8	100.3	104.3
1963	264.1	129.6	142.5	157.6	74.8	86.2	196.3	99.9	103.1
1964	239.2	125.1	127.4	136.2	71.7	71.0	198.5	97.7	112.8
1965	269.1	141.7	152.2	137.6	73.8	74.5	311.5	141.4	172.3
1966	355.4	164.9	194.0	172.0	75.9	96.9	430.3	173.4	203.8
1967	436.3	198.8	197.7	228.7	94.5	105.0	370.9	188.4	157.1
1968	422.2	225.3	185.5	234.0	112.6	104.8	354.1	200.9	144.9
1969	396.0	223.8	184.8	222.7	118.3	111.4	306.7	172.2	116.5
1970	351.7	205.0	170.7	208.8	118.3	106.9	240.0	123.3	98.8
1971	314.5	198.6	156.3	184.2	117.5	95.9	264.8	141.3	113.4
1972	350.3	206.3	169.0	199.0	123.4	102.3	322.3	127.0	115.8
1973	394.4	216.0	188.2	212.0	130.9	100.6	432.1	142.9	199.3
1974	500.4	221.8	239.0	263.0	117.2	129.1	506.9	208.6	214.7
1975	575.9	241.2	262.5	339.5	136.0	160.7	303.7	138.2	140.5
1976	535.7	189.8	259.1	355.6	120.3	165.3	293.4	104.9	178.2
1977	533.5	196.1	329.4	326.9	118.9	184.0	479.0	140.3	328.3
1978	712.5	232.5	468.7	379.2	116.9	239.1	829.4	246.6	489.3
1979	983.0	301.2	567.7	579.7	155.6	346.3	615.4	226.1	297.8
1980	1 026.5	295.8	504.0	696.7	163.7	351.5	425.9	188.8	188.9

Continued

Table A1. *Continued*

Year	TSB			SSB			Recruitment (age 2)		
	SD 25–32	SD 25	SD 26 and 28	SD 25–32	SD 25	SD 26 and 28	SD 25–32	SD 25	SD 26 and 28
1981	984.2	346.2	469.3	666.1	192.0	308.6	689.8	282.0	314.2
1982	1 057.4	370.1	495.9	670.9	193.5	310.9	693.6	297.6	305.3
1983	1 003.1	370.6	447.0	645.3	215.0	294.9	472.4	196.6	209.3
1984	920.3	330.4	449.0	657.7	219.1	317.7	302.9	106.2	142.9
1985	737.7	256.5	360.3	544.9	160.2	268.0	253.1	100.1	127.7
1986	547.6	236.9	283.1	399.4	151.0	204.6	260.2	117.6	120.9
1987	492.3	255.7	235.9	320.4	141.0	162.1	368.0	172.3	125.1
1988	462.3	240.4	190.3	299.2	134.6	134.4	224.2	108.0	64.8
1989	352.7	199.5	132.2	240.2	123.4	101.2	122.1	55.8	37.4
1990	271.2	161.3	128.7	215.7	116.8	100.1	128.2	86.6	34.0
1991	192.6	117.4	90.6	151.0	83.2	67.0	83.2	48.3	31.6
1992	133.6	100.3	78.6	92.5	61.3	51.0	140.3	90.4	45.6
1993	173.9	141.8	88.8	113.5	82.9	53.7	182.8	122.0	55.0
1994	268.5	184.6	97.7	193.8	128.8	65.7	127.1	73.2	39.5
1995	316.6	180.3	112.2	242.3	132.3	79.9	119.3	68.0	42.3
1996	229.4	158.1	108.4	168.8	115.2	77.7	115.3	57.6	37.0
1997	206.7	108.8	90.0	146.4	80.1	63.8	87.8	44.8	32.7
1998	177.3	91.2	78.9	111.0	54.6	53.8	149.3	71.5	41.6
1999	179.4	104.6	70.1	89.3	60.6	46.9	152.6	76.0	32.3
2000	213.5	99.2	60.1	114.7	58.4	41.2	175.0	72.2	27.4
2001	170.8	92.7	54.3	103.9	58.0	35.6	135.7	57.7	32.1
2002	140.3	117.1	42.8	82.9	84.1	28.0	122.0	61.5	22.2
2003	134.2	71.3	44.1	80.5	48.0	28.3	102.1	25.1	31.3

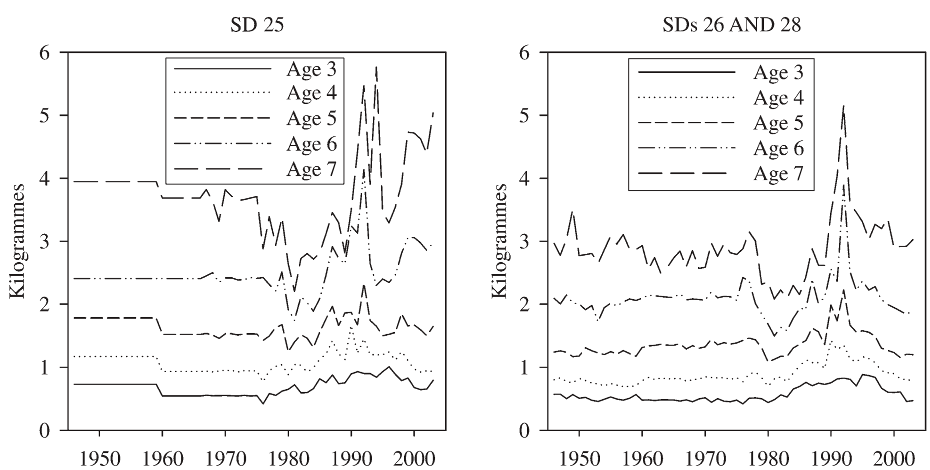

Figure A1. Input data on weight-at-age for age groups 3–7 in SD 25 and SDs 26 and 28, 1946–2003.

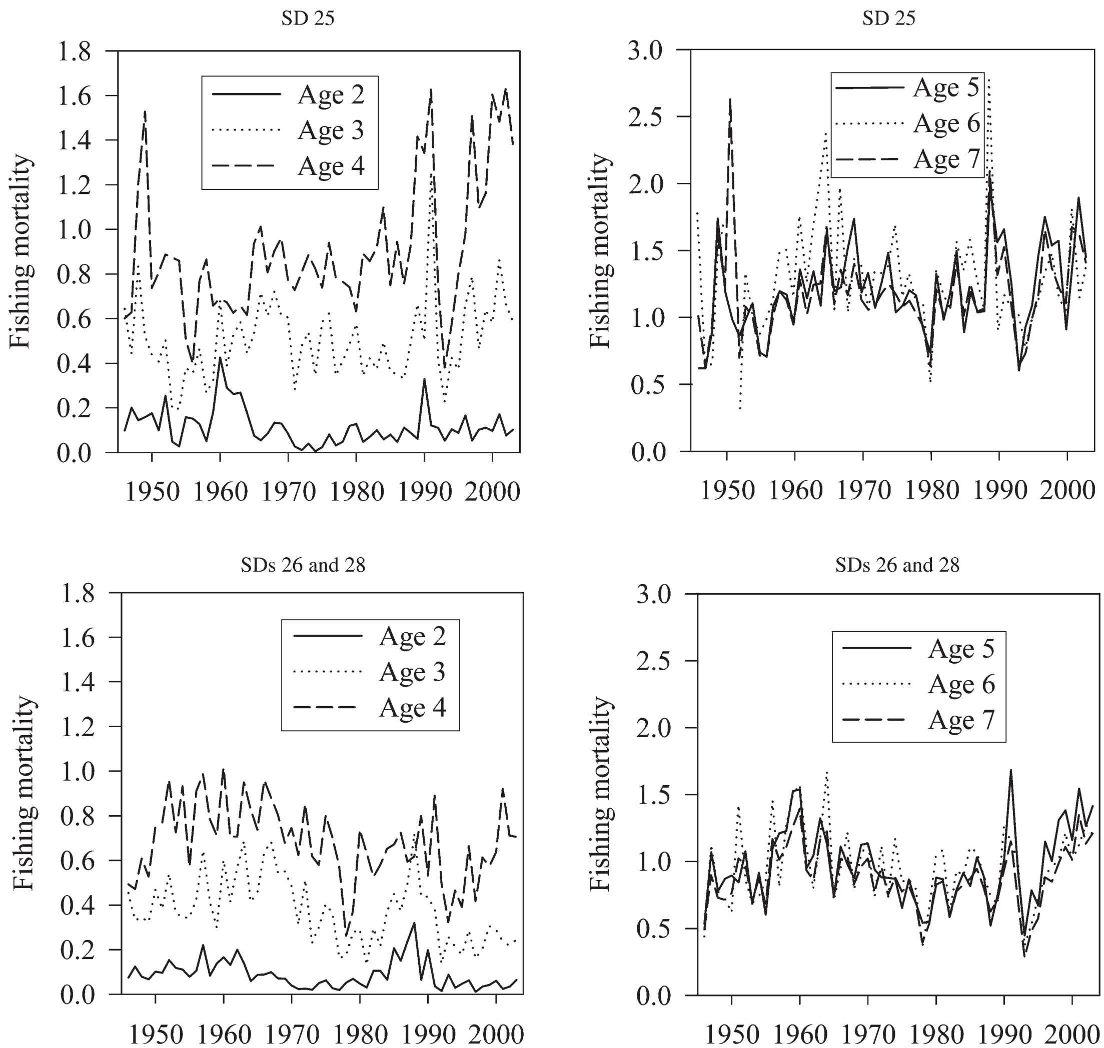

Figure A2. Estimates of fishing mortality *F* from the VPA analysis for SD 25 and SDs 26 and 28 separately by age group 2–7.

doi:10.1093/icesjms/fsm114

Paper III

Reconstructing historical stock development of the eastern Baltic cod (*Gadus morhua*) before the beginning of intensive exploitation

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Abstract

The landings of the eastern Baltic cod (*Gadus morhua*) in the early decades of the 20th century were below 50 000 tonnes, and therefore lower than in recent years at very low stock size. These low landings have largely contributed to a perception that the stock size was also low before the 1950s. In this investigation, we demonstrate that cod spawning stock biomass in the years 1925-1944 fluctuated in a similar range as in the periods from the 1950s to the mid-1970s and from the late 1980s onwards, and was in most of these years at least twice as high as at present. Fishing mortality before the 1940s was below 0.2, but reached moderate levels during the Second World War. The stock size before the war may be considered as a reference level of biomass at low fishing impact, providing important information for the management of fisheries and the Baltic ecosystem.

Introduction

Most of the regular fish stock assessments in the North Atlantic area cover only the recent 3-4 decades and the available time-series of stock developments begin after the onset of intensive exploitation. Consequently, the baselines for rebuilding depleted fish stocks may only refer to contemporary developments (Pitcher 2001) whereas a longer term historical perspective is important for evaluating the state of marine ecosystems and setting achievable goals for their management (Jackson et al. 2001; Pinnegar and Engelhard 2008). Several major shifts that have occurred in the abundances of fish stocks over decades or centuries have been related to exploitation. For example, studies on historical developments of cod stocks near Newfoundland (Rose 2004) and on the Scotian Shelf, eastern Canada (Rosenberg et al. 2005) showed that fishing was the dominant factor responsible for century-scale declines of these populations. Jackson et al. (2001) have also concluded that stock abundances of several predator species at the time of lower fishing pressure were much higher compared to the present low levels.

In the Baltic Sea, the low landings in the first decades of the 20th century suggest the opposite. The annual cod landings before the 1940s were below 50 000 t, which is not only lower than during the more recent decades, but is low also when compared with landing in neighbouring areas. Before the 1940s, the cod landings for example in the North Sea were up to hundred times higher than in the Baltic, whereas the landings from the two areas in the later decades have been at a relatively similar level (Fig. 1). However, the low Baltic cod landings in the early decades of the 20th century may not reflect the stock size but could also be due to an undeveloped fishery or low local demand for cod (MacKenzie et al. 2002; Bager et al. 2007; Eero et al. 2007b).

Biomass estimates for the eastern Baltic cod are available from ICES assessments from 1966 on (e.g., ICES 2007) and the time series has recently been extended back to 1946 (Eero et al. 2007*a*). Throughout this period the stock has been relatively heavily exploited. The stock size and the exploitation rate earlier in the 20th century are at present poorly known as the available estimates (Thurow 1999) are uncertain. The fishing intensity before the 1950s is considered to have been lower than in the later decades (Bagge et al. 1994). However, even at relatively low effort, fishing could still have had significant impact on the stock if the biomass was as low as suggested by Thurow (1999). The apparently low biomass of fish stocks in the early decades of the 20th century has been considered to be related to low productivity of the Baltic Sea before the 1950s (Thurow 1997*a*).

The uncertainty in the cod biomass before the mid-1940s is related to scarcity of data for estimating the stock size by standard methods with satisfactory reliability. In this paper we compile the available historical evidence that could be utilized to provide an indication of the cod stock size in the period from 1925 to 1944. We use multiple approaches based on independent datasets that enable us to evaluate the consistency of the information provided by the different analyses. The estimated biomass and fishing mortality allow us to evaluate whether the stock size in these years can be used as a baseline before the onset of heavy fishing pressure. Our analyses contribute to improving the understanding of the relative importance of environmental and human factors on development of the cod stock and provide new knowledge for management of fisheries and the Baltic ecosystem.

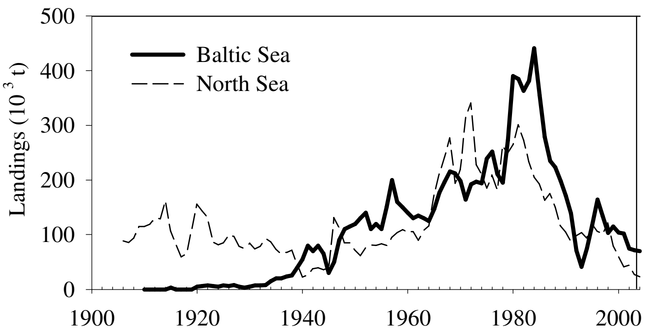

Fig. 1. Cod landings in the Baltic (Sparholt 1994; ICES 2007) compared with the North Sea (Daan et al. 1994; ICES 2005).

Materials and methods

We used four approaches to estimate the stock size of eastern Baltic cod (ICES Subdivisions (SD) 25-32, Fig. 2) in 1925-1944. First, spawning stock biomass (SSB) was estimated based on total mortalities obtained from catch curve analyses. This included analyses of length distribution data, compilation of catch numbers at length and subsequently estimation of mortality and biomass. Secondly, an indication of the level of SSB was obtained by comparing the catch rates of RV “Poseidon” in the period from 1925 to 1938 with the data from RV “Solea” for the years 1975-1992. Thirdly, we analysed cod landings in the northernmost areas in the Baltic and in the Gulf of Riga where cod abundance is more variable and dependent on stock size. Fourthly, we compared egg abundances from ichthyoplankton surveys in the 1920s and 1930s with more contemporary data. All the utilized data refer to the eastern Baltic stock (SD 25-32). All four methodologies used here, as do all methods for quantifying population sizes of wild organisms, involve different assumptions and are associated with different levels of uncertainty, partly resulting from incomplete data coverage in time and space. The major uncertainties related to these approaches are addressed in the discussion. The data sources and treatments concerning each of the analyses are described below.

Length distribution data

Length distributions of cod in the catches by German cutters and steamers for the period from 1940 to 1944 and by the former USSR, Poland, Federal Republic of Germany and former German Democratic Republic for the period from 1947 to 1975 (Table 1) were included in estimating mortalities in respective time periods. For the period before the 1940s, average length distributions were additionally presented for German trawl surveys conducted in the period from 1925 to 1938 between March and July by RV “Poseidon” using commercial trawl (Kändler 1944). For comparison, average length frequency was presented for surveys by RV “Anton Dohrn” in the years 1962-1970 during April-May (Tiews 1974). In order to compare commercial length distributions in the 1940s with later decades we have also included average length structure of Danish commercial cod landings in the years 2002-2006 obtained from the national database. Differences in the proportions of cod ≥ 50 cm in length in the catches in different time periods were analysed using Wilcoxon rank test.

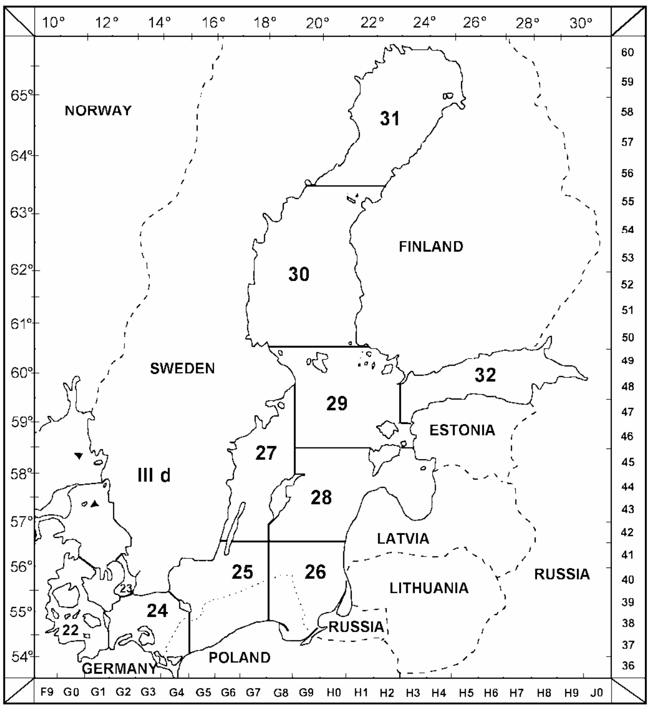

Fig. 2. ICES Subdivisions in the Baltic Sea.

Calculation of catch numbers by length-groups

<u>1940-1944:</u>

The Baltic cod landings in 1940-1944 were mainly taken by German steam trawlers. These corresponded to ca 80% of the total annual eastern Baltic cod landings based on the data utilized in this study. The recorded landings of steamers included all species, however ca 99% was reported to have been cod (Meyer 1952*b*). The German steamer fleet operated in offshore areas in the Baltic, mainly in Bornholm Basin, Gdansk Deep and Gotland Basin

Table 1. Availability of length composition data for the landings by German cutters and steamers in 1940-1944 and for the landings by the former USSR, Poland, former German Democratic Republic (GDR) and Federal Republic of Germany (FRG) in 1947-1975 by year, time and Subdivision (SD) and respective data sources.

Country	Years	Time	SD	Source
German cutters	1940	May, June	25	Meyer 1952*b*
	1941	Feb.	26	
	1943	Mar., Nov.	26	
	1944	Jan.	26	
German steamers	1940	May-July	25, 26, 28	Meyer 1952*b*
	1941	Mar., Feb., Dec.	25, 26, 28	
	1942	Jan., Apr.-June	25, 26	
	1943	Mar., July, Sept.	25, 26, 28	
	1944	Feb., Apr., June	26, 28	
USSR	1947-56	Spawning time	26-32	Dementjeva 1959
	1966-75	Annual mean	26-32	presented to ICES
Poland	1947	Annual mean	26	Chrzan 1950
	1948-51	Annual mean	26	Chrzan 1954
	1952-54*	Annual mean	26	Chrzan 1957
	1955-56*	Annual mean	26	Rutkowicz 1959
	1953-54	Annual mean	25	Reimann 1962
	1955-56	Annual mean	25	Stanek 1962
	1957-60	Annual mean	25	Stanek 1965
	1966-75	Quarter 1	25, 26	Kosior 1967, 1969, 1970 1971, 1972, 1973, 1974, 1976
GDR	1954-60	Quarters 1 and 2	25	Berner, M., unpublished
	1967-75	Quarters 1 and 2	25	Berner and Borrmann 1980; Berner, M., unpublished
FRG	1969-75	Quarters 1 and 2	25-28	presented to ICES

* Length distributions in weight were converted into numbers of fish applying mean weight at length in 1947-54 (Chrzan 1962).

(Meyer 1952*a*) which correspond to the spawning areas of the eastern Baltic cod (Bagge et al. 1994). The major part of the German cod catches in the Baltic in 1940-1944 was taken during spawning season (Meyer 1952*a*). The fishing effort of steam trawlers during the years from 1940 to 1944 was relatively stable: number of fishing trips in the Baltic in these years varied between 1011 and 1177 without a temporal trend, whereas the number of fishing days per trip increased from 9.9 to 11.7 during 1940-1944 (Meyer 1952*a*).

Danish landings in the years 1940-1944 were included for the harbours located at Christiansø and at the east coast of Bornholm Island assuming that the cod landed in these ports was caught in the waters east of Bornholm, i.e. in SD 25-32. The data were extracted from the statistics of the Danish Directorate of Fisheries stored in the Danish National Archive. Swedish landings were also included for the counties bordering SDs 25-32 (Awebro 2002).

Length compositions from German cutters (Meyer 1952*b*) were assumed to represent the part of cod landings not taken by German steamers in 1940-1944. The average length composition in the years 1941 and 1943 was applied for 1942. The data for different months in 1940 and in 1943 were averaged to obtain annual means. The length compositions of the steamer catches by month were averaged by using respective landings as weights (Meyer 1952*a*). Mean weights at length from Polish data for the years 1947-1954 (Chrzan 1962) were used to calculate landings in numbers by length-groups in 1940-1944.

<u>1947-1975:</u>

Catch numbers at length were calculated for the years 1953-1960 for SD 25, for the years 1947-1956 for SDs 26 and 28 and for the years 1966-1975 both for SD 25 and for SDs 26 and 28. Whenever length distributions from several countries for a given year and area were available, these were averaged, weighting by respective landings. Landings data by countries and SDs before the year 1972 were compiled by Eero et al. (2007*a*); from 1972 on, the data are available in ICES (e.g., ICES 2007). Average weights at length in the years 1953-1954 (Reimann 1962) and 1954-1962 (Berner, M., unpublished) and the average weights in the years 1967-1975 (Berner, M., unpublished) were applied in calculating catch numbers at length for SD 25 in 1953-1960 and in 1966-1975, respectively. The catch numbers in SDs 26 and 28 in 1947-1956 and in 1966-1975 were calculated using mean weights at length for the years 1947-1954 (Chrzan 1962) and 1960-1975 (data from the former USSR, presented to ICES Working Group on Demersal Fish Stocks in the Baltic), respectively.

Estimation of mortality and biomass based on catch-curve analyses

The length-converted catch curve method (Sparre and Venema 1998) was used to calculate total mortalities. Before the mid-1940s, mortalities were estimated based on average catch numbers at length in 1940-1941, in 1942-1944 and for comparison in 1940-1944 combined. The two time periods were kept separate due to large differences in length frequency. For comparison, we estimated mortalities based on the length data also for the period from 1947 to 1975, as for these years the estimates from age-based VPA were available for validation (Eero et al. 2007*a*).

The length-converted catch curve method uses the von Bertalanffy growth equation to convert length into age. Three sets of growth parameters estimated for the 1960s and 1970s for SD 25 (Kosior 1976; Berner and Borrmann 1980; Steffensen and Bagge 1983) and for SD 26 (Draganik and Netzel 1966; Lablaika et al. 1975; Kosior 1976) were applied in estimating mortalities in SD 25 and in SDs 26 and 28, respectively. The mortalities for the years 1940-1944 were estimated for all six sets of growth parameter values. Different values were applied in order to evaluate the sensitivity of mortality estimates to growth parameters. Length-groups from 45 to 70 cm were included in catch curves that after converting into age corresponded approximately to ages 4-7.

To have an indication of possible differences in growth in the 1940s compared to the later years we used the information on condition of cod. Fulton's condition factors (K) for cod in SD 25 in the first quarter of 1943 were estimated by Meyer (1952*c*). His calculations were based on weights of the fillets multiplied by two as the fillets formed approximately half of the total weight of the fish. As the exact proportions of the fillets in the total weight were also given (between 50 and 60 %; Meyer 1952*c*), we used these data to adjust Meyer's estimates of condition factors for more accurate values. The average condition factor of cod in SD 25 in the first quarter of the years 1991-2007 was calculated based on length and total weight data from the Baltic International Trawl Surveys (BITS, ICES database).

Our catch curve analyses were based on average catch at length over a number of years, not following the development of single year-classes. In order to evaluate the consequent possible bias in mortality estimates for 1947-1975, we additionally estimated mortalities in this period from age-based catch curves. Catch numbers at age (Eero et al. 2007*a*) were averaged over the same time periods as the length-based data. Age-groups 4-7 were included in catch curves. The mortality estimates from catch curves were then compared with the results from VPA (Eero et al. 2007*a*).

Fishing mortalities in 1940-1941 and in 1942-1944 were calculated from respective total mortality values, assuming a natural mortality rate of 0.2 that corresponds to the value applied in the assessment of this stock (ICES 2007). The biomass was estimated as the ratio between the landings and the fraction of the stock removed by the fishery. The estimated biomass was considered to represent the size of the spawning stock as the mortality estimates did not include small fish. This was supported by the data for the years 1966-2006 where the ratio between the landings and the fraction removed due to fishing mortality of the ages 4-7 produced values similar to the estimates of SSB (r^2=0.979, p<0.01; ICES 2007).

Catch per unit of effort

Catch rates (kg·hour^{-1}) of RV “Poseidon” (Table 2) in Bornholm Basin (SD 25) in the period from 1925 to 1938 (Kändler 1944) were compared with catch rates by RV “Anton Dohrn” in the years 1964-1971 (Tiews 1974 and unpublished) and from RV “Solea” for the years 1975-1992 (Thurow and Weber 1992).

The catch rates by RV “Anton Dohrn” and by RV “Solea” in SD 25 were both significantly correlated with cod SSB in SD 25-32 in respective years (r^2=0.673, p<0.05; r^2=0.441, p<0.01, respectively). The average ratio between CPUE and SSB was 0.66 (± 0.21) for RV “Solea” and 1.2 (± 0.45) for RV “Anton Dohrn”. The technical characteristics of the gear in use and the vessels (Table 2) indicated that catchability of RV “Poseidon” was closer to RV “Solea” than to RV “Anton Dohrn”. Therefore, the average ratio between CPUE and SSB from RV “Solea” was applied for calculating SSB in the 1920s and 1930s based on the catch rates of RV “Poseidon”.

Table 2. Availability of CPUE data from German research surveys in Bornholm Basin by vessel and year and characteristics of the vessels and fishing gear.

Vessel	Length, m	BRT	HP	Gear	Years	No. of stations	Month
"Poseidon"	46	453	480	120-feet trawl	1925-1926	11	Apr., July
					1929, 1931	21	Apr.-June
					1933, 1935	22	Mar.-Apr.
					1938	19	Mar., Aug.
"Anton Dohrn"	62	999	850	180-feet standard	1964	13	Apr.-May
				herring trawl and	1966	14	Apr.
				140-feet fish trawl with	1968	11	Apr.
				herring cod-end	1969	23	Apr.
					1970	13	Apr.-May
					1971	12	Apr.-May
"Solea"	35	337	870	Sonderburg trawl	1975-1992	ca 25 per year	Mar.-May
				Cod hopper; 107-feet trawl*	annual		

* The length of the groundrope was not provided as an official technical measure of the trawl, respective measurement was obtained from the design plan in order to compare with the measures of the trawls used by "Poseidon" and "Anton Dohrn" (Manfred Stein, pers. comm., Sea Fisheries Institute in Hamburg).

Cod landings in the northern Baltic and in the Gulf of Riga

Increased cod landings in the northern Baltic and in the gulfs can be used as an indicator of increased distribution area and stock abundance (Aro and Sjöblom 1982; Ojaveer et al. 1985; Ojaveer et al. 1999; MacKenzie et al. 2002). Therefore, we compared cod landings in the Gulf of Riga and in SDs 29-32 in the period from the mid-1920s until the early 1940s with the landings in these areas after the 1970s. Similar amounts of landings in the 1920s - 1940s compared to the landings in the later period were assumed to indicate similar levels of SSB.

The development of landings in the Gulf of Riga was represented by Latvian data extracted from national fisheries statistical reports. In the years 1925-1938, the landings reported for the harbours located along the Gulf of Riga were assumed to have been taken from the gulf. For SDs 29-32, two time series of landings were analysed: (*i*) Swedish landings in SDs 29-31; and (*ii*) Estonian and the former USSR landings in SDs 29 and 32. The Estonian statistics refers to the years 1934-1938 and 1991-2004; in 1973-1990 the landings reported by the former USSR in SDs 29 and 32 were utilized. Swedish data until the year 1974 were from national fisheries statistics (Awebro 2002) and included landings for the counties corresponding to the location of SDs 29-31. From 1975 onwards, the landings by SDs were available from ICES (e.g., ICES 2007). Estonian landings by counties in 1934-1938 were extracted from the national fisheries statistical reports and included for the areas located at the west and north coast corresponding to SDs 29 and 32. From 1973 on, the data by SDs were taken from ICES (ICES 2007).

Our comparisons of landings in the northern Baltic and in the Gulf of Riga assumed that the proportions of the stock dwelling in these areas were similar in the time periods compared. The expansion of the cod distribution north-eastwards at higher population sizes is related to increased salinities that favour cod reproduction (Lablaika and Lishev 1961; Plikshs et al. 1993; Köster et al. 2005). In order to account for possible differences in stock distribution due to different salinities, we compared only the landings from time periods with similar salinity conditions in the bottom water. The landings from the mid-1980s on were therefore only used in comparisons with the landings in the early 1930s, when the salinities were similarly low (Fonselius 1962; Köster et al. 2005). The landings in the mid-1920s and late 1930s were compared to data for the 1970s.

Egg abundance

Potential egg production of eastern Baltic cod stock taking into account maturity, sex ratio and relative fecundity has been shown to be highly correlated with realized egg production from ichthyoplankton surveys in SD 25 (Kraus et al. 2002). Based on this information, a recent attempt to estimate SSB from egg abundance for SD 25 (Kraus, G., Hinrichsen, H.-H., Voss, R., Tomkiewicz, J., Teschner, E., Schaber, M., Köster, F.W., submitted) indicated that the method is sensitive to the hydrographic conditions with a good agreement in inflow years, but less in stagnation periods. As sufficient information for the period before the 1940s is not available for utilizing the relationship between potential and realized egg production for estimating SSB, we followed a simpler approach to obtain a proxy for the level of SSB from available egg abundances for the 1920s and 1930s. We compared egg abundances in SD 25 in 1926, 1931 and 1938 (Mielck and Künne 1935; Kändler 1944) with data from 1966 on (Köster et al. 2005). To account for possible differences in buoyancy of eggs at different hydrographic conditions (Wieland and Jarre-Teichmann 1997) egg abundances were compared only for years where the bottom water salinities (80 m depth; Mielck and Künne 1935; Kändler 1944; Fonselius and Valderrama 2003; ICES Oceanographic Database) were similar. Similar egg abundances observed at similar salinities were assumed to reflect similar level of SSB.

The egg data for 1926, 1931 and 1938 were from July, May-June and July-August, respectively. The data for the later period represented three month peak in spawning time, i.e. April-June up to 1989 and was successively shifted to mid April-July (1990), May-July (1991-1992), mid May-mid August (1993-1995), and mid June-mid September (1996 to 1999) corresponding to the shift in spawning time (Köster et al. 2005). In 1926, 1931 and 1938, data were available from 7, 8 and 40 stations, respectively. For the later years, data were in general from 3 surveys per year, with the number of stations ranging from 24 to 46 per survey (CORE 1998).

Results

Changes in length composition of the landings and condition of cod

In the years 1940-1941, more than 60 % of cod in the landings by German steamers were ≥ 50 cm in length. Thereafter, the proportion of large fish declined and in 1942-1944 they formed as an average only 49 % of the landings (Fig. 3), with the difference in the proportion being significant (W=69; $p<0.05$). An even larger reduction in the percentage of cod ≥ 50 cm was indicated in the landings of cutters. The proportion of fish at this size in the landings in 1938-1941 was on average more than twice as high as during 1942-1944. However, the difference was not found significant likely due to a low number of samples.

The average length distribution of cutter catches in the years 1942-1944 was similar to the average commercial catch compositions in the later time periods, i.e. in 1947-1960, in 1966-1975 and in 2002-2006 (Fig. 3). The average proportion of cod ≥ 50 cm in these years was between 16 and 19 percent. Similar length structures were observed in research catches in the period from 1962 to 1970, whereas in research catches from 1925 to 1938 up to 60% of cod was ≥ 50 cm in length, similarly to the length structure of commercial catches by steamers in 1940-1941.

The condition of cod during the war was indicated to have been lower compared to the recent 15 years period. Fulton's condition factor in SD 25 in the first quarter of 1943 was estimated at 0.80, while the average in the years 1991-2007 in the equivalent area and season was estimated at 0.97.

Mortality estimates from catch curve analyses

Total mortality (Z) of cod in SD 25-32 in the years 1940-1941 was estimated at 0.44 and increased to the level of 0.81 in 1942-1944 (Table 3). The slopes of the catch curves for the years 1940-1941 and 1942-1944 were found significantly different ($t_{2,8}=3.746$; $p<0.01$). The corresponding SSB in 1940-1941 was estimated at around 300 000 t and thereafter it declined to 113 000 t in 1944.

Length based mortality estimates for the years 1953-1960 and 1966-1975 for SDs 26 and 28 were in line with the results from VPA and with the mortalities estimated from age-based catch curve analyses for the same time periods (Table 3). For SD 25, the average length-based total mortalities were estimated at 1.0 and 1.2 in 1953-1960 and 1966-1975, respectively. These values suggest lower fishing mortality in both periods than obtained from the VPA (Table 3).

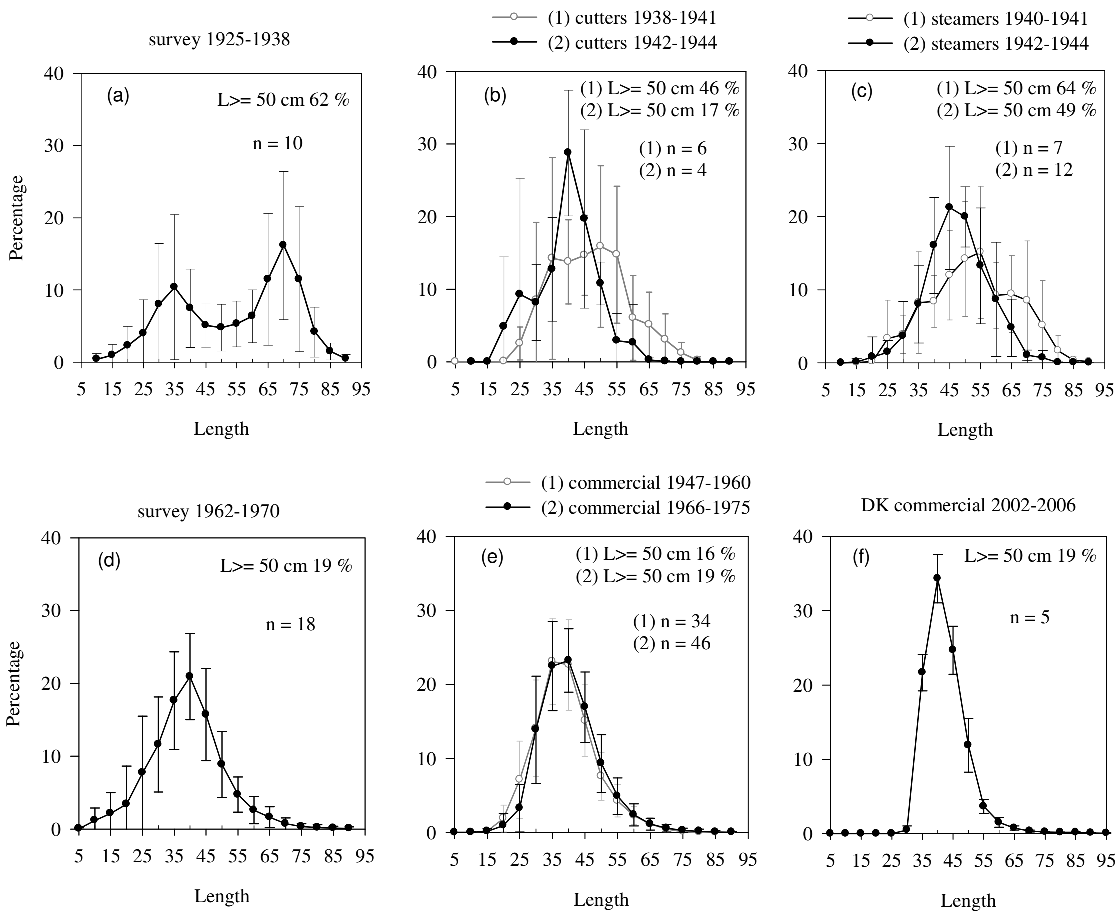

Fig. 3. Average length distributions of cod in a) catches by RV "Poseidon" in 1925-1938, b) catches by German cutters in 1938-1940 and in 1941-1944, c) catches by German steamers in 1940-1941 and in 1942-1944, d) catches by RV "Anton Dohrn" in 1962-1970 e) commercial catches in 1947-1960 and in 1966-1975, f) Danish commercial catches in 2002-2006. Error bars represent variability in the data sets that were available by a) year and area; b) year and for some years by month; c) year and in some years by area and/or month; d) year and area; e) year, country and SD; f) year. Each panel shows the number of available datasets (n) and the average percentage of fish $\geq$ 50 cm in length. The length distributions are presented by 5 cm groups, the length shown on the x-axis indicates the first cm of a length-group.

Table 3. Estimates of total mortality (Z) and confidence intervals based on length-converted catch curve analyses in comparison with total mortalities from age-based catch curve analyses and fishing mortalities from VPA (Eero et al. 2007*a*). The range of the mortality estimates and confidence intervals obtained applying different von Bertalanffy growth parameter values are shown in brackets.

Years	Area	XSA F (4-7)	Age based catch-curve Z (4-7)	Length-converted catch-curve Z (45-70cm)
1940-1944	SD 25-28	-	-	0.67 (0.62-0.73) ± 0.20 (0.17-0.23)
1940-1941	SD 25-28	-	-	0.44 (0.41-0.48) ± 0.36 (0.31-0.40)
1942-1944	SD 25-28	-	-	0.81 (0.75-0.89) ± 0.21 (0.17-0.25)
1953-1960	SD 25	0.96	1.04 ± 0.43	1.01 (0.94-1.10) ± 0.05 (0.04-0.06)
1966-1975	SD 25	1.17	1.36 ± 0.54	1.18 (1.11-1.29) ± 0.02 (0.01-0.03)
1947-1956	SDs 26 and 28	0.85	1.05 ± 0.19	1.12 (1.02-1.19) ± 0.15 (0.13-0.16)
1966-1975	SDs 26 and 28	0.89	1.14 ± 0.24	1.08 (0.98-1.15) ± 0.07 (0.06-0.08)

Analyses of catch per unit of effort

The average catch rate of RV “Poseidon” in SD 25 in 1925-1926 was 102 kg·hour^{-1}. Similar catch rates were recorded in the years 1933-1935 and 1938 (91 and 126 kg·hour^{-1}, respectively), while in 1929-1931 the average CPUE was 3-4 times lower (Fig. 4). The catch rates by RV “Poseidon” were at a similar level as the catches per hour by RV “Solea” in the early 1990s and by RV “Anton Dohrn” in the mid-1960s (Fig. 4), whereas the catchability of the RV “Poseidon” should be considered as the lowest among the three vessels (Table 2). The average SSBs in SD 25-32 based on the catch rates of RV “Poseidon” were estimated at 155, 44, 138 and 191 thousand tonnes in the years 1925-1926, 1929-1931, 1933-1935 and in 1938, respectively.

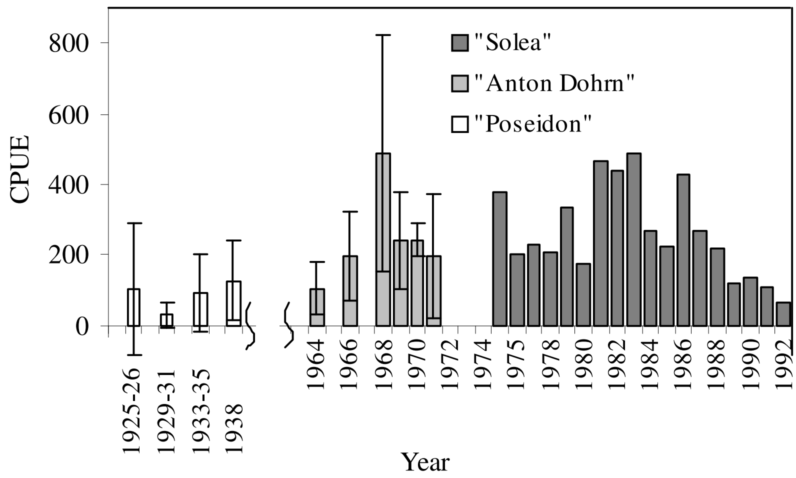

Fig. 4. Average CPUE (kg·hour^{-1}) by RV "Poseidon" (Kändler 1944) in the period from 1925 to 1938, by RV "Anton Dohrn" (Tiews 1974 and unpublished) in the period from 1964 to 1971 and by RV "Solea" (Thurow and Weber 1992) in 1975-1992 in SD 25.

Development of cod landings in the northern Baltic and in the Gulf of Riga

Swedish cod landings in SDs 29-31 were between 2 and 20 t in the years 1925-1939 and rose up to 350 t in the early 1940s (Fig. 5). The lowest landings in this period were recorded in the early 1930s, similar to the low level of landings in recent years (Table 4). The landings in the mid-1920s and late 1930s were comparable to the amounts of cod taken in these areas in the early 1970s when the average SSB in SD 25-32 was between 200 and 225 thousand tonnes (Table 4). Estonian cod landings in SDs 29 and 32 increased from 50 t in 1934 to over 800 t in 1938. For comparison, in recent years the catches from this area have been negligible (Fig. 5). Similar average landings as in the years 1934-1935 and 1936-1938 were taken from this area in 1989-1991 and in 1973-1977, respectively. The corresponding average SSB in SD 25-32 was between 200 and 300 thousand tonnes. The average Latvian landings in the Gulf of Riga in the years 1929-1931 were 7 t. Similar low landings were recorded in the years 1990-1992 when the SSB was around 150 000 t. The landings in the late 1930s were about 35 times higher, corresponding to the level of landings in the first half of the 1970s at an average SSB of 240 000 t (Table 4).

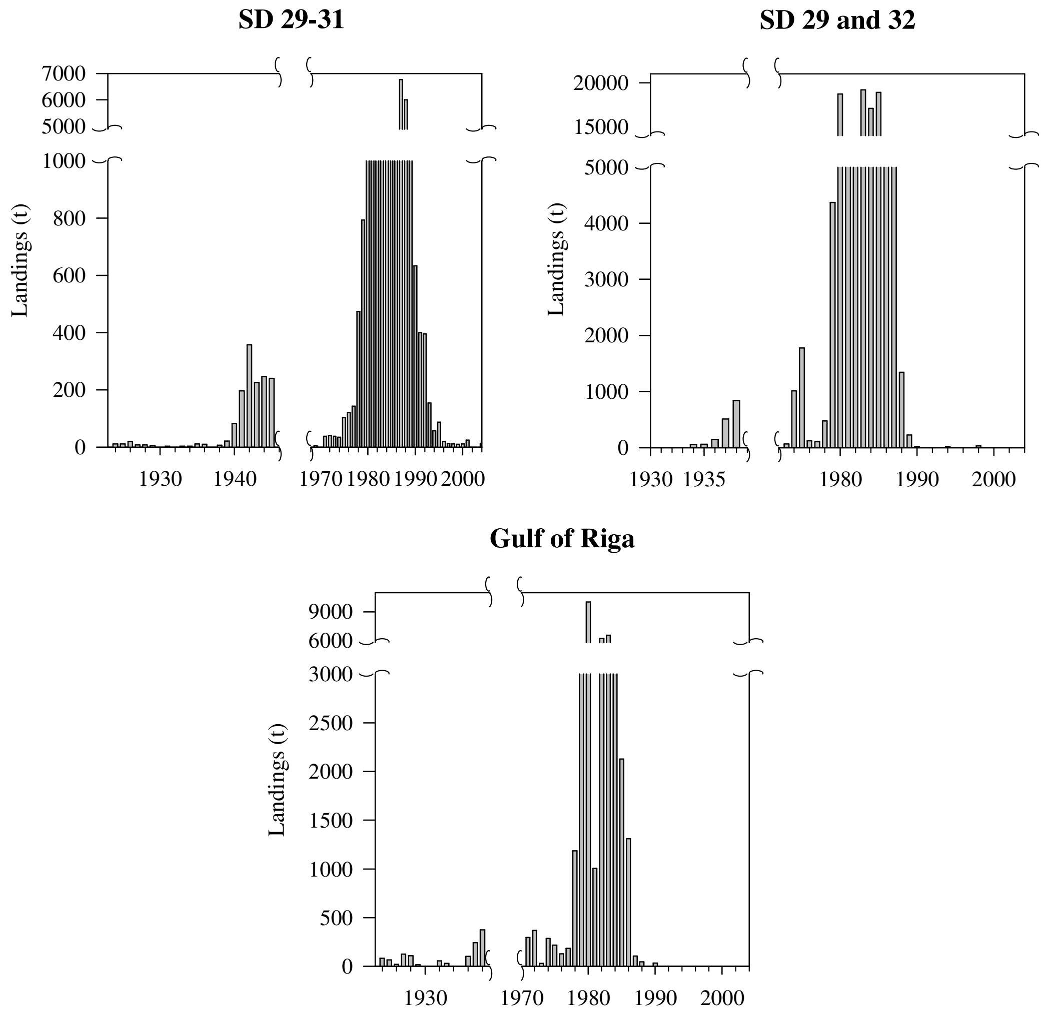

Fig. 5. Cod landings by Sweden in SDs 29-31, by Estonia in SDs 29 and 32 and by Latvia in the Gulf of Riga.

Egg abundances

The abundances of cod eggs in SD 25 in 1926, 1931 and 1938 were most similar to egg abundances observed in 1997, 1992 and 1976, respectively, when considering the time series from 1966-1999. The corresponding SSB values were 146, 92 and 355 thousand tonnes (ICES 2007), respectively (Table 5).

Table 4. Average cod landings by Sweden in SD 29-31, by Estonia in SDs 29 and 32 and by Latvia in the Gulf of Riga in the mid-1920s, in the late 1920s-early 1930s and in the late 1930s-early 1940s compared to the corresponding levels of average landings and spawning stock biomasses in the period after the 1970s.

Area	Years	Landings (t)	Years	Landings (t)	SSB (10^3 t)
SD 29-31	1925-1927	13	1969-1971	15	205
	1930-1932	2	2002-2004	4	81
	1938-1940	36	1972-1974	37	225
SD 29 and 32	1934-1935	59	1989-1991	82	202
	1936-1938	500	1973-1977	667	299
Gulf of Riga	1929-1931	7	1990-1992	11	153
	1936-1938	240	1971-1975	239	240

Table 5. Cod egg abundances (ind·m^{-2}) and corresponding salinities (80 m depth) in Bornholm Basin in the years 1926, 1931 and 1938 and spawning stock biomasses (10^3 t) in the period from 1966-1999, in the years when the egg abundances were similar to the values observed in 1926, 1931 and 1938.

Year	1926	1931	1938
Egg abundance / Salinity	39 / ~16	11 / ~15	89 / 16.8
Egg abundance / Salinity in comparative year	45 / 15.8 (1997)	9 / 14.9 (1992)	96 / 16 (1976)
SSB	146	92	355

Comparison of the indications of spawning stock biomass and corresponding fishing mortalities

The three estimates of SSB for the mid-1920s were between 150 and 200 thousand tonnes. The estimates for the late 1920s and early 1930s indicated a lower level of SSB, between 45 and 150 thousand tonnes. In the late 1930s, the SSB estimates were in the range of 190 to 355 thousand tonnes (Fig. 6). The lowest estimates in each time period were generally obtained from comparing catch rates of RVs “Poseidon” and “Solea”. The highest level of

SSB in the late 1930s was indicated from egg abundance data, similar to the estimate from catch curve analyses for the early 1940s (Fig. 6).

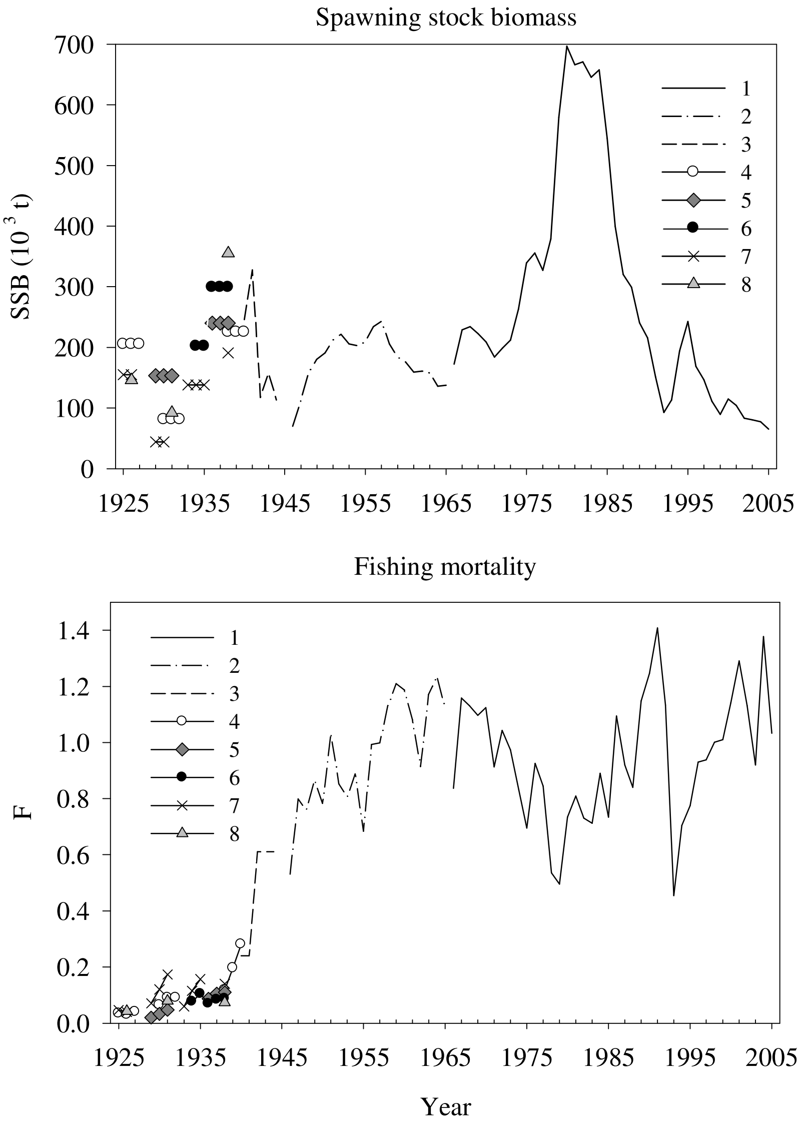

Fig. 6. Estimates of cod SSB and fishing mortality for the years 1925-2005 by different methods. 1- ICES assessment (ICES 2007); 2- VPA (Eero, et al. 2007a); 3- Based on mortality estimates from length based catch curve analysis; 4- Based on landings in SD 29-31; 5- Based on landings in the Gulf of Riga; 6-Based on landings in SDs 29 and 32; 7-Based on CPUE data; 8- Based on egg abundances.

Fishing mortalities were estimated on basis of the ratio between total cod landings and SSB, except from the catch curve analyses where mortalities were used to calculate biomass values. Fishing mortalities were below 0.2 from the mid-1920s until the mid-1930s, increased up to 0.3 by the early 1940s followed by a sharp increase to the level of 0.6 during the war (Fig. 6).

Discussion

Historical development of the cod fishery and perception of the stock size

Technological developments in the Baltic fisheries occurred much later compared to e.g. North Sea. Trawling was conducted by steamers in the North Sea already in the 19th century (e.g., Haines 1998) while in the Baltic motorization of the boats only started in the beginning of the 20th century and trawls were introduced in the 1920s (Hessle 1947; Jensen 1954; Bager et al. 2007; Eero et al. 2007*b*). Trawls were initially small and adopted to catch flatfish that gave high yields in the 1920s and early 1930s (Molander 1955; Jensen 1959; Temming 1989). After severe reduction of flatfish catches in the mid-1930s, the trawls became larger and better adapted to catch cod (Hessle 1947; Sahlin 1959). Until then cod was mainly caught by hand-lines and long lines (Hessle 1947; Jensen 1954).

With the Second World War, Germany lost its offshore fishing grounds in the North-East Atlantic and had to confine the fishery to more coastal areas, i.e. southern part of the North Sea, Skagerrak, Kattegat and the Baltic Sea (Meyer 1952*a*). It was seen as a crisis for the fishing industry as before the war these areas were of very little importance for the fishery by steamers due to low profitability. In the Baltic a commercial fishery by steamers had so far not taken place, except for unsuccessful trials during the First World War. The Baltic generally had a reputation as an overfished and low fish abundance area. This concept developed mainly in relation to the decline of flatfish stocks that were considered to be depleted due to the development of the trawl fishery (Meyer 1952*a*). In contrast to their expectations, the German steamer fleet found abundant resources of cod in the eastern Baltic (SD 25-28) that formed a major part of total German landings during the war. The steamers' cod fishery was from the beginning accompanied by scientific investigations, first of all related to economical interests (Meyer 1952*a*, 1952*b*, 1952*c*). Consequently, although it may appear surprising, the first extensive materials related to the commercial fishery of eastern Baltic cod are from the investigations conducted during the war and these provide important information for our study.

The cod fishery by steamers during the war changed the perception of the Baltic in terms of its productivity and fish abundance. Although an increase in cod landings in the local fisheries was observed already in the late 1930s (e.g. Eero et al. 2007b), their level was still much lower compared to the landings by German steamers during the war. After the war, the cod fishery in the Baltic developed rapidly (e.g., Lablaika et al. 1991) and in the 1950s the exploitation rate was already at a high level (Eero et al. 2007*a*). Research on status of fish stocks in the Baltic developed in the eastern countries shortly after the war, but was mainly focusing on predicting future fishing possibilities, not on historical developments or their causes. The first attempt to estimate the stock size of the eastern Baltic cod in the early decades of the 20th century was made by Thurow (1999). Based on the results from his study and on the landings statistics, the cod stock is generally considered to have been at a very low level until it started to increase in the late 1930s. Consequently, the current understanding of the long-term impacts of major human-induced changes in the Baltic ecosystem (e.g. eradication of marine mammals, eutrophication) on fish populations is based on the perception of very low cod stock in the early 20th century (e.g. Österblom et al. 2007). However, the level of landings in the period when the fishery was undeveloped and when cod fishing effort was low (e.g., Bagge et al. 1994; Kändler and Thurow 1959) may not represent the level of the stock size (MacKenzie et al. 2002). Furthermore, the biomass estimates by Thurow (1999) before the 1940s are based on few data and rely on rough assumptions (e.g. the mortality estimates of the population are largely based on data from young fish surveys, which did not catch larger fish; Thurow 1997*b*), that inevitably lead to uncertain estimates. Therefore, the current perception of the development of cod stock and fish productivity of the Baltic ecosystem before the 1950s needs to be evaluated by alternative approaches such as those used in this investigation.

Uncertainties in the biomass estimates

A well-known general problem for estimating fish stock biomass based on commercial landings is the accuracy of reported statistics. In this study, total cod landings were utilized in one of the four methods, i.e. catch curve analyses covering the years 1940-1944. Cod fishery in the eastern Baltic in these years was mainly conducted by German steamers and their landings were closely monitored (Meyer 1952a). Therefore, potentially under-reported landings during these years are not expected to have a major impact on the results of this study.

One of the shortcomings with our catch-curve analysis is the assumption of relatively constant year-class strength. The year-class strength of the eastern Baltic cod is partly related to hydrographic conditions (e.g. Kosior and Netzel 1989; Lablaika et al. 1989; Jarre-Teichmann et al. 2000; Köster et al. 2001) that are determined by inflows of North Sea water into the Baltic (Schinke and Matthäus 1998). The average inflow data (Matthäus 2006) for the years corresponding to hatching of the year-classes appearing as 4-7 year olds in 1940-1941 and in 1942-1944 indicate that possible differences in year-class strength due to variable hydrographic conditions may have led to overestimation of mortality. The oldest length-converted age-group included in the catch curve estimates has in both periods as an average been exposed to weaker inflow conditions at hatching compared to younger ages. These weaker year-classes could have contributed to the steepness of the catch curve and consequently resulted in overestimation of mortality. In addition to relatively high uncertainty in the total mortality estimate for 1940-1941, the fishing mortality and biomass for this period were also sensitive to the assumption of natural mortality as the level of total mortality was estimated to be relatively low. The natural mortality could have been higher taking into account predation mortality by marine mammals that were more abundant in this period compared to the recent decades (Harding and Härkonen 1999). The length based catch curve estimates also rely on the assumption that the growth of the fish was similar in the 1940s compared to the 1960s-1970s. Lower condition factor of cod in 1943 compared to the recent decades indicates that the growth rates were likely not higher in the earlier period. If the growth rate was lower, e.g. due to lower food availability, the biomasses based on catch curve analysis are underestimated, similarly to the effect of variable year-class strength and underestimated natural mortality.

Our biomass estimates based on comparison of catch rates from research surveys assume similar catchability of RVs “Poseidon” and “Solea”. This is a rough assumption as catchabilities of vessels are known to differ. However, the catchability of “Poseidon” is not expected to have been higher compared to “Solea”. Although the trawl used by “Solea” was smaller in terms of groundrope length, this was likely compensated by modern technology and double horse power of the engine. The information on exact trawling speed of “Poseidon” is unavailable, but there are indications that it could have been low. During 1-2.5 hours it covered 2.5-5 nautical mails in earlier expeditions (Strodtmann 1905) suggesting an average trawling speed of about 2 knots; “Solea” trawled at 3-3.5 knots (ICES 1988). Therefore, at a similar stock size, the catch rates of “Poseidon” could hardly be higher than these of “Solea” and our SSBs from catch rate analyses are likely under- rather than overestimated.

The landings in the northern Baltic and in the Gulf of Riga in the 1920s-1930s were at a similar level to the landings in these areas in the 1970s and 1990s while the total Baltic cod landings in the earlier period were about ten times lower (Fig. 1). This could be due to different cod distribution pattern in the Baltic in the early decades or it may indicate that fishermen were able to take similar landings in these relatively coastal areas, while the offshore areas were proportionally much less exploited. We have taken into account possible differences in stock distribution caused by variations in salinity (Lablaika and Lishev 1961; Tomkiewicz et al. 1998) by comparing only time periods with similar salinity conditions. Our analyses assume similar fishing effort in the two time periods, though the effort in the earlier period could be expected to have been lower. However, the differences in effort in these areas are likely not as large as for the total Baltic, as the higher effort in the cod fishery in the later period has been mainly directed to offshore areas, not to the nearshore areas of the northern Baltic or the Gulf of Riga. It should be noted that in some cases, especially concerning the SDs 29 and 32, the compared landings in the 1930s and in the period after the 1970s were not entirely similar. The lower landings in the 1930s indicate that the respective SSB value in the 1930s could be overestimated.

Among the data used in comparisons between the 1920s -1930s and the more recent decades, the egg abundances should be considered as the most comparable in terms of technological developments. Catchability differences between the standard gear used by the former USSR and later by Latvia, i.e. the IKS80, and the standard gear used by Denmark and Germany since the early 1970s, i.e. a Bongo-net, are negligible (CORE 1998). As earlier German sampling was conducted with a gear similar to the IKS-80, it can be assumed that catchability differences are marginal between all three gears used for sampling ichthyoplankton in the 20th century. The egg abundances for the period from 1966 refer to the main three month spawning season, whereas this may not be the case with the earlier data. A mis-match of spawning season and sampling time would result in an underestimation of the spawner biomass in earlier years. As the conducted comparison is based on egg abundances, i.e. integrating over all egg developmental stages, a pronounced difference in egg mortality would affect the validity of the approach as well. However, as only periods with similar hydrography, i.e. salinity, were compared, a large differences in salinity-related egg mortality are not expected. Another factor potentially decoupling egg abundance and spawning stock size is fecundity that is related to prey availability (Kraus et al. 2002). Based on the estimation for the early 1940s, the condition of cod in the late 1930s was likely lower than in the 1990s. Therefore, it appears to be unlikely that fecundity was higher and consequently the spawner biomasses at least in the mid-1920s and early 1930s that are based on the egg data from the 1990s are under- rather than overestimated. A factor which however may result in an overestimation of spawner biomass is the fact that in a stock characterized by the presence of old fish, the proportion of female cod will be higher (Tomkiewicz et al. 1997) and consequently the egg production per unit of spawner biomass will as well be higher.

The level of stock size and fishing intensity

The SSB of cod in the mid-1920s and in the period from the late 1930s to the beginning of the 1940s was estimated about 2-5 times higher compared to the current stock size. The estimates for the late 1920s-early 1930s were in a similar range as the SSB in recent years. The highest SSB during 1925-44, up to 350 000 t, was estimated for the late 1930s-early 1940s, similar to the level in the mid- 1970s and in the mid-1980s. The spawning stock could have been close to this level also in the mid-1950s as the stock size in SD 25 in this period from the VPA was considered underestimated (Eero et al. 2007*a*). This is further confirmed by our length-based catch curve analyses indicating lower fishing mortality in SD 25 in the 1950s-1970s than obtained from age-based VPA in a previous study (Table 3). This can be explained by the fact that the available length data represented a larger part of the catches in SD 25 compared to the age specific data utilized by Eero et al. (2007*a*).

The relatively high level of stock size in the 1930s-early 1940s as estimated here is supported by additional indicators. Abundance of cod larvae in the 1930s was similar to the 1960s- early 1970s and much higher compared to the 1990s (MacKenzie et al. 1996). Relatively high cod biomass in the early 1940s is also supported by cod stomach investigations. Cod cannibalism, which is generally related to high stock abundance (Neuenfeldt and Köster 2000), was observed during the Second World War in all central Baltic areas (Meyer 1952*c*). Tiews (1974) compared the catch rates of RV "Anthon Dohrn" in the 1960s with those of German steamers during the Second World War and found that the catch rates in 1962-1970 in Bornholm Basin and in 1962-1968 also in Gdansk and Gotland areas were generally lower or at the same level as during the war. The fishing gear of the vessels is reported to have been similar (Meyer-Waarden and Tiews 1967); however it should be noted that the capacity (BRT) of the steamers fishing in the Baltic during the war was about two or three times lower compared to RV "Anton Dohrn" (Meyer 1952*a*; Table 2). The total fish biomass in the Baltic during the war is also indicated to have been higher than in neighboring areas. Daily catch rates (all species) during the war were about twice as high in the Baltic as in the southern North Sea, Skagerrak and Kattegat (Meyer 1952*a*). Also, average catch rates of all fish species in the total North Sea and in Skagerrak before the war were lower than in the Baltic during the war, not taking into account the North Sea herring fishery (Meyer 1952*a*).

Our results concerning the reduction in cod stock at the end of the war were supported by comparison of the catch rates of steamers during the war and the catch rates of cutters in the following years. The catch rates after the war were about two times lower while the fishing power of these fleets was considered comparable (Meyer 1952*a*). The estimated level of stock size at the end of the war is also in line with results from an analytical assessment (Eero et al. 2007*a*) for the second half of the 1940s (Fig. 6). The reduction in cod stock size in the first half of the 1940s corresponds to a sharp increase in fishing mortality in preceding years and the catch rates declined from 1940 to 1944 (Meyer 1952*a*). The impact of fishing on the cod population during the war is also indicated by the change in size composition of catches. In addition to sampled length distributions (Fig. 3), a reduction in the proportion of larger cod in the landings during the 1940s is evident also in the market categories of total landings. The proportion of cod in the category of large fish (above 40 cm) nearly halved during the war in all fishing areas of the central Baltic (Meyer 1952*b*). In addition to the fishery by German steamers on relatively large cod, Sweden carried out intensive fishery with small-meshed trawls catching large quantities of small cod (Alander 1946). According to observations by Alander (1946), the mean weight of cod in Swedish catches during the war years was only 100–200 g. Heavy fishery was therefore likely the major factor contributing to the reduction in stock size in the first half of the 1940s. The Baltic cod, which likely for the first time in history was intensively exploited during the Second World War, thereby provides a contrasting example to many other fish stocks in the North-East Atlantic which were almost not exploited during the war (Pope and Macer 1996; Hylen 2002) and some consequently increased in abundance (e.g., Rijnsdorp and van Leeuwen 1992).

The fishing mortality on the eastern Baltic cod in the 1920s-1930s was estimated below 0.2, which is much lower than the mortality rate on cod for example in the North Sea (0.5) in the same time period (Pope and Macer 1996). Lower fishing pressure in the Baltic at this time is in line with the much less developed fishing technology in the Baltic compared to the North Sea. Despite the low fishing pressure, the level of stock size in the Baltic before the war was estimated to be lower than observed in the late 1970s-1980s. The Baltic thereby differs from many other areas where fish abundances before the beginning of intensive fishery were much higher than observed since then (e.g., Jackson et al. 2001; Myers and Worm 2003). Relatively low fish biomass in the Baltic before the onset of intensive fishery is likely related to lower productivity of the Baltic ecosystem. The net biomass productivity in the 1920s-1930s was estimated by a factor of 2.5 lower compared to the recent decade (Schneider and Kuss 2004). The food limitation for cod in the early 1940s is also indicated by relatively low condition factor. Additionally, the abundances of potential cod predators, i.e. seals were higher in the 1920s-1930s compared to the later period (Harding and Härkönen 1999).

In summary, our spawning stock estimates are based on different proxies that vary in precision. Several of our analyses were considered to under-estimate the SSB in the 1920s-1930s. Therefore, the true stock might have been larger than shown here; however based on present knowledge there are no indications that it could have reached the level close to the highest recorded biomass in the early 1980s. The level of landings by a relatively intensive fishery during the war was still about 5 times lower than in the late 1970s-early 1980s, while the impact of fishery on the stock during the war at this level of landings was obvious. The multiple proxies are consistent in terms of the level of stock size in each time period, which increases the confidence in results. However, the exact biomass values should be treated with suitable caution.

Our study demonstrates that cod biomass in the Baltic in the 1920s-1940s was higher and showed different trajectory than previously believed. The fishing mortality was low until the Second World War, when it increased sharply to moderate levels. The biomasses in the earlier years therefore provide a new baseline for the level and variability of stock size at low fishing pressure, and improve the basis for estimating the relative roles of multiple human impacts and climate on the long-term development of the cod population.

Acknowledgements

The authors thank Marie Storr-Paulsen for help with BITS data and for fruitful discussions on the analyses. The cooperation of the staff in the Institute for Baltic Sea Fisheries in Rostock and Sea Fisheries Institute in Hamburg in compiling some of the datasets is greatly appreciated. Special thanks to Hildrun Müller, Manfred Stein, Wolfgang Weber and Fritz Thurow. We thank Henrik Gislason for discussions and advice on the manuscript. The first author received support from the Danish Research School for Studies in Marine and Coastal Environment, Heritage and Sustainable Tourism (MAST), which is gratefully acknowledged. The study was supported by the History of Marine Animal Populations project of the Census of Marine Life and by the Commission of the European Communities FP6 Specific Targeted Research Project 022717 (UNCOVER) as a contribution to the FP6 NoE 511106-2 (EUROCEANS). Contributions from participants of these projects are acknowledged here.

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Paper IV

The Baltic Sea bio-manipulation experiment of the 20th century–resolving impacts of fishing, eutrophication, marine mammals and climate on a cod population

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Abstract

The Baltic Sea has experienced major human-induced changes during the 20th century, including increased fishing, eutrophication and declines in the abundance of marine mammal predators. In addition, major variations have occurred in salinity and oxygen conditions related to large scale climatic variability. In this paper we evaluate the impact of these changes on the eastern Baltic cod (*Gadus morhua*) population dynamics since 1925. Long time series of data covering the periods of large contrasts provide an unusual opportunity to demonstrate how various human activities interacted with a fish population in a large marine ecosystem. Changes in trends of the cod abundance coincided with major variations in climate forcing, whereas the level of stock size at similar climatic conditions was mainly determined by compensatory and cumulative effects of different human impacts.

Introduction

Several fish populations at higher trophic levels have shown declines over the past decades or centuries (Jackson et al. 2001; Myers and Worm 2003; Brander 2005). The concern of overfishing tends to set the focus on fishing as a cause of stock declines. However, abundances of fish stocks have been observed to increase under intense fishing pressure (e.g., Rothschild 1998), whereas fishing stop has in several cases not resulted in immediate stock recovery (e.g., Hutchings and Reynolds 2004). In order to aid the recovery of fish stocks by suitable management actions, understanding of the mechanisms driving the dynamics of fish populations is essential.

Understanding of these mechanisms is often limited due to complexity of ecosystems. In addition to fishing, changes in climate and trophic interactions play important roles in the dynamics of fish populations (Cushing 1982; Harwood and Croxall 1988; Frank et al. 2007). The responses of an ecosystem to various changes can easier be investigated in lakes by bio-manipulation experiments (Kasprzak et al. 2003); these are however difficult to conduct in large marine ecosystems. Difficulties to separate the effects of different factors on fish populations are in many cases also related to the shortness of available time series and to co-varying driving forces. A long-term historical perspective has a greater probability of representing a wider range of both natural and human impacts, and therefore can potentially identify and quantify their relative importance for development of fish populations (Southward 1995; MacKenzie et al. 2002; Holm 2003).

The Baltic Sea is an exceptional case in many of these aspects. It is a relatively well-studied area with several long time series of climatic and ecosystem parameters available. Furthermore, the Baltic ecosystem has been subjected to different human perturbations at a multi-decadal scale and can therefore be seen as a large-scale eco-engineering experiment. During the period from the early 1900s to the 1940s the abundance of top predators (i.e. seals) was reduced more than five-fold by intensive hunting (Harding and Härkönen 1999). As a consequence of increased use of fertilizers and intensified industrialization after the Second World War nutrient inputs during the 1940s-1980s increased three to five-fold (Larsson et al. 1985; Jansson and Dahlberg 1999). Fishing mortality on eastern Baltic cod was below 0.2 until the late 1930s and increased to above 1.0 by the 1960s (Eero et al. submitted). In addition, climatic and hydrographic conditions influencing cod recruitment (e.g., Köster et al. 2005) varied widely in the past century (e.g., Matthäus 2006). The spawner biomass of eastern Baltic cod consequently exhibited up to 7-fold fluctuations during the last century (Fig. 1).

Due to large changes in the stock size and in major forcing factors, cod in the Baltic Sea provides a unique opportunity for investigating the relative influences of the key factors, i.e. climate, fishing and bottom-up and top-down forcing on a fish population in a large marine ecosystem. The paper improves the understanding of human impacts on cod in the Baltic Sea compared to natural variability that is essential for sustainable management of the fisheries and the ecosystem.

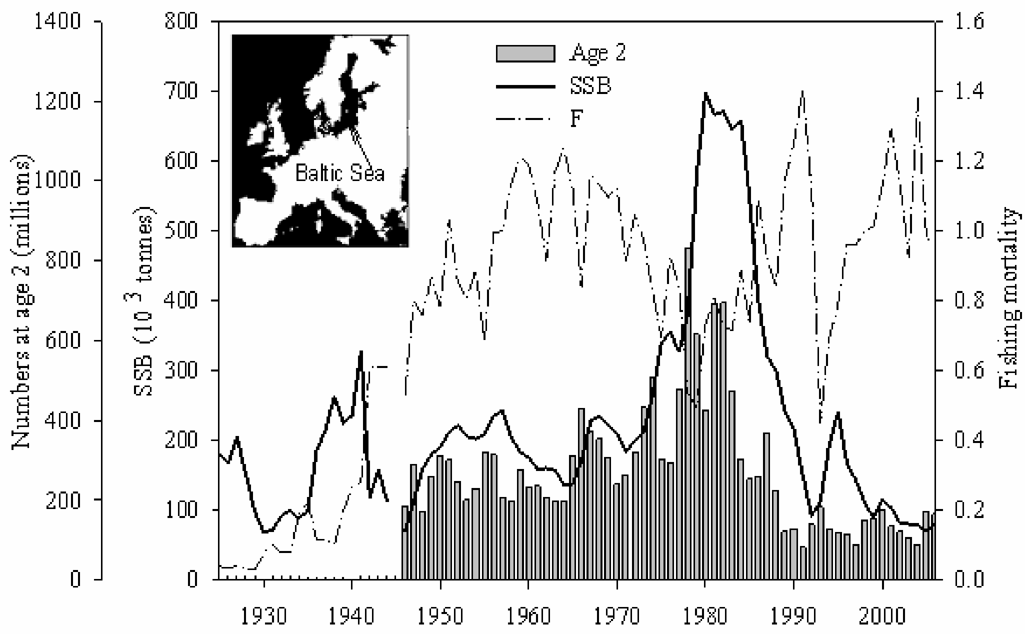

Figure 1. Eastern Baltic cod spawning stock biomass (SSB), recruitment (age 2) and fishing mortality (for 1925-1944 the level of F on SSB, from 1946 onwards average F on ages 4-7) in 1925-2006 (ICES 2007; Eero et al. 2007; and modifications from Eero et al. submitted).

Material and methods

Cod stock development

The eastern Baltic cod (ICES Subdivisions 25-32, for location of Subdivisions see http://www.ices.dk/aboutus/icesareas/ICES_areas_Arc9_Baltic_300.pdf) spawning stock biomass (SSB), stock numbers and fishing mortalities for the total stock and by Subdivisions (SD) were available from ICES (International Council for the Exploration of the Sea) assessments from 1966 and 1976 onwards, respectively (ICES 2006, 2007). The estimates back to 1946 were taken from Eero et al. (2007). The annual SSB and fishing mortality rates in 1925-1944 were based on the estimates by Eero et al. (submitted), combined with the annual catch per unit of effort (CPUE) data.

We utilized CPUE data from hook and line fisheries by Sweden in SDs 25 and 28 and by Latvia in the central Baltic in 1925-1938. The effort represented total numbers of motorboats and fishing days in the Swedish and Latvian fisheries in the particular areas, respectively. The data were obtained from official national statistics. The levels of SSB estimated by different methods by Eero et al. (submitted) were averaged. The SSB and the standardized average CPUE in 1925-1938 were significantly correlated ($r^2 = 0.695$, $p<0.01$), however discrepancies in the annual developments were observed in the mid-1930s. As the SSBs by Eero et al. (submitted) represented the average stock levels by time periods rather than inter-annual developments, the annual variability was considered to be better represented by CPUE data. Therefore, we used the relationship between CPUE and SSB in 1925-1929 to scale the CPUE values for 1930-1938 to the absolute level. Annual fishing mortalities were adjusted accordingly as estimated based on the ratio between landings (Eero et al. submitted) and SSB.

Comparing the anomalies of cod recruitment with changes in the intensity of major Baltic inflows

The recruitment of eastern Baltic cod in recent decades has been shown to be related to hydrographic conditions (e.g., Jarre-Teichmann et al. 2000; Köster et al. 2005), determined by major inflows of saline and oxygen-rich water from the North Sea into the Baltic (Matthäus 2006). We evaluated whether anomalies in cod year-class strength in the earlier decades of the 20th century co-occurred with major changes in the intensity of major Baltic inflows. To do this, indices of major inflow events (Matthäus 2006) between September 1 (in the preceding year) and April 30 were summed up to obtain an annual index, potentially influencing cod reproduction in a given year (MacKenzie et al. 1996; Hinrichsen et al. 2002b). Because we focused on decadal scale changes rather than inter-annual variability, time series of logged inflow data (ln (x + 1)) and corresponding recruitment (age 2, lagged for 2 years) from 1948 onwards were smoothed by taking five-year running means. Anomalies in the inflow index were presented as deviations from the long-term average over the years 1898-2003.

Due to incomplete data coverage for SD 25 in the period before the 1970s (Eero et al. 2007) the combined recruitment estimates for cod subpopulations in ICES SDs 26 and 28 were used to represent relative trends in recruitment of the total stock (SD 25-32). In 1976-2003, recruitment estimates for the total stock and for SDs 26 and 28 were highly correlated (r^2=0.939, p<0.01).

In the years before the 1940s, trends in the spawning stock were assumed to reflect the pattern of major changes in recruitment level. Based on size composition data (Eero et al. submitted), age-groups 3-7 were considered to form a major part of the spawning stock. Therefore, the SSB was compared with the average inflow index 3-7 years earlier, corresponding to the birth-years of the five respective year-classes.

Comparing the developments in the cod stock with changes in fishing mortality, seal abundance and nutrient load

<u>1920s -1950s</u>

Changes in the level of cod SSB in the time periods when the average hydrographic conditions for the development of respective year-classes were similarly favourable were compared with changes in fishing mortality, abundance of seals and nutrient loading.

The developments in cod SSB (considered to be represented by age-groups 3-7) were compared with the average abundance of predators, i.e. grey seals (*Halichoerus grypus*) over the preceding 1-6 years, corresponding to the time interval back to when the oldest age-group contributing significantly to the spawning stock biomass (age 7) recruited to the stock as 1-year-old. The fishing mortalities were averaged over the preceding four years for representing the impact on SSB in a given year.

The approximate level of nutrient loading in the 1920s-1940s was taken from Jansson and Dahlberg (1999). For the 1950s, we used the values suggested by Wulff et al. (1990). Changes in cod SSB were compared with the average nitrogen and phosphorus loadings 1-7 years earlier covering the years since the oldest age-group in the SSB (age 7) was born.

<u>1950s-1990</u>

The stock numbers and the fishing mortalities by age were available from the mid-1940s onwards. The data for SDs 26 and 28 were used to investigate temporal changes in adult survival and in recruitment production expressed as the number of recruits (age 2) produced per unit of SSB. Survival was estimated as the fraction of the stock numbers at age 2 surviving to a given age. As natural mortality in this period is assumed constant

(Eero et al. 2007; ICES 2007), the differences in survival represent changes in fishing mortality.

In order to demonstrate the effect of reduced fishing mortality on the spawning stock in 1975-1987, we simulated cod spawning stock numbers by modifying the fishing mortalities by age and year influencing the stock (SD 25-32, ages 3-7) in 1975-1987 (e.g. the stock in 1975 was affected by fishing mortalities on ages 2-6 in 1974, on ages 2-5 in 1973 etc.). The fishing mortalities by age in this period were set equal to the average values experienced by years-classes forming the stock in 1960-1974 (e.g. mortality on age 2 in all the years influencing stock numbers in 1975-1987 was set equal to the average mortality on age 2 in the years influencing the stock in 1960-1974 etc.).

The simulated stock numbers were calculated based on the standard stock numbers equation (e.g., Hilborn and Walter 1992) applying the modified fishing mortalities. The recruitment in respective years was modified according to the difference between the simulated and observed SSB. The ratio of the number of recruits produced per unit of spawning stock biomass in each year was kept equal to the original value and the recruitment was adjusted accordingly.

Results

Fluctuations in cod recruitment and major Baltic inflows

Since the mid-1980s, the average inflow intensity has been far below the long-term mean (Fig. 2d). In parallel with a dramatic decline in the inflow index, the average cod recruitment declined to very low levels after a peak in the late 1970s. An equally long stagnation period as observed in recent decades has not been recorded before in the 20th century. Shorter periods with weak or lacking inflow events occurred in the late 1920s and 1950s that coincided with respective changes in the average cod year-class strength

(Fig. 2). The stock size in the early and mid-1930s was estimated lower than in the adjacent time periods and a reduction in the average recruitment in the late 1950s-early 1960s was also observed. Average recruitment was relatively low also in the late 1960s-early 1970s coinciding with reduced inflow intensity. Consequently, the peaks in the stock size in the mid-1920s and in the late 1930s-early 1940s and in the average recruitment in the late 1940s-mid 1950s, in the mid-1960s and from the mid- 1970s to the early 1980s coincided with periods when the average inflow index was above the long-term mean (Fig. 2).

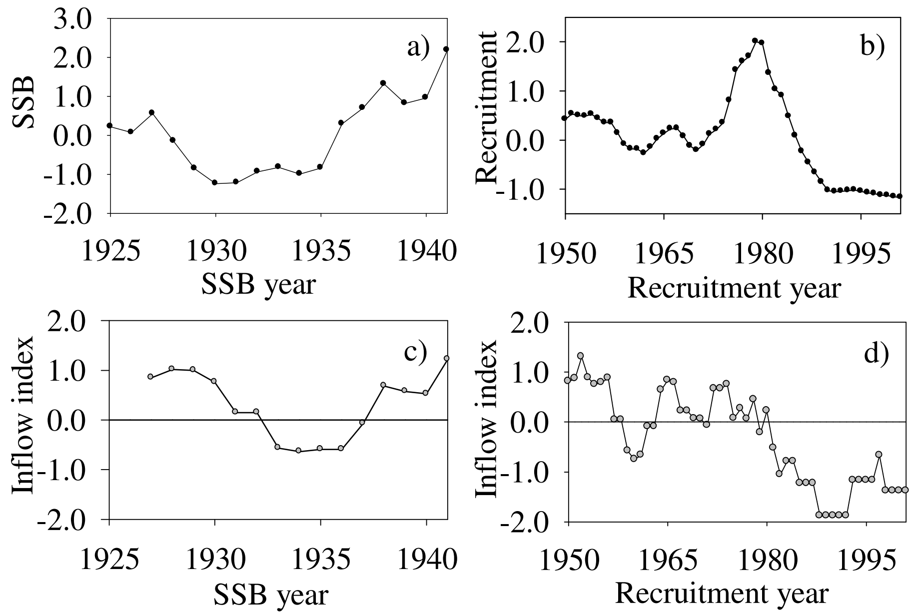

Figure 2. a) Standardized spawning stock biomass (SSB) b) Standardized recruitment presented as a running mean of 5 years; the years on the x-axis correspond to the middle of a 5-year period. c) Anomalies of inflow index (Matthäus 2006; running mean of 5 years) lagged for 3-7 years in relation to SSB in the years indicated on the x-axis. d) Anomalies of inflow index (running mean of 5 years) lagged for 2 years in relation to the recruitment (age 2) in the years indicated on the x-axis.

Despite the similar favourable inflow conditions, pronounced differences were observed in the level of recruitment and stock size between these periods, e.g. the average recruitment in the late 1970s-early 1980s was about twice as high as in the 1950s or mid-1960s. Although the major trends in cod recruitment coincided with major fluctuations in inflow intensity, other factors appear to have been involved influencing the differences in stock level.

Cod SSB and major changes in the Baltic ecosystem in the 1920s-1950s

The cod year-classes corresponding to the average spawning stock biomass in 1926-1927, 1938-1940 and in 1956-1958 were in general exposed to similar favourable hydrographic conditions at the development of their early life stages (Fig. 2). The level of SSB in 1938-1940 was indicated higher than in 1926-1927. In 1956-1958, the SSB was estimated similar to the average level in 1938-1940, however the range of different estimates for 1938-1940 suggest that the stock in this period might have been larger than in 1956-1958 (Fig. 3a).

During the period from the 1920s to 1950s, a shift occurred in the causes of cod mortality in a post-larval phase. The abundance of predators, i.e. grey seals declined from about 65 thousand individuals in the first half of the 1920s to 35 and 22 thousand individuals in the mid-1930s and 1950s, respectively (Fig. 3b; Harding and Härkönen 1999). In contrast, the average fishing mortality during this period increased sharply from 0.04 to 0.16 and further to 0.78, influencing the stock size in 1926-1927, 1938-1940 and 1956-1958, respectively.

Comparing the period 1926-1927 with 1938-1940, a nearly halving of the grey seal population coincided with a threefold increase in fishing mortality. The cod SSB in the later period was higher suggesting that seal predation had a larger impact on the cod stock in 1926-1927 than fishing. Comparing the periods 1938-1940 and 1956-1958, the total mortality on the cod stock in the later period was apparently substantially higher. This is indicated by a nearly fivefold increase in fishing mortality compared to about forty percent reduction in predator abundance. Corresponding large difference in the level of SSB in 1938-1940 and 1956-1958 is however not indicated.

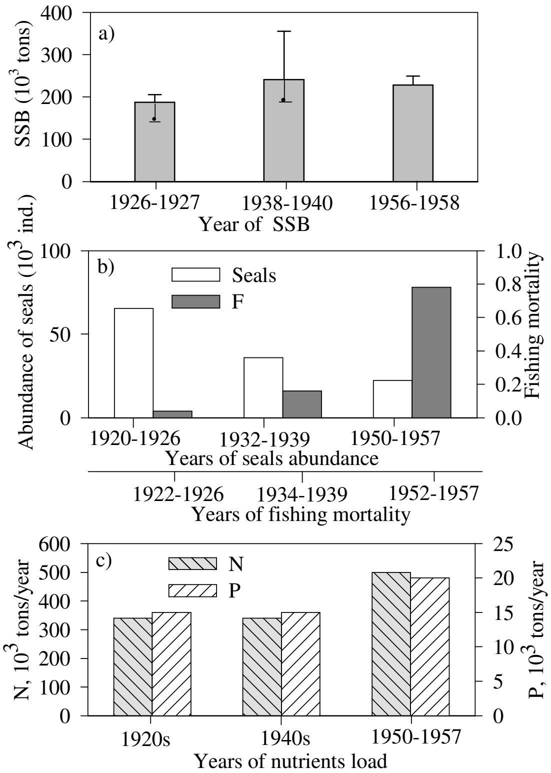

Figure 3. a) The average spawning stock biomass of cod (SSB, SD 25-32) in 1926-1927, 1938-1940 and 1956-1958; b) the average abundance of grey seals (Harding and Härkönen, 1999) and fishing mortality in the preceding 1-6 and 1-4 years, respectively; and c) the average annual loads of nitrogen (N) and phosphorus (P) in the 1920s, 1940s and in 1950-1957 (Jansson and Dahlberg 1999; Wulff et al. 1990). The error bars for cod SSB in the first two periods represent the range of estimates from different analyses (Eero et al. submitted). For the period 1956-1958, the error bar indicates the SSB obtained when applying by 0.2 lower fishing mortality (x - 0.2) on the subpopulation in SD 25, as the fishing mortality in this area and period was considered as possibly overestimated by this level (Eero et al. submitted) by Eero et al. (2007).

The nutrient input to the Baltic has been estimated to approximately 340 thousand tonnes of nitrogen and 15 thousand tonnes of phosphorus per year in the 1940s (Jansson and Dahlberg 1999). In the first half of the 1950s, the annual average inputs have been suggested at approximately 500 thousand tonnes of nitrogen and 20 thousand tonnes of phosphorus (Wulff et al. 1990). This corresponds roughly to an increase of 30 and 25 percent compared to the earlier period, respectively (Fig. 3c). Increased nutrient loadings can be expected to have enhanced ecosystem productivity. Therefore, enhanced cod recruitment and/or increased individual growth could have partly compensated for the substantial increase in fishing mortality.

Major changes in the cod stock and in the Baltic ecosystem from the 1950s to 1990

The concentration of nitrogen in the Baltic increased from about 15 mmol/m^3 in 1950 to approximately 27 mmol/m^3 in the late 1970s (Wulff et al. 1990). An even larger increase took place with respect to phosphorus, from 0.3 to 0.9 mmol/m^3. However, this increase in the nutrient concentration did not appear to have increased the productivity of cod stock during this period. The number of recruits produced per unit of SSB showed large variability during 1948-1990, but did not exhibit an increasing trend (Fig. 4).

The high values of recruits per SSB observed around 1950, in the mid-1960s and in late 1970s were all at a similar level (Fig. 4) and coincided with favourable hydrographic conditions for recruitment (Fig. 2). The substantially higher recruitment observed in the late 1970s - early 1980s (Fig. 1) must therefore be caused by a higher SSB. The high SSB in the late 1970s was related to higher survival of a number of year-classes in the post-recruitment phase. The survival of year-classes from age 2 until reaching age-classes 3 - 6 was 10-25 percent higher in the late 1970s compared to the adjacent time periods (Fig. 4).

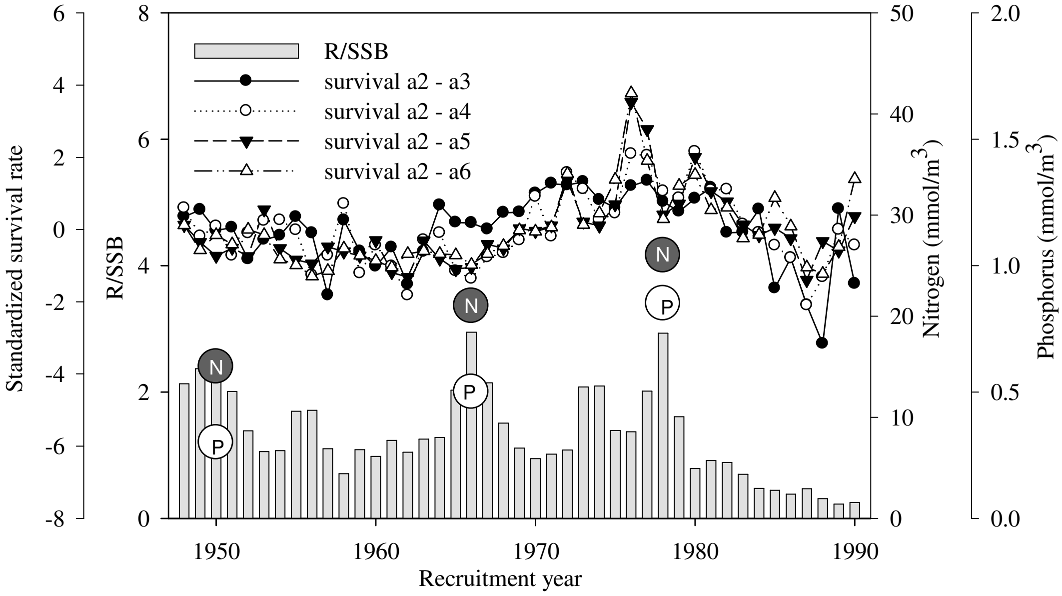

Figure 4. Numbers of recruits (age 2) produced per unit of spawning stock biomass (R/SSB) and concentrations of nitrogen and phosphorus (Wulff et al. 1990) in selected years corresponding to the peaks in R/SSB. The lines represent the survival of respective year classes from being 2-year-old in the years indicated on the x-axis until reaching the ages 3-6.

The effect of reduction in fishing mortality in the late 1970s on the stock was further illustrated by a simulation exercise. Applying similar fishing mortalities as exerted on the stock in the 1960s - early 1970s on the year-classes contributing to the stock in the late 1970s - early 1980s resulted in nearly 50 percent lower spawning stock numbers in the early 1980s compared to the observed level (Fig. 5).

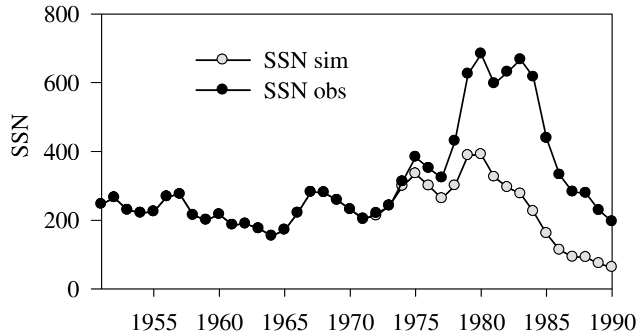

Figure 5. Observed and simulated cod spawning stock numbers (SSN, age 2-8+, SD 25-32). SSNs were simulated from 1975 onwards by applying the average age-based fishing mortalities that influenced the stock in 1960-1974 on the year-classes contributing to the SSNs in 1975-1987 (see Material and Methods for details).

Discussion

Influence of climate and bottom-up forcing on cod stock dynamics

Climatic influences on cod recruitment in the Baltic are mainly related to inflows of saline and oxygenated water from the North Sea (e.g., Hinrichsen et al. 2002b), determined by particular pressure and wind conditions over the Baltic region (Schinke and Matthäus 1998). Since the late 1980s, a decline in salinity and oxygen concentration has reduced the reproductive success of the eastern Baltic cod (Köster et al. 2005). Although comparable periods with so few major inflow events have not occurred earlier in the 20th century (Matthäus 2006), shorter-term variability in inflow intensity during the 1920s-1970s was indicated to have had a major impact on cod recruitment trends. In addition to the direct effect on egg survival (e.g., Kosior and Netzel 1989; Lablaika et al. 1989) low inflow situations increase predation on cod eggs by sprat and herring (Köster and Möllmann 2000; Köster et al. 2005), and low salinity reduces cod larval survival by reducing their prey abundance (Möllmann et al. 2000; Voss et al. 2003; Hinrichsen et al. 2002a). In addition to improving salinity and oxygen conditions, inflows force nutrients from the bottom to the photic zone, stimulating primary production (Nehring 1982) that potentially has a positive influence on the development of cod larvae (Bagge and Thurow 1994). The strongest inflow event since 1898 was recorded in 1951 and it has been suggested to have contributed to the shift from an oligotrophic to a more eutrophic sea (Österblom et al. 2007).

Given that fish production in several marine ecosystems is functionally related to levels of primary production (e.g., Ware and Thompson 2005), one might hypothesize that eutrophication in the Baltic may have stimulated not only primary production, but also production at higher trophic levels. However, finding quantitative evidence for increased secondary and fish production as a response to eutrophication in marine systems is surprisingly difficult, partly due to lack of sufficiently long comparable datasets and due to multiple simultaneous changes in the ecosystems (Nixon et al. 1986; Nixon and Buckley 2002). In a few cases, for example on the Faroe Shelf, dramatic variations in phytoplankton production in the 1990s allowed demonstrating a relationship between phytoplankton production and cod production; the causal mechanism likely being increased production of food organisms for cod (Steingrund and Gaard, 2005). In the central Baltic, clear trends in phytoplankton or zooplankton abundance as a response to increased nutrient input during the 1940s-1980s have been difficult to demonstrate, and the results from different studies are inconsistent (Larsson et al. 1985 and references therein). However, indirect measures of biological production such as Secchi depth in 1919-1939 and in 1969-1991 indicated lower water transparency and higher chlorophyll values in the later period (Sandén and Håkansson 1996). Also, the benthic biomass was shown to have increased significantly from 1920-1923 to 1976-1977 (Cederwall and Elmgren 1980).

Our results do not indicate a major positive effect of the increasing nutrient concentration on cod productivity in the period from the 1950s to 1980s (Fig. 4). Also the growth of cod during the 1950s-1970s was stable (Eero et al. 2007). It is more likely that eutrophication had a negative impact on cod recruitment in this period due to increased occurrence and duration of hypoxia and anoxia (Elmgren 1989). However, our findings suggest that the increased nutrient load had a positive influence on cod SSB in the 1950s compared to the earlier period. The potential impact of increased nutrient load on cod recruitment in this period cannot be evaluated with the available data. Therefore, both increased productivity and/or enhanced individual growth could have contributed to the relatively high spawning stock biomass in the 1950s counteracting the pronounced increase in fishing mortality.

Quantifying the potential influence of increased ecosystem productivity on cod SSB in this period is difficult as the stock size estimates for the late 1930s-early 1940s are associated with larger uncertainties compared to the later period (Fig. 3). The higher values of SSB among the different estimates for the 1930s-1940s correspondingly suggest lower positive effect of increased nutrient loading on the cod stock. However, improved growth in the 1950s compared to earlier period is indicated by Fulton's condition factor, being estimated at 0.8 in Bornholm Basin in the first quarter in the early 1940s (Eero et al. submitted) and at about 1.0 in the same area and season in 1955-1960 (Stanek 1964). Also, qualitative information from the fisheries suggests that the cod in the catches before the late 1940s was extremely thin and of bad quality (Alander 1949).

Influence of predation and fishing on cod stock dynamics

Interactions between seals, their prey populations and fisheries are complex and evaluating the impact of seals on individual fish stocks is difficult (Harwood and Croxall 1988). Concerning the relative impacts of predation and fishing on the eastern Baltic cod, in the early decades of the 20th century when fishing mortality was very low and seal populations were abundant, the consumption of cod by seals likely exceeded the removals by the fishery. The level of predation mortality by seals is however difficult to estimate due to scarcity of relevant information. Elmgren (1989) suggested average daily fish consumption of grey seals to be 3.2 kg·day^{-1}·ind^{-1} that corresponds approximately to 75,000 tonnes of fish at the level of grey seal abundance in the mid-1920s. In the investigations of the grey seal diet in the late 1960s - early 1970s, cod was found in about 20 percent of stomachs (Söderberg 1975). Assuming similar proportion of cod in the diet of grey seals also back in time would suggest a consumption of 15,000 tonnes of cod in the mid-1920s. For comparison, the eastern Baltic cod landings in this period were below 10,000 tonnes (Sparholt 1994). Predation mortality on cod by seals was likely concentrated on younger age groups as indicated by data on prey size composition (Thurow 1997a).

The abundance of seals declined three-fold from the 1920s to 1940s (Harding and Härkönen 1999). Assuming similar reduction in the predation mortality on cod would indicate 5,000 tonnes of cod consumed annually by grey seals at their population level in the 1940s-1960s. The influence of seal predation on cod population dynamics in this period can be expected to have been minor, considering the biomass of cod that just for the recruiting age-group (age 2) was as a minimum 50,000 tonnes in the 1940s-1960s.

Consequently, seals were not considered as a major factor influencing cod population dynamics from the 1940s onwards. If the higher seal abundances in the 1940s-1960s compared to the later period (Harding and Härkönen 1999) had a measurable influence on the natural mortality on cod (currently assumed constant since the mid-1940s), this would indicate that the recruitment for this period is a certain degree underestimated and consequently the fishing mortality, especially on younger ages overestimated. The influence on our conclusions would be minor, as R/SSB in the 1950s-1960s would be even higher compared to later period and survival of recruits would be indicated even lower, although a fraction of it could be due to higher predation mortality. Cod has also been found in the stomachs of ringed seals (*Phoca hispida*) (Söderberg 1975). However, due to limited spatial overlap with the cod population, their predation on cod is expected to have been much lower compared to grey seals (Söderberg 1975). Consequently, ringed seals were not considered as a major factor influencing cod stock dynamics in the 20th century. The relative population development of the two seal species was similar (Harding and Härkönen 1999).

By the end of the first half of the 20th century, the role of natural top-predators in the Baltic ecosystem had been taken over by the fishery. The impact of fishing on the cod stock was first apparent during the Second World War and intensive fishery was likely a major factor contributing to the stock decline in the first half of the 1940s (Eero et al. submitted). Unfortunately, data on hydrographic conditions for the war years are not available. Nevertheless, the strong inflows in 1938 and 1939 (Matthäus 2006) likely favoured at least these respective year-classes contributing to the spawning stock in the first half of the 1940s.

After a period with high fishing intensity in the 1950s-1960s, fishing pressure was gradually reduced. The reduction in mortality was first apparent on younger cod (Fig. 4) that was partly due to technical measures introduced to protect the stock (e.g., Kosior 1974). The overall reduction in cod targeting in the 1970s was related to the development of the more profitable pelagic fishery for herring and sprat (Lablaika et al. 1991). Cod fishery intensified again in the 1980s, stimulated by the observed large increase in stock size. Our results show that the higher survival of cod caused by reduction in fishing mortality was the major factor contributing to the record high stock size in the late 1970s-early 1980s, twice as high compared to the simulated scenario at previous high exploitation rates (Fig. 5).

The relative impacts of human activities and climate on cod stock dynamics: summary and conclusions

Earlier ecosystem modelling studies have addressed the relative roles of human-induced ecosystem changes, i.e. eradication of top predators and increased bottom-up forcing (eutrophication) in the Baltic in the 20th century on fish populations, including the cod stock (e.g., Österblom et al. 2007). These analyses were however based on the perception of very low fish biomasses in the Baltic in the early decades on the 20th century as indicated by low landings and earlier biomass estimates (Thurow 1999), which are however associated with large uncertainties. Major effort has recently been made to improve the knowledge of the eastern Baltic cod stock dynamics since 1925 and the results revealed a different level and trajectory of the stock size before the 1950s than previously believed (Eero et al. submitted). This advance in knowledge of the historical population dynamics motivated our investigations on the long-term impacts of different forcing factors on the eastern Baltic cod.

Our study is the first to consider the historical developments in all the four key factors, i.e. climate, fishing, eutrophication and marine mammals, as potentially influencing long-term stock dynamic of cod in the Baltic Sea. The cumulative and compensatory effects of different factors that influenced the stock at different time periods emphasize the importance of looking at different ecosystem changes in parallel and at a relatively high time resolution in order to improve the understanding of relative roles of single parameters.

Before the 1940s, the cod biomass in the Baltic was likely restricted by high abundance of predators and low level of nutrients (Fig. 6). By the 1950s-1960s, these limiting factors were replaced by fishing. The opposite effects of different human activities on the cod stock implied that despite of substantial changes in each of the forcing factors, the cod stock fluctuated at a relatively constant level during the 1920s-1960s, the trends being mainly driven by climate variations. The drastic decline in the stock from the late 1980s to the present is considered to be a consequence of a combination of recruitment failure due to unfavorable salinity and oxygen conditions and a heavy fishing pressure (Bagge et al. 1994; Köster et al. 2003). The period corresponding to the record high cod biomass in the late 1970s - early 1980s clearly stands out as representing milder pressures on the cod stock compared to the other periods in the 20th century (Fig. 6).

The example of the Baltic cod demonstrates the importance of a long-term perspective in order to understand major changes in a fish population. The peak in the Baltic cod stock in the late 1970s - early 1980s has previously been ascribed to the effect of eutrophication, combined with favourable hydrographic conditions (Thurow 1997b; Österblom et al. 2007). Here we show that favourable combination of all four major drivers was necessary for the record high stock size to occur, i.e. favourable climate, low predation, high ecosystem productivity and reduced fishing pressure (Fig. 6). A similar combination has not occurred in other time periods in the 20th century. This pattern can hardly be seen when looking only at short-term developments.

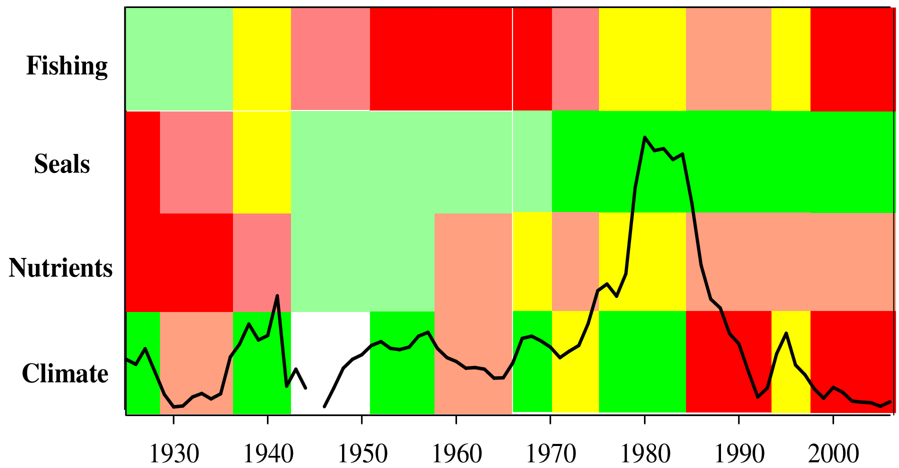

Figure 6. Major changes in the impact of climate, nutrients, seal abundance and fishing on the spawning stock biomass of eastern Baltic cod (represented by the line) in 1925-2006. The years on the x-axis refer to the cod spawning stock biomass. The colours represent schematically the changes in different factors corresponding to major fluctuations in the cod biomass. The colour scale from red to green denotes restricting and favouring influence of the changes in forcing factors on the cod stock, respectively.

Different human perturbations on the Baltic ecosystem apparently contributed to the highest recorded cod biomass, higher than estimated for the early decades of the 20th century when the human impacts on the ecosystem were much lower. This is a contrasting example to the developments in a large number of other marine fish stocks that showed much higher abundances in pre-industrialized time periods (e.g., Jackson et al. 2001; Myers and Worm 2003). Moreover, a continuous trend in an ecosystem parameter as a consequence of evolving anthropogenic interference may result in a reversed impact on fish populations over time, as illustrated by the influence of increased nutrient concentrations on the eastern Baltic cod. In the early decades of the 20th century the low productivity of the ecosystem likely partly limited cod biomass in the Baltic, while from the 1960s onwards, the high level of nutrients contributed to the deterioration of cod spawning conditions due to oxygen deficiency, especially during the periods of low inflow activity (Fig. 6).

In conclusion, our results highlight the potential and limitations of human manipulations for influencing fish stock dynamics in a marine ecosystem, on the example of the eastern Baltic cod. During the last ca 80 years, major trends in the cod stock dynamics coincided with climate variations. However, the level of stock size at similar climatic conditions was largely determined by different human impacts on the ecosystem. This indicates that in cases where fish populations are sensitive to climate, like the eastern Baltic cod, recovering the depleted stocks by management measures has certain limitations. This emphasizes the need for taking into account climate variability in defining the target levels for fisheries management. However, besides the large influence of climate on the eastern Baltic cod, different human activities have historically had a significant impact on the stock size. Our results provide a new understanding of the relative influences of fishing and human-induced changes in the upper and lower trophic levels on the cod stock dynamics and can potentially help to define the limit and target reference levels for fishing mortality and other ecosystem parameters that can be modified by management actions.

Acknowledgements

The first author received support from the Danish Research School for Studies in Marine and Coastal Environment, Heritage and Sustainable Tourism (MAST), which is gratefully acknowledged. The study was supported by the History of Marine Animal Populations project of the Census of Marine Life and by the Commission of the European Communities FP6 Specific Targeted Research Projects 022717 (UNCOVER) and 044133 (RECLAIM).

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