UNIVERSITY OF LATVIA

Faculty of Biology

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IMPACT OF ENVIRONMENTAL VARIABILITY ON YEAR-CLASS STRENGTH OF BALTIC COD (*GADUS MORHUA CALLLARIAS* L.)

Doctoral Thesis

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The doctoral thesis was developed in Departments of Hydrobiology and Zoology and Animal Ecology, Faculty of Biology, University of Latvia as well as in Latvian Fisheries Research Institute (LATFRI), Institute of Food Safety, Animal Health and Environment (BIOR) and Institute of Marine Science (IFM) at University of Kiel, Germany during 1997 – 2013

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TABLE OF CONTENTS

ANNOTATION

This thesis assesses spatial and temporal variability in conditions affecting the survival of cod eggs in three distinct spawning sites in the Baltic Sea – Bornholm, Gdansk and Gotland. The cod reproduction habitat or so called 'reproductive volume' (RV) at each of the spawning sites is defined as the volume of water where salinity is higher than 11psu and dissolved oxygen content higher than 2ml l^{-1} permitting successful egg development. Cod RV annual dynamic and the factors determining it are analyzed in connection with climate change in the Baltic Sea. In order to assess cod biomass and recruitment dynamics the calculated RV are being tested as the environmental variables in the classical Ricker stock recruitment model.

In addition, the influence of cannibalism on annual stock recruitment dynamics is analyzed. The thesis is summary of five publications.

The study underpaying proposed Doctoral thesis is carried out in Latvian Fisheries Research Institute (LATFRI), Institute of Food Safety, Animal Health and Environment (BIOR), Institute of Marine Science (IFM) at University of Kiel (Germany) and Departments of Hydrobiology and Zoology and Animal Ecology of Faculty of Biology, Latvian University.

Key words: Baltic cod, recruitment, reproduction volume, stock – recruitment relationship, cannibalism.

1. INTRODUCTION

1.Eastern Baltic cod and their its role in the sea ecosystem

The cod (*Gadus morhua*) is a temperate marine fish that spawns in high salinity bottom water layers of the continental shelf and produces pelagic eggs. In contrast to other Gadidae such as haddock (*Melanogrammus aeglifinius*) and whiting (*Merlangius merlangus*) the cod is able to penetrate into the brackish waters of the semi-enclosed Baltic Sea (Svetovidov, 1986). However, conditions in the Baltic with a surface salinity of 7-8 psu and bottom salinities up to 10-23psu are marginal for marine species. This generally confines cod spawning to four deep high salinity areas: the Bornholm Deep, Slupsk Furrow, Gdansk Deep and Gotland Deep. Dissolved oxygen concentration at the surface is typically 6-8 ml l^{-1} but on the bottom of the deeps can be depleted to zero. High eutrophication and irregular water exchange with the North Sea has resulted in highly variable conditions on these spawning grounds.

The Baltic cod stock has shown great variation in abundance in the past. The maximum abundance in recent history was observed after the major inflows of highly saline water into the Baltic before 1980. After that time the Baltic was characterised by a deep stagnation process, development of anoxic layers and reduction of successful cod recruitment. Since then major inflows in the Baltic were registered only twice: in 1993/1994 and in 2003 (Matthäus et al., 2003; Matthäus, 2006). In spite of these two single inflows, heavy fishing during this period resulted in a dramatic decline in stock abundance of cod (ICES, 2013).

During the spawning time (April-August) cod performs the migrations to the Baltic deeps where only in saline waters they can successfully spawn (Bagge and Thurow, 1993). The volume of water that provides minimum environmental conditions for spawning and successful egg development and survival, has been variously named as the 'spawning layer' (Grauman, 1973), 'spawning volume' (Lablaika and Lishev, 1964) 'zone of egg survival' (Uzars et al., 1991) or 'reproduction volume' (P.-O. Larsson pers.com.). The latter seems more appropriate, because insures both spawning and egg survival. It should be noticed that spawning cod concentrations have been observed below the critical oxygen and salinity values (Plikshs and Kalejs, 1998; Neuenfeldt et al., 2009; Schaber et al., 2011).

The aim of the present investigation is to examine whether variations of this reproduction volume can explain the fluctuations of Baltic cod recruitment that have occurred over the past 50 years. *In situ* observations suggest that cod reproduction is confined to areas with salinity >10-12 psu and oxygen content >1.5 - 2 ml l^{-1} (Kändler, 1944; Grauman, 1973). It has been found in experimental studies that a salinity of at least 11 psu is necessary to ensure spermatozoon motility and at least 12 psu for neutral egg buoyancy (Westin and Nissling, 1991; Nissling et al. 1994; Nissling and Westin, 1991a). Furthermore, salinity over 10 psu is necessary for normal hatching of cod eggs (Westin and Nissling, 1991b). Minimum dissolved oxygen requirement for egg development was found to be 2.0 ml l^{-1} (Wieland et al., 1995). For the purposes of the present study the limits of the reproductive volume were defined as salinity >11 psu and dissolved oxygen concentration >2.0 ml l^{-1}.

1.2. Cod spawning ecology and possible mechanisms influencing recruitment

During recent years lot of effort has been invested to understand the mechanisms that drive Eastern Baltic cod recruitment. Although Baltic cod is adapted to low salinity environment in the Baltic Sea there are certain limits to its adaptation capacity. The only cod spawning grounds are in the deep basins where salinity is high enough to keep cod eggs floating to ensure successful fertilization and development and hatching. Hence the physical environment factors like salinity, temperature and oxygen have been considered as the factors determining production of viable cod larvae and juvenile fish (Berner et al, 1989; Grauman, 1973; Wieland et al., 1994, Plikshs et al., 1993, Lablaika et al., 1989; Nissling and Westin, 1997; **IV**; **V**). Besides the abiotic environment parameters a number of biotic interactions has been analysed in connection to variation in recruitment:

- Size and condition of spawning stock size (especially female), that affect spawned egg quality and condition and thus the viable egg production. Large females produce larger and more buoyant eggs than smaller fish (Nissling et al. 1994). Large fish also produce more batches during spawning season and spawns over the longer period (Kjesbu et al, 1996).
- Spawning stock biomass (Ricker, 1958). However, SSB is not always the best estimate for stock reproduction potential (Marshall et al., 1998).
- Variability of larvae mortality. As suggested by the match and mismatch hypothesis, until larvae mortality may be caused by starvation due to time mismatch in occurrence of cod larvae and their zooplankton pray (*nauplii*) in some years (Hinrichsen et al., 2002; Cushing, 1990).
- Egg predation by sprat. As clupeids have been identified as major predators on cod eggs and larvae in the Baltic, increased predation may be an important factor influencing cod recruitment abundance. Especially at the beginning of the cod-spawning season, characterized by low zooplankton availability, sprat consumed a considerable proportion of the eggs produced (Köster and Möllmann, 2000). However the total proportion of consumed eggs is related to total sprat stock size and this phenomenon is recorded in the Southern Baltic (Bornholm Basin) only where cod and sprat spawning areas overlap.
- Larvae drift from spawning sites. Retention or dispersion of larvae from the spawning grounds has been identified as one of the key processes influencing recruitment success in fish stocks. A rapid transport of larvae from the spawning grounds towards the shallow coastal regions of the Bornholm Basin may be beneficial for larvae growth and survival. The years with a large number of low-pressure systems passing over the Baltic Sea characterized by strong westerly winds, 80–90% of larvae hatched in the centre of the Bornholm Basin may be transported to the northern coastal areas. Conversely, high-pressure systems over Scandinavia and the eastern Baltic Sea during the spawning season result in weak easterly and/or northerly winds and the larvae might be largely retained within the deepwater region of the Bornholm Basin (Voss et al., 1999; Hinrichsen et al., 2001). As it is indicated by modelling recruitment improves with increasing southerly or westerly winds (**I**).
- Cannibalism. As indicated by Multispecies stock assessment models the estimated cannibalism in second half of year was a major cause of mortality until 1988, i.e. responsible for removing 32–60% of the initial abundance of age group 0. Since 1989, predation pressure has declined to 14–25% removal. Cannibalism on age 1 accounted for 14–31% of the initial abundance, with highest values also in the first half of the 1980s and a decline to <10% in recent years (Neuenfeldt and Köster , 2000).

Recent 20 years the cod spawning timing has gradually changed from spring to summer (Wieland et al., 2000). One of the reasons for such a delay could be changes of cod spawning stock structure in favour of younger individuals (Kraus et al, 2002). It is well known that elder gadoid fishes mature and spawn earlier than younger ones (Nikolsky, 1965; Kjesbu, 1994; Tomkiewicz et al., 1998). These changes may also reflect an adaptive response to environmental changes (Rolf, 1992, cit. after Eero, 2000).

Figure 1 shows a simplified conceptual model of those factors that potentially influencing the survival of Baltic cod from eggs till recruitment of catchable stock.

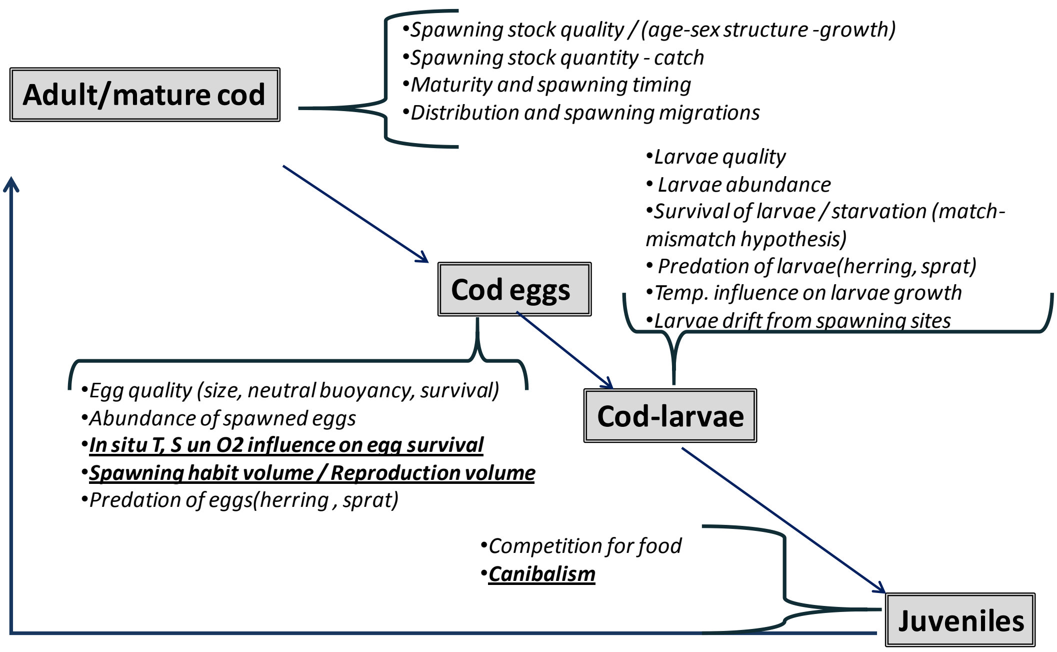

Figure 1. The conceptual model of processes influencing the Eastern Baltic cod egg, larvae and juvenile survival. Processes that have been analysed in the present theses are highlighted in bold and underlined.

1.3. The Baltic Sea environment and adaptive response of Baltic cod reproduction in the Baltic Sea

The Baltic Sea is small marginal sea that has meridian extension about 659 km and longitudinal extension about 1500 km (Ehlin, 1981). The Baltic Sea is considered as a new sea, it has formed after Baltic Glacier period and during its geologic history has been connected with the Atlantic (as it still is) and probably with the Arctic Oceans (Ignatius *et al.*, 1981). The fish fauna of the brackish Baltic Sea is relatively young, yet diverse in terms of origin, including the species both of marine and freshwater origin. The marine species including cod have invaded the sea from the North Sea approximately 8000-4000 years ago during the relatively saline and warm Litorina Sea period. Since then, the environmental conditions have gradually worsened for marine species and under the present low and variable salinity conditions most of those suffer high physiological stress resulting in slower growth and higher recruitment variability compared to their Atlantic relatives.

From fish species for which the random inflows of saline water from the North Sea play vital role ensuring successful breeding, the Baltic cod *Gadus morhua callarias* L., inhabiting the edge of the natural distribution area of the *Gadus morhua*, is among those in the most critical conditions. The spawning success of cod depends on extent of water with sufficient density (salinity) in order to keep eggs floating in oxygen-rich layer ("reproduction volume"). Due to higher salinity in the area, the cod in the south-western Baltic enjoys somewhat better environmental conditions, while good recruitment in the eastern and northern parts seems to be rather an exception than a rule. The present brackish nature of the sea is the main reason why in the Baltic the marine ichthyofauna is relatively poor and is dominated by only three species: cod, sprat and herring.

The Baltic cod is assessed as two separate stocks, covering south-western (Sub-divisions 22-24) and north-eastern Baltic (Sub-divisions 25-32), respectively (Fig.2). Eastern Baltic cod is distributed eastwards of Bornholm Island. The difference between the two cod stocks in the Baltic Sea is demonstrated by genetic (electrophoresis and DNA analyses), morfometric characters, migration patterns, distinct spawning areas and timing and otolith structure and form (Bagge and Steffensen, 1989; Aro, 1989; Jamieson and Otterlind, 1971; Berner and Vaske, 1985, Nielsen et al., 2003; Nielsen et al., 2005).

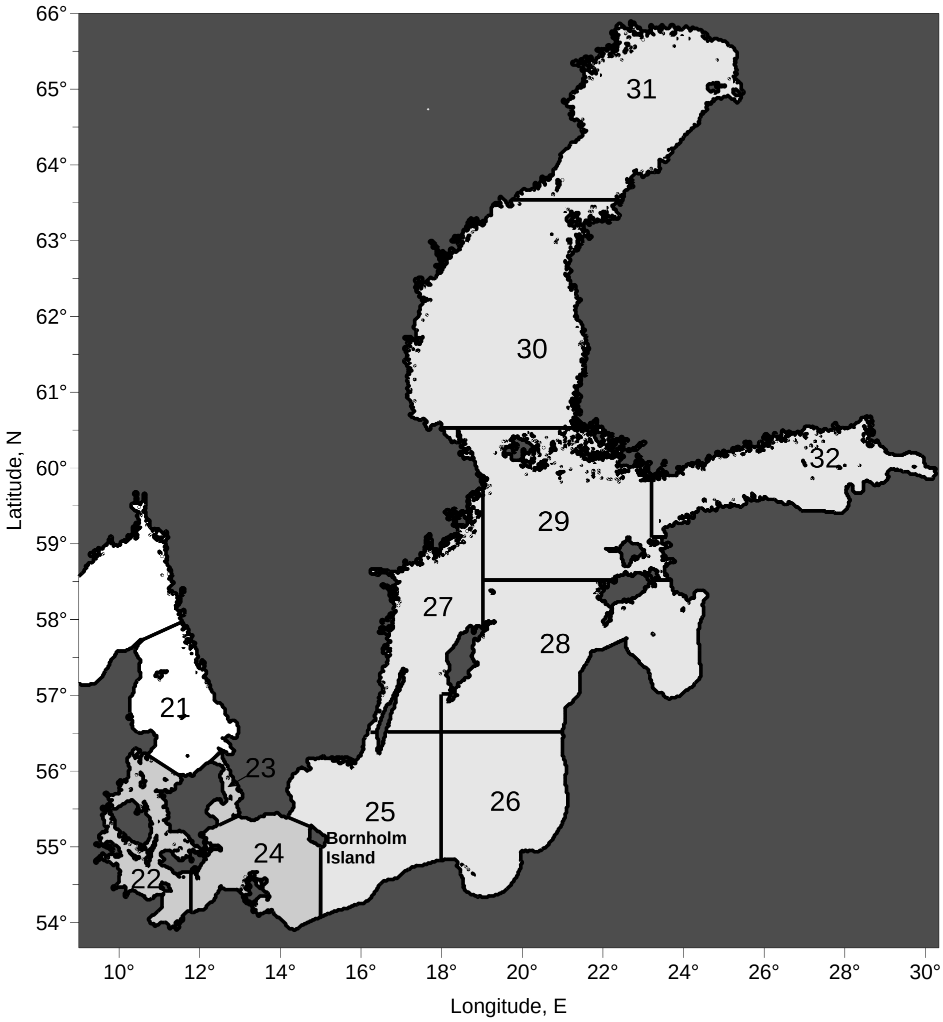

Figure 2.ICES Sub-divisions in the Baltic Sea and the Western and Eastern cod stock distribution areas. Distribution area of Eastern Baltic cod is marked in light gray, Western Baltic cod – dark gray.

1.4. The main objective of the thesis

The overarching objective of this study is to improve the knowledge on Eastern cod reproduction dependence from changing environmental conditions caused largely by climate regime shift in the Baltic. It is very important to incorporate this knowledge in the stock assessment process in order to understand the mechanisms of stock dynamics formation and developing stock management strategies and plans.

The abovementioned objective was further divided into several tasks:

1) identify and describe the physical oceanographic processes that influence the year-class strength of Eastern Baltic cod;

2) describe the stock - recruitment relationship of the Baltic cod and its dependence from reproduction volume;

3) evaluate the role of cod cannibalism in determining the year-class strength.

1.5. Promoted thesis of the study

- The reproduction volume is the primary term for formation of abundant year classes of Eastern Baltic cod;
- The abundant year classes of Eastern Baltic cod was observed in years that was favourable for egg survival in all major spawning grounds;
- The diminishing of cod year class strength since 1990-ies was determined mainly by development of stagnation processes in the Eastern deeps and inadequate management of Eastern Baltic cod fishery;
- Inclusion of reproduction volume as an environmental variable in the stock recruitment models significantly improve the credibility of these estimates;
- Cod cannibalism is mainly determined by abundance of juveniles that increase their distribution area. The possibility of cannibalism increases with expansion of distribution area, but not with abundance of possible predators (adult cod).

1.6. Scientific novelty of research work

In World-wide ichthyology we were the first who quantified the „Reproduction volume "and applied this hypothesis to explain the variation in dynamics of the Eastern Baltic cod recruitment. This hypothesis is based on a suggestion that salinity and oxygen in the Baltic Sea are limiting factors for successful development of early life (eggs) stages of fishes with pelagic eggs. In our case it is the Eastern Baltic cod. The Reproduction volume (RV) may be easily calculated using oceanographic measurements (salinity, oxygen and temperature) and it allow to obtain Baltic cod year-class strength estimates at age 2 years at least with advance of 2 years. This hypothesis is also confirmed by several internationally reviewed publications.

Long-term investigations of cod cannibalism in case of Eastern Baltic cod revealed that it mainly depends from the abundance and distribution of juvenile cod although in internationally accepted multispecies stock assessment models cannibalism usually assumed as dependent from adult fish abundance e.g. potential predator stock size.

1.7. The approbation of the research

The main results of the study were described in five internationally reviewed publications and in nine other publications covering the cod reproduction ecology and stock assessment in the Baltic Sea. The results of research were also presented in 15 international and two national conferences. The complete list of publications and corresponding citation indexes can be seen under http://scholar.google.com/citations (name Maris Plikshs).

I. Jarre-Teichman, A., Wieland, K., MacKenzie, B.R., Hinrichsen, H.-H., **Plikshs, M.**, and Aro, E., 1997. Stock-recruitment relationship for cod (*Gadus morhua callarias* L.) in the central Baltic sea incorporating environmental variability. Arch. Fish. Mar. Res. 48(2):97-123.

II. MacKenzie, B.R., Hinrichsen, H-H., M.A., **Plikshs, M**., Wieland, K. and Zazera, A.S., 2000. Quantifying environmental heterogeneity: estimating the size of habitat for successful cod egg development in the Baltic Sea. Mar. Ecol. Prog. Ser. 193: 143-156.

III. Uzars, D. and **Plikshs,M.,** 2000. Cod (*Gadus morhua calla*rias L.) cannibalism in the Central Baltic: interannual variability and influence of recruitment abundance and distribution. ICES J. Mar. Sci., 57: 324-329.

IV. Köster, F.W., Hinrichsen, H-H., St.John, M.A., Schnack, D., MacKenzie, B., Tomkiewicz, J. and **Plikshs, M**., 2001. Developing Baltic cod recruitment models II: Incorporation of environmental variability and species interaction. Can. J. Fish. Aqua. Scie., 58(8): 1534-1556.

V. **Plikshs , M.,** Hinrichsen., H.-H., Elferts. D., Sics, I. Kornilovs, G. and Köster, F.W., 2014. Baltic cod reproduction in the Gotland Basin: causes of annual variability. (submitted to Acta Ichthyologica et Piscatoria).

The corresponding sequence numbers of these publications are shown in the Materials and methods and Result chapters.

Other related publications

1. **Pliksh, M.A.** and Kaleis, M.V.,1990. Cod distribution during the spawning period in the eastern Baltic in 1986-1988. Fischerei-Forschung 28(2): 39-43 [In Russian].
2. Malkin, E.M. and **Pliksh, M.A**.,1993. Application of Biostatistical Method for Assessment of Abundance of Eastern Baltic Cod, *Gadus morhua callarias*. J. Ichthyol. 33(8): 96-110.
3. Köster, F.W., Möllmann, C., Neuenfeldt, S., St.John, M.A., **Plikshs, M**.and Voss, R., 2001. Developing Baltic cod recruitment models I: Resolving spatial and temporal dynamics of spawning stock and recruitment for cod, herring and sprat. Can. Journal of Fisheries and Aquatic Sciences. 58(8): 1516-1533.
4. Köster, F.W., Hinrichsen, H-H., Schnack, D., St.John, M.A., MacKenzie, B., Tomkiewicz, J., Möllmann, C., Kraus, G., **Plikshs, M.,** Makarchouk, A., and Aro, E., 2003. Recruitment of Baltic Cod and sprat stocks: identification of critical life stages and incorporation of environmental variability into stock-recruitment relationships. Sci.Mar., 67 (Supl.1): 129-154.
5. 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 J. Mar. Sci., 64: 1257–1271.
6. Köster, F.W., Vinther, M., MacKenzie, B.R., Eero, M., and **Plikshs, M,** 2009. Environmental Effects on Recruitment and Implications for Biological Reference Points of Eastern Baltic Cod (*Gadus morhua*). J. Northw. Atl. Fish. Sci., Vol. 41: 205–220.
7. Möllmann, C., Dieckmann, R., Muller-Karulis, B., Kornilovs, G., **Plikshs, M.**, and Axe, P. 2009. Reorganization of a large marine ecosystem due to atmospheric and anthropogenic pressure: a discontinuous regime shift in the Central Baltic Sea. Global Change Biology, 15:1377-1393.
8. Rossing, P., **Plikshs., M.,** Booth, S., Veitch, L., and Zeller, D., 2010. Catch reconstruction for Latvia in the Baltic sea from 1950–2007. In: Total marine fisheries

extractions by country in the Baltic Sea: 1950-present. Rossing, Booth and Zeller (eds.) Fisheries Centre Research Reports 18(1): 127-144.

9. Casini, M., Blenckner, T., Möllmann, C., Gårdmark, A., Lindegren, M., Llope, M., Kornilovs, G., **Plikshs, M.** and Stenseth N.C., 2012. Predator transitory spillover induces trophic cascades in ecological sinks, PNAS, 109(21):8185-8189.

International conferences

ICES symposia"Recruitment Dynamics of Exploited Marine Populations: Physical-Biological Interactions". Baltimora, Marilenda, ASV 22-24 September 1997.

1. Jarre-Teichman, A;. Wieland, K., MacKenzie, B.R., Hinrichsen, H.-H., **Plikshs, M.,** and Aro, E., 1997. Stock-recruitment relationship for cod (*Gadus morhua callarias* L.) in the central Baltic sea incorporating environmental variability (oral presentation).
2. Uzars, D. and **Plikshs, M.,** 1997. Cod (*Gadus morhua callarias* L.) cannibalism in the central Baltic: interannual variability and influence of recruitment abundance and distribution (oral presentation).

Alaska See Grant Symposia "Resiliency of Gadoid Stocks to Fishing and Climate Change", Anchorage, Alaska, USA, 31st October- 3rd November, 2006.

1. **Plikshs,** M. and Raid, T., 2006. Recent failure of the Baltic cod recruitment: is it determined by environmental regime change or overexploitation? (oral presentation)
2. Raid, T. and **Plikshs, M.**, 2006. Cod in the Baltic Sea: assessment and management of marginal cod stocks (oral presentation).

ICES Annual Science Conferences:

1. Uzars,D., **Plikshs,** M., Grauman, G., Kalejs, M. and Baranova, T., 1991. Cod distribution and spawning in the Gotland Basin in the 1980-ies. ICES-CM-1991/J:15 (La Rochelle, France, September 1991).
2. **Plikshs, M.,** Kalejs, M. & Grauman, -G., 1993. The influence of environmental conditions and spawning stock size on the year-class strength of the eastern Baltic cod. ICES-CM-1993/J:22 (Dublin, Ireland, September 1993).
3. **Plikshs, M**., 1996. Recent changes in Cod spawning stock abundance and reproduction success in the Gotland area: is the cod stock recovery possible? ICES-CM-1996/J:23 (Reykjavik, Iceland, September 1996).
4. MacKenzie, B.R., St.John M.A., **Plikshs, M.,** Hinrichsen, H. H. and Wieland,K., 1996. Oceanographic processes influencing seasonal and interannual variability in cod spawning habitat in the eastern Baltic Sea. ICES-CM-1996/ C+J:4 (Reykjavik, Iceland, September 1996).
5. **Plikhs, M.,** Hinrichsen, H. H., Köster, F., Tomkiewicz, J., and Berzins, V., 1999. Baltic cod reproduction in the Gotland Basin: annual variability and possible causes. ICES-CM-1999/Y:31 (Stockholm, Sweden, September 1999).
6. MacKenzie, B.R., **Plikshs, M.,** Köster, F.W. and Hinrichsen, H H., K., 1999. Does spatial match-mismatch of spawning and environmental conditions affect recruitment in Baltic cod. ICES C.M. 1999/Y:16 (Stockholm, Sweden, September 1999).
7. Köster, F.W., Hinrichsen, H. H., St. John, M.A, MacKenzie, B. and **Plikshs, M.,** 1999. Stock-recruitment relationship of Baltic cod incorporating environmental variability and spatial heterogeneity. ICES C,M. 1999/Y:26 (Stockholm, Sweden, September 1999).
8. Möllmann, C., Müller-Karulis, B., Diekmann, R., Flinkman, J., Kornilovs, G., Lysiak-Pastuszak, E., Modin, J., **Plikshs, M.,** Walther, Y. and N. Wasmund.,N., 2006. An integrated ecosystem assessment of the Central Baltic Sea and the Gulf of Riga. ICES-CM-2006/P:03 (Maastricht, Netherland, September 2006).
9. Baranova, T., Müller-Karulis,B., Šics, I, and **Plikshs, M**., 2011. Changes in the annual life cycle of Eastern Baltic Cod during 1950-2010. ICES CM 2011/R: 10 (Gdansk, Poland, September 2011).

10. Gröger, J., Möllmann, C., Blenckner, T., Gårdmark, A., Lindegren, M., Müller-Karulis, B., Axe, P., **Plikshs, M.** and G. Kornilovs, G, 2011. Applying the shiftogram approach for identifying ecosystem changes—the Baltic Sea as a multivariate test case. ICES CM 2011/J:09 (Gdansk, Poland, September 2011).
11. Baranova, T., Zilniece D. and **Plikshs,M.,** 2012. Some results of long-term investigations of morphological parameters of Baltic cod otoliths. ICES CM 2012/J:35 –poster (Bergen, Norway, September 2012).

National Conferences

IV. Latvian University 65. Scientific conference „Climate change in water environment" February 2007:

1. Maris **Plikšs** un Bärbel Müller-Karulis. Baltijas mencas (*Gadus morhua callarias* L.) paaudžu ražības samazināšanās pēdējās desmitgadēs: hidroloģiskā režīma izmaiņu vai pārzvejas rezultāts? (posters- in Latvian).
2. Bärbel Müller-Karulis, Christian Möllmann, Maris **Plikšs**, Georgs Kornilovs. Svarīgākie signāli Baltijas jūras un Rīgas līča vides monitoringa datu rindās: 1973 – 2004 (oral presentation-in Latvian).

V. Latvian University 66. Scientific conference „Climate change in water environment" March 2008:

1. Maris Plikšs un Bärbel Müller-Karulis. Nārsta tilpums kā mencas paaudzes ražības galvenais rādītājs (oral presentation-in Latvian).

1.8. Structure of Doctoral thesis

The doctoral thesis is a summary of the five publications and covers the main findings and results.

2. MATERIAL AND METHODS

2.1 The definition of Reproduction volume

Thee reproduction volume (RV) of Eastern Baltic cod we define as water volume that lies in pelagic or near bottom layers and which upper border is determined by isochaline 11psu and lower border – by isooxygen 2ml l^{-1} (Plikshs et al., 1993; **II**).

In Gotland Basin during stagnation years, when isooxygen 2ml l^{-1} is placed shallower when isochaline 11psu the calculated water volume we named as unsuitable reproduction habitat volume of cod (UV) –**V**.

2.2 Hydrological observations and evaluation of Reproductive volume (RV) - "Latvian method".

Calculations of Baltic cod RV were based on standard oceanographic stations from sampling in February, May and August in the central parts of the main spawning deeps (Fig. 3):

- Bornholm Deep -station BY5A (55°15'E, 15°59'N, depth 90m);
- Gdansk Deep -station P1 (55°05'E, 19°15'N, 105m);
- Gotland Deep -station BY9A (56°05'E, 19°10'N, 125m),
  -station 43 (56°42', 19°52',153 m) and
  -station BY15A (75°18'E, 20°04'N 240m.)

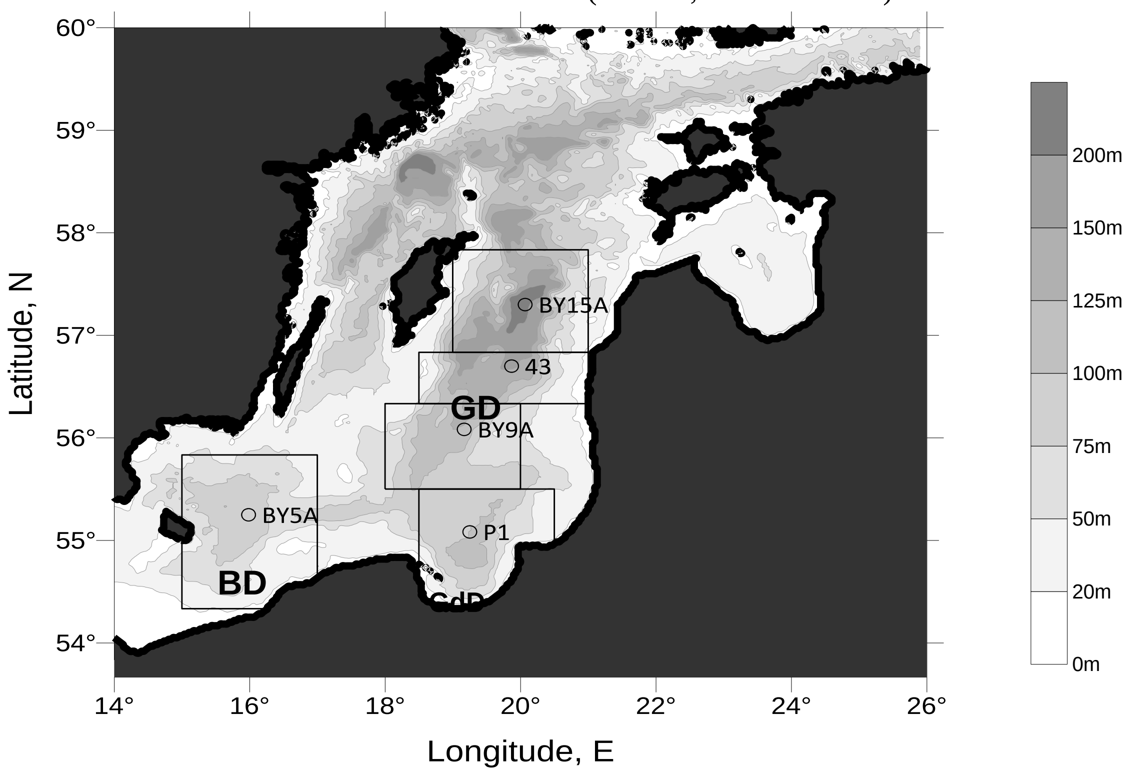

Figure 3. Standard oceanographic stations in the central Baltic deeps. Squares indicate area for which the Reproduction volume was calculated: BD – Bornholm Deep, GdD – Gdansk Deep, GD – Gotland Deep.

The oceanographic data sources used in the calculations of RV are shown in Table1.

Table 1.

Data sources of oceanographic stations

	Stations				
	BY 5A	P1	BY 9A	43	BY 15A
1952-1963	Annales Biologique (ICES); Bulletin Hydrographique (ICES)	Annales Biologique (ICES), Bulletin Hydrographique (ICES); Glowinska, 1963	Annales Biologique (ICES), Bulletin Hydrographique (ICES); Sea hydro-meteorological annals. Baltic Sea, USSR (in Russian).	Sea hydro-meteorological annals. Baltic Sea, USSR (in Russian).	Sea hydro-meteorological annals. Baltic Sea, USSR (in Russian).
1963-1991	BALNIIRH	BALNIIRH	BALNIIRH	BALNIIRH	BALNIIRH
1991-2011	http://www.smhi.se ; H-H.Hinrichsen –IFM-GEOMAR (pers.com); P.Axe – SMHI - (pers.com)	P.Morgonsky SFI (pers.com); H-H.Hinrichsen –IFM-GEOMAR (pers.com) A.Zezera ATLANTNIRO (pers.com.)	LATFRI, LATFRA, BIOR	LATFRI, LATFRA, BIOR	LATFRI, LATFRA, BIOR

BIOR – Institute of Food Safety, Animal Health and Environment.
BALTNIIRH - Baltic Scientific Research institute of Fisheries).
LATFRI - Latvian Fisheries Research Institute.
LATFRA - Latvian Fisheries Resource Agency.
SMHI – Swedish Meteorological and Hydrological Institute, Sweden.
IFM-GEOMAR – Leibniz-Institute of Marine Sciences, Kiel, Germany.
IFM – National Marine Fisheries Research Institute, Gdynia, Poland.
ICES – International Council for the Exploration of the Sea.
ATLANTNIRO – Atlantic Research Institute of Marine Fisheries and Oceanography, Kaliningrad, Russia.

Salinity and oxygen saturation measurements of BALTNIIRH during 1963-1991 were performed in samples obtained using a Nansen's bathometer. Samples at each station were taken at 10 m intervals between 0-50 m and 100-240 m depths and at 5m intervals between 55 - 95 m depth.

The positions of the salinity (11 psu) and oxygen (2.0 ml l^{-1}) depth limits of the RV were calculated with the precision of 1 m. These values were then applied to the bathymetry of the Baltic Sea using the contouring software "Balthypsograph" (Wulf and Anderson, University of Stockholm) to evaluate the volume of water in a given area. The contouring software used for the volume estimations employs the hypsographic function for the Baltic proper derived from a gridded 5' X 5' bathymetric database by Stigebrandt (1987) and Stigebrandt & Wulff (1987). This function quantifies the volumes of water below horizontal surfaces at given depth levels. The depth levels at which horizontal surfaces are chosen for calculating water volumes are defined by the vertical profile of hydrographic data collected at the station in the basin. Hence, the volume of water between any 2 surfaces (e.g. those represented by the 11 psu and 2 ml l^{-1} oxygen levels) can be derived by assuming horizontal homogeneity of water mass within the rectangular calculation units (Fig. 3). This involves some simplifications and assumptions and only the three largest cod spawning grounds were covered (**I, II, IV,V**).

Cod spawning and egg production that occurred in some years in the northern and north-western Baltic (Grauman, 1984) outside the rectangular calculation areas presented in Figure 3 were not included in the analysis.

2.3. Alternative methods of estimation of reproduction volume in the basins taking into account the water mass heterogeneity.

In Bornholm Basin estimation methodology of Institute of Marine Science (IFM-GEOMAR, Kiel) was used. It was based on the hydrographic data set consisting of measurements from 16 cruises carried out in the Bornholm Basin between May 1989 and April 1996 (Hinrichsen & Wieland 1996). The station grid represents the Bornholm Basin enclosed by the 60 m isobaths. During all surveys 36 standard stations were covered with a mean horizontal resolution of -10 nautical miles with exception of 1989 when 21 stations were carried out (Fig.4). The survey data were used to calculate the thickness of the reproduction volume of Baltic cod, i.e. the vertical extension of the water body considered suitable for successful egg development (salinity >11 psu, oxygen >2 ml l^{-1}, temperature >1.5^{O}C). Horizontal fields of the thickness of the spawning layer were constructed by objective analysis (Bretherton et al. 1976) based on a standard statistical approach - the Gauss-Markov theorem - which yields an expression for the linear least-square error estimate of the variables. For each of the 36 stations, the thickness of the reproduction volume was compared with the total reproductive volume obtained for the dates in the period 1991 to 1996 using linear regression analysis.

In the Gotland Basin in order to compare the RV estimates from single point stations with hydrographic heterogeneity within the basin, the hydrographic data set of measurements from 11 cruises carried out in the Gotland Basin between February 1969 and May 1999 on stations at two transects of the Central Gotland Basin was used: northern - stations 36, BY15A, 38 and 38A and southern – stations 42, 43, 44 enclosed by 80 m isobath (Fig.5). On average, the spatial resolution was about 30 nm in latitude and 15 nm in longitude. The survey data were used to calculate the thickness of the reproduction layer of Baltic cod with respect to its classical definition (S > 11 psu; O2 > 2 ml l^{-1}) as well as with regard to suboptimal oxygen and salinity conditions –unsuitable habitat (UV) (O2< 2 ml/ l and salinity < 11 psu).

The hydrographic data set was used to construct horizontal fields of the thickness of reproduction layers by a multi-dimensional linear function:

$$F_{(x,y)} = \sum_{i=1}^{N} \sum_{j=1}^{N} A_{ij} \times x^{(i-1)} \times y^{(j-1)} \qquad (1)$$

which is determined by a multiple regression analysis using the least square criteria.

For the present analysis of the fields of the reproduction layers it was assumed that a horizontal trend of the data could be approximated by (1) fitted to the data using a multiple regression scheme. Applying this method a unit array configuration with dx=dy=5km was provided for depths >80 m, with each grid point being representative for the positive or negative layer thickness centred around it. The RV of the Central Gotland Basin area was calculated for each of the different surveys by simply integrating the fields of reproduction layer thickness horizontally.

This method (IFM-GEOMAR) allows taking into consideration the basin-wide trends in the depths of oxygen concentrations and in the haline stratification and thus, the method is able to include spatial variability.

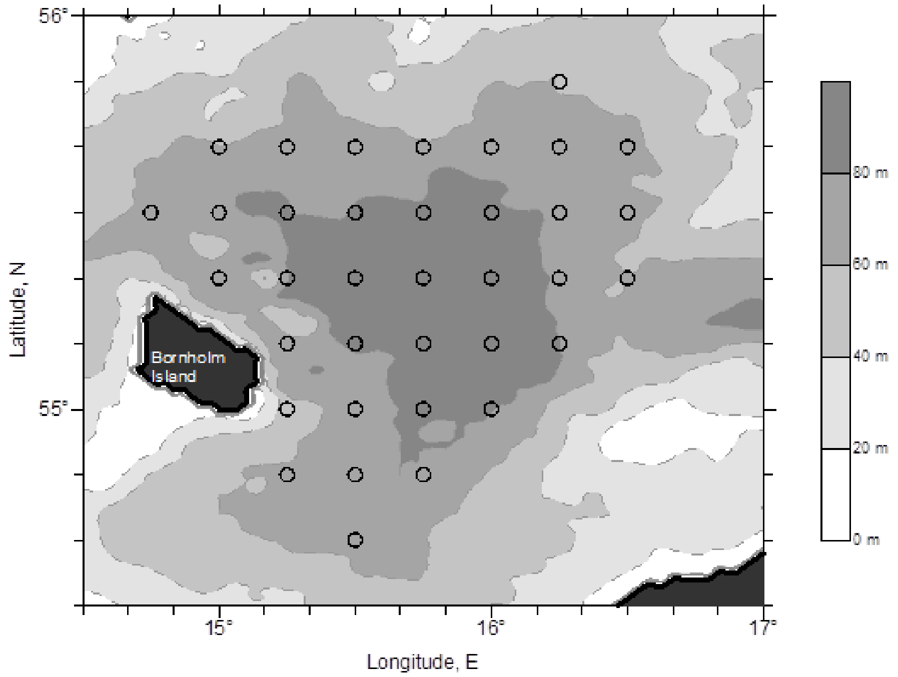

Figure 4.Grid of hydrographic stations in Bornholm Basin used by University of Kiel research vessels for determining reproductive volumes during 1991-1996 (○:36 stations).

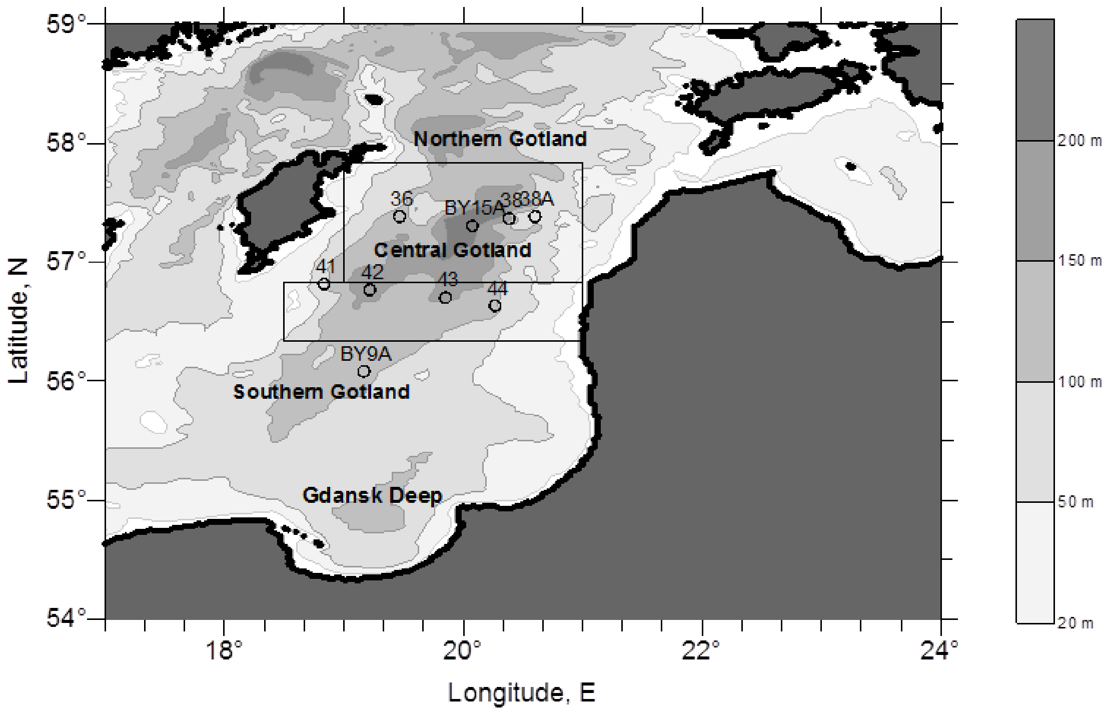

Figure 5. . Hydrological monitoring stations in the Gotland Basin. Squares indicate suitable (RV) and unsuitable (UV) reproduction volume calculation areas based on single station observations: BY15A, 43 in the Central Gotland.

2.3. Estimation of cod egg survival index.

During 1954 to 1990, 125 ichthyoplankton surveys were carried out in the Baltic Sea. The water column was sampled at each station using a standard vertical tow IKS-80 net (mesh size 0.5 mm, net opening 0.5 m^2). At each station, cod eggs were counted and the results were standardised to the number per m^2 of sea surface. All sampled eggs were sorted and assigned to development stages. Four egg development stages were recognised:

> Stage I - blastula stage, from fertilisation to the appearance of a distinct primitive streak on the embryonic shield;
> Stage II - gastrulation stage, from end of stage I until to the closure of the blastopore;
> Stage III- from the end of stage II until embryo tail growth extends to the equator of the egg;
> Stage IV- from when the tail-tip of the embryo grows through equator until hatching.

The eggs were further segregated into viable and dead eggs in each development stage. The fraction of live eggs by development stages were calculated from each survey within each basin as:

$$F_n = NA_n / ND_n + NA_n \qquad (2)$$

where NA - total number of live eggs during one survey within rectangle,

ND - total number of dead eggs during one survey within rectangle,

n – egg development stage (1, 2, 3, or 4).

It was not possible to fit a satisfactory exponential mortality model to the egg numbers at different stages (Gunderson, 1994). Therefore a survival index was used for evaluation of annual egg mortality (Grauman, 1973). The survival index combines the data from all the egg stages in the following way:

$$SI = F_1 * F_2 * F_3 * F_4 \qquad (3)$$

where SI –is egg survival index in a given basin and F is fraction of viable cod eggs in stages 1, 2, 3 and 4 respectively.

Since the durations of the stages are different, survival index may not be equal to true egg survival to stage 4. However, the index provides a convenient means of comparing egg survival from year to year. This analysis was available for years from 1954 till 1989 when BALTNIIRH ichthyoplankton sampling covers all Eastern Baltic Basins. The obtained survival index values there taken from Grauman (1984) and Plikshs et al. (1993).

2.5. The estimates of cod year-class strength.

The year class strength estimation of cod from research surveys data in Eastern Baltic was performed by two different methods: for evaluation of (1) cannibalism and (2) spawning condition influence (**III** and **V**).

1. An annual index of the cod recruitment (age group 1) in the Eastern Baltic was calculated from the results of research surveys by demersal trawling in 1975-1990. Although the surveys were carried out with the same trawl, the area coverage varied. Due to this, single haul catch per unit of effort (CPUE) data could not be combined together directly. Therefore General Linear Model (GML) was applied on weighted by depth strata area mean and log transformed CPUE data (SAS, 1989). The applied model was:

N (Age1)= Y+A+S+D+A*D+S*A+e (4)

where

N – recruitment index of one year old fishes,

Y - year effect,

A - sub-area effect. Following sub-areas were introduced - Southern Gotland, Central Gotland Northern Gotland and Gdansk Deep.

S - season effect. Following seasons were used combining the data: January-February, March-April and November-December. It was assumed that season reflects the same distribution pattern;

D - depth strata effect. The following depth strata were used: 21-40 m, 41-60 m, 61-100 m, 101-120 m and 121-140 m.

A* D and S* A interaction terms;

E – error term.

Descriptive statistics for the model were df = 371, R_{square} = 0.53, F =8.71, p<0.0001. Obtained age group 1 year class strength index was related to frequency of cod cannibalism (**III**).

2. As there is strong non linear effect on estimated index, in later works a new approach was used (**V**). Annual indices of cod recruitment and adult cod (ages 3+) stock were calculated from Latvian research surveys in the Southern and Central Gotland Basin during 1975-2011. As the surveys are carried out in February-March, direct estimation of spawning stock is not appropriate because of changes of cod spawning timing from spring months to summer (Wieland et al., 2000).

In total 1181 single trawl hauls were carried out. Although the surveys were standardized to new TV3 trawl, the area coverage varied. The number of hauls used was separated by years, areas (Southern and Central Gotland) and depth strata (DSTR) - 21-40 m, 41-60 m, 61-100 m, 101-120 m and 121-140 m. Abundance index for the age 1 and age group 3+ for each year was calculated, first, by calculating mean number of actual catch in each Year, Area and DSTR combination (strata). Then those mean strata numbers where multiplied by the coefficients of area for corresponding DSTR to obtain estimated abundance index for each strata. Estimated indices then were averaged for each year (R Core Team 2013).

During research surveys in 1982-1994 I participated in majority of cases as a cruise leader and sampled demersal trawl data as well as oceanographic and ichthyoplankton data.

2.6. Estimation of frequency of cod cannibalism.

Cannibalism was characterized by the percentage contribution of cod to the total stomach content weight and the frequency of occurrence of cod in non-empty stomachs. Cod cannibalism was analysed for three periods separately, which differ either in major oceanographic characteristics or in recruitment level (HELCOM, 1990; ICES, 1996):

- 1969–1975. Inflow of high-saline water was intense and stagnation below the halocline was short and rare. Recruitment and biomass of cod were relatively stable.
- 1976–1979. Oxygen and salinity conditions in the near-bottom water layers were favourable for cod reproduction. Abundance of cod increased sharply owing to successful recruitment.
- 1980–1990. This period is characterized by deepwater stagnation. The biomass of cod reached a maximum in the early 1980s and decreased sharply from 1986 onwards.

2.7. Stock- recruitment analyses.

The eastern Baltic cod stock recruitment analyses is based on classical Ricker stock recruitment model (Ricker, 1958; **I**):

$$R = \alpha SSBe^{-\beta SSB} \quad , \tag{5}$$

where R – recruitment at age 2, SSB – spawning stock biomass, α un β – coefficient.

In order to evaluate the influence of environmental variable, in our case the Reproduction volume, the equation (5) was updated by additional variable c*RV:

$$R = \alpha SSBe^{-\beta SSB + cRV} \tag{6}$$

where RV- Reproduction volume and c -coefficient.

The coefficients α, β and c can be estimated using multiple standard linear regression analysis based on equation:

$$\log\left(\frac{R}{SSB}\right) = \alpha + \beta SSB + cRV \tag{7}$$

The obtained values of coefficients were applied in equitation (6) to obtain theoretical recruitment abundance at age 2. The observed Eastern Baltic cod abundance at age group 2 and spawning stock biomass were taken from recent ICES Baltic Fisheries assessment working group data (ICES, 2013).

3. RESULTS

3.1. Comparison of Reproduction volume estimates from single and multiple oceanographic station observations

Bornholm Basin

Monthly (February, May, August and October) reproduction volume estimates by BIOR and IFM-GEOMAR methods were compared in the Bornholm Basin (**II**). Month-specific regression analyses between two data series generally indicated a strong correspondence between estimates by the two methods (Fig. 6). All regressions were highly significant ($p < 0.0001$) and the explained variation (R^2) was 44 to 82%. None of the slopes differed significantly from 1. However, the intercepts were close to being significantly different from zero for some months, and the intercept was highly significant when all months were combined for an overall analysis. Intercept values ranged from -15.8 to 47.4 for individual months, and equalled 24.5 for the model combining all months.

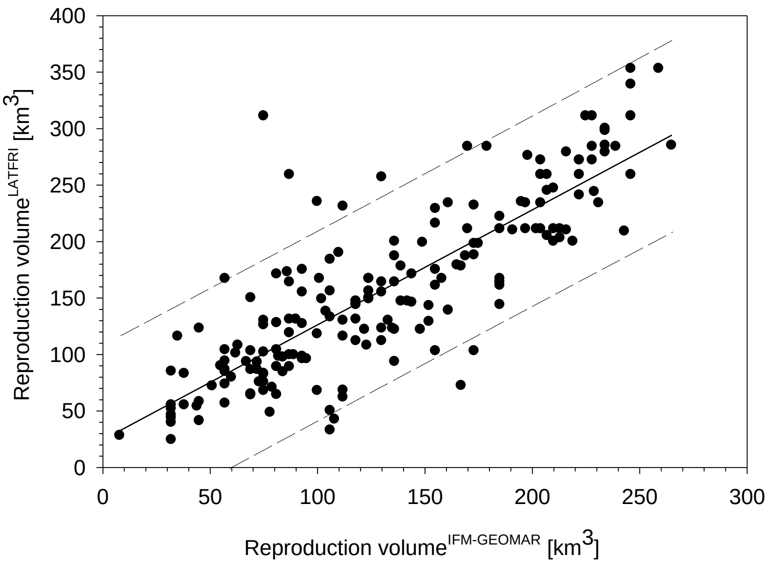

Figure 6. Regression model comparing reproductive volumes in the Bornholm Basin for all months for which data were available during 1958-1992. Reproductive volumes were estimated by 2 different methods employing different input hydrographic datasets; (-----) 95 % prediction limits.

Gotland Basin.

Oceanographic data sets allowed a comparison of 15 monthly estimates of RV as well as unsuitable habitat (UV) volumes in the Gotland Basin (**V**). Regression analysis between two data series generally showed that there is a strong correspondence between estimates obtained from 2 single stations in the centre of the basin and estimates obtained taking into account spatial heterogeneity of salinity and oxygen content (Fig. 7). The regression is highly significant ($p<0.0001$) and explains 91% of variation. Largest deviations (15-23%) were observed during inflow months, when the dynamic of water mass transport was the highest. Salinity and oxygen transects performed during the inflow periods show that in the eastern part of the basin, the isohaline 11 psu is located shallower while the isooxygen of 2 ml l^{-1} lays deeper than in the western part of the basin, i.e. the influence of the inflows is the highest in the eastern part of the basin.

During stagnation periods, the deviations in volumes estimated by both methods were much smaller – from 1 to 8% while the isohaline 11psu as well as the isooxygen 2ml l^{-1} are more evenly distributed in west – east direction. Bagge and Thurow (1994) observed a similar pattern of even distributions of salinity and oxygen across the Gotland basin during the stagnation period in 1991. Although the present comparison covered only 15 monthly observations, we can conclude that single point estimates sufficiently quantify the reproduction volume conditions and thus similarly as in the Bornholm basin can be used for estimation of the RV for the whole basin.

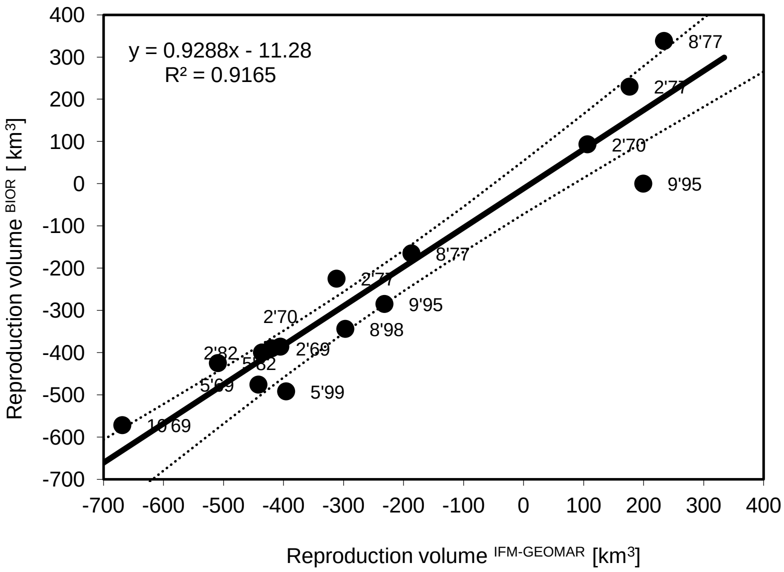

Figure7. Comparison of BIOR and IFM-GEOMAR estimates of reproduction and unsuitable habitat (presented as negative values) volumes in the Gotland Basin; (········) 95 % confidence limits. Labels to the right of data points indicate the month and year of observation.

3.2. Inter-annual variation and spatial characteristics of the reproduction volume.

The Baltic cod RV has shown great inter-annual variation during the last 60 years with a total maximum of 635.2 km^3 in 1972 and a minimum of 35.8 km^3 in 1999 (Fig. 8). Only the Bornholm Deep sustained sufficient spawning conditions throughout the sampling period. Occurrence on RV in the south-eastern Baltic spawning grounds (Gdansk and Southern Gotland) was sporadic, after major inflows (in 1952-57, 1961-62, 1964-67, 1969-70, 1972-80, 1983-86, 1993 and 2003), and in the Central Gotland only in 1952-55, 1961-62, 1964, 1972, 1975-1977 and 1994)

The largest RV in the Bornholm deep occurred in May 1972 at approximately 353km^3 which is close to the total water volume in this area beneath the halocline. In the Gdansk deep and Gotland deeps observed maxima were 125 and 256 km^3 respectively. Annual formation of the RV in the Gdansk and Gotland areas until the beginning of 1980s was relatively regular. Stagnation periods lasted only one or two years. From 1980s until the end of the study period the RV was often very low not exceeding 100 km^3 and was restricted almost entirely to the Bornholm deep. Only the inflows in 1993 and 2003 resulted in several-fold increase of RV.

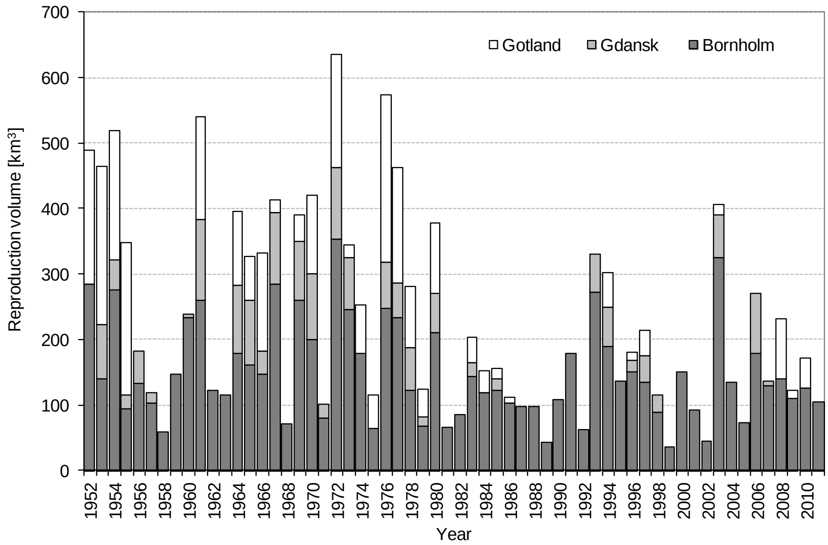

Figure 8. Potential reproduction volume of eastern Baltic cod in the main principal spawning grounds (km^3).

The character of RV distribution among the different spawning grounds it is possible to distinguish three typical situations or years:

1) Aeration years, when RV is observed in all the spawning grounds and volume within each area is large. The near bottom layers are characterised by high dissolved oxygen concentrations: 3-4 ml l^{-1}. Such conditions have been observed in 1953-55, 1964-67, 1969-70, 1972-1973, 1976-80, 1994 and 2003 (23 cases out of 60, 17 of which were observed before 1981);

2) Intermediate years, when RV has been observed in Bornholm, Gdansk and Southern Gotland. Relatively high oxygen levels remain in the near bottom layers of the Bornholm deep but in the eastern Baltic the oxygen levels are close to the limiting value of 2 ml l^{-1}, sometimes with oxygen deficiency in intermediate layers. This situation is usually observed one to two years after major inflows (16 cases);

3) Stagnation years, when RV is only present in the Bornholm spawning ground. Also an oxygen-depleted bottom layer develops in the deeper central parts of the Gdansk and Gotland spawning areas. (21 cases, 16 of which observed after 1981).

The timing of the RV maximum within a year differs between the spawning grounds. In the Bornholm Basin the maximum RV was usually in February - March, in the south-eastern Baltic (Gdansk and southern Gotland) the maximum was mainly in May, but in the Central Gotland the maximum was most often in August.

Analysing the RV anomalies during 1952-2011 it can be seen that significant change has happened in 1981 when negative anomalies started to prevail in all spawning grounds (Fig.9). Obviously it is related to decrease of North Sea/Kattegat water inflow intensity (Matthäus and Naush, 2003). This suggests that cod reproduction in the Baltic substantially worsened after 1981. Exceptional situations are observed only after 1993 and 2003 inflows.

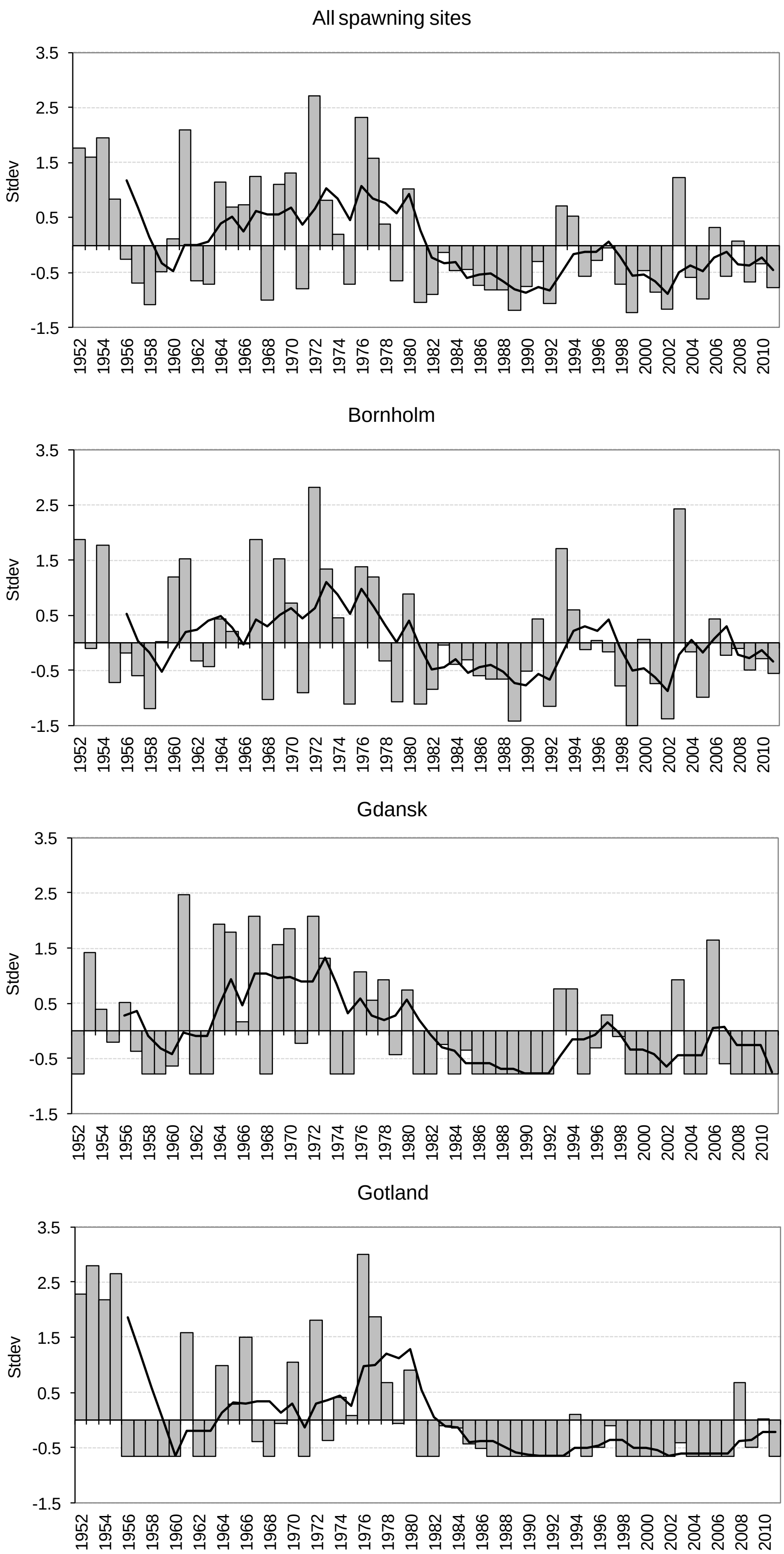

Figure 9. Anomalies of Eastern Baltic cod reproduction volume by principal spawning grounds. Stdev - standard deviation of the yearly RV estimate adjusted to cod spawning time during the whole observation period 1952-2011. Line shows 5 year moving average.

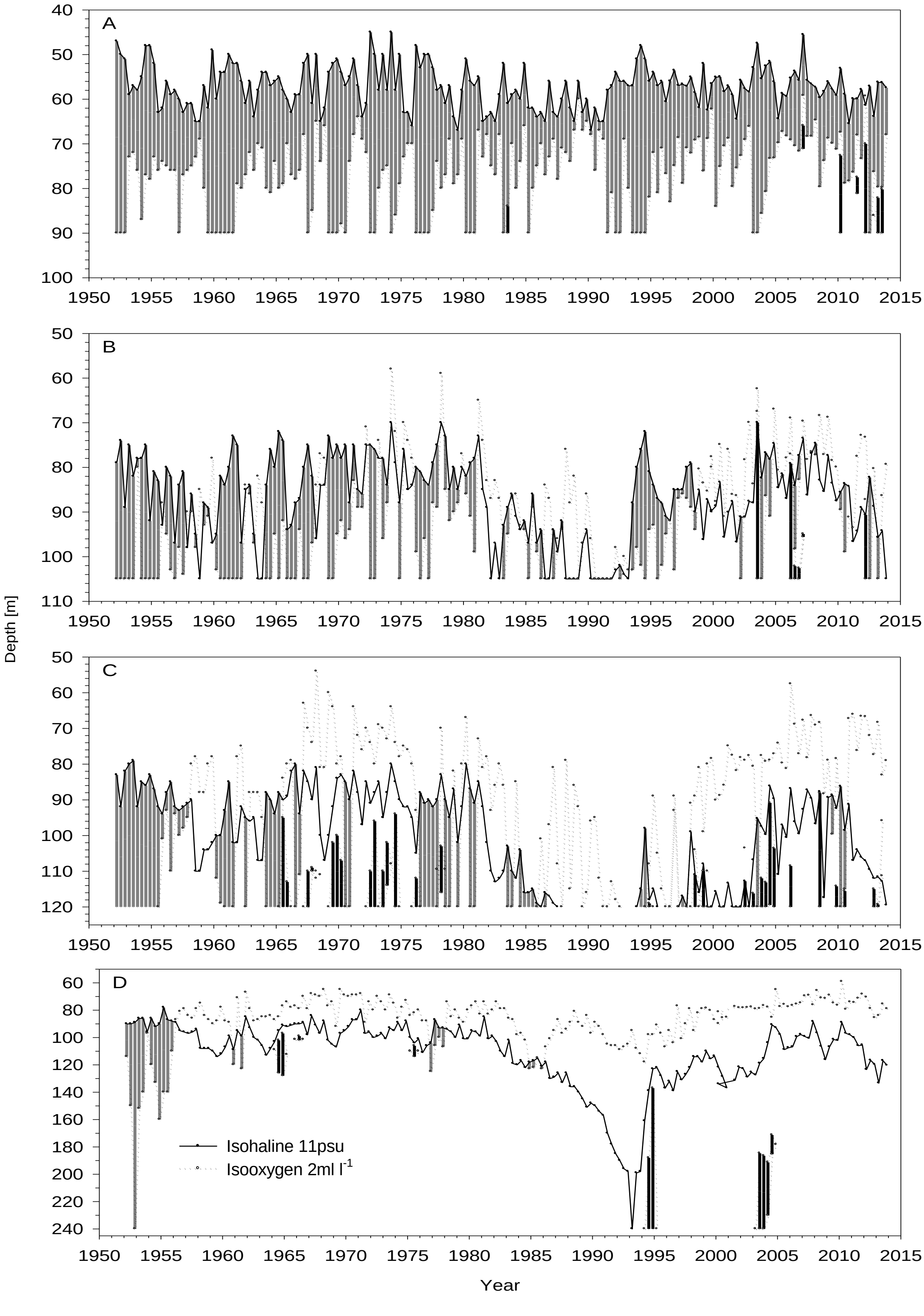

Figure 10. Vertical distribution of limiting factors for successful cod egg development in the principal spawning grounds of the Eastern Baltic cod. Grey bars indicate extent of the reproductive volume; black bars – reproduction volume below intermediate low oxygen content layer. A- Bornholm Deep, B – Gdansk Deep, C – Sothern Gotland Deep, D – Central Gotland Deep.

Inspection of vertical distribution of the depths of the isohaline 11 psu and isooxygen 2ml l^{-1} shows great variation from year to year and by principal spawning grounds (Fig.10). In the Bornholm Deep the 11psu isohaline fluctuates between 47-68 m without any trend. The 2.0ml l^{-1} isooxygen fluctuates more regularly between 65 m and the bottom (more than 90m) (Fig10). These fluctuations tend to be of opposite phase so that decrease in the 2.0 ml l^{-1} isooxygen depth is associated with increase of isohaline 11psu depth. The main determinants of the RV thickness are advection of Kattegat waters, and gradual decrease of oxygen content of the bottom layers in the years between inflows through oxygen consumption associated with bacterial degradation of organic matter in the bottom layers. Increase of the 11 psu isohaline depth is associated mainly with water column vertical mixing and river fresh water runoff. During the stagnation period from 1985 to 1990 the 2.0 ml l^{-1} isooxygen depth rose from the bottom (93 m) to about 60 m but the isohaline level remained relatively constant.

In the eastern Baltic cod spawning grounds (e.g. Central Gotland Basin) RV formation occurs in deeper water layers below 80 m. The post 1985 stagnation period was dominated by a decrease in salinity descending into the deep layers, so that the 11psu isohaline depth reached about 160 m by 1991 and totally disappeared from deep in second half of 1993. In previous stagnation periods only minor decrease in salinity occurred (during 1951-1980 the 11psu isohaline never went below 110 m) and the salinity regime was restored by each inflow. Increases in the 2.0 ml l^{-1} isooxygen depth are usually associated only with strong or very strong major inflows according to Matthäus and Franck classification (Matthäus and Franck, 1992). Increase in oxygen content observed in 1984-85 was apparently caused by vertical water convection.

3.3. Reproduction volume influence on cod egg survival

Egg survival dependence from RV analyses was available only for period 1954-1990 (Grauman, 1984; Plikshs et al., 1993). Egg abundance in samples after 1990 especially in the Gotland Basin was so small that estimation of survival index was not possible. It should be mentioned that analyses covers the period before the Eastern Baltic cod shift in spawning timing (Wieland et al, 2000).

There is a clear positive linear relationship between reproductive volume in May (cod peak spawning time) and the egg survival index calculated for the period April-August of the same year (Fig.11). It explains 44% of the variation (p=0.0001, F=27.57, df=36, R^2=0.44). RV larger then 300km^3 ensures the high survival index (above 5). This is observed in years when all spawning ground provide sufficient habitat for cod egg successful development. The abundant year-classes of 1954, 1964, 1972, 1976, 1977 and 1980 have higher indices because larger reproduction volume ensures higher survival at egg stage of development. However, RV in range of 100-200km3 has high annual survival index variation – from 1.5 till 9.1. Higher index was recorded in 1956, 1957, 1962, 1963, 1981, 1984 and 1985 when successful reproduction also was possible in eastern spawning grounds although the total RV was relatively small. These results confirm how important that all potential spawning sites of Baltic cod are involved in reproduction.

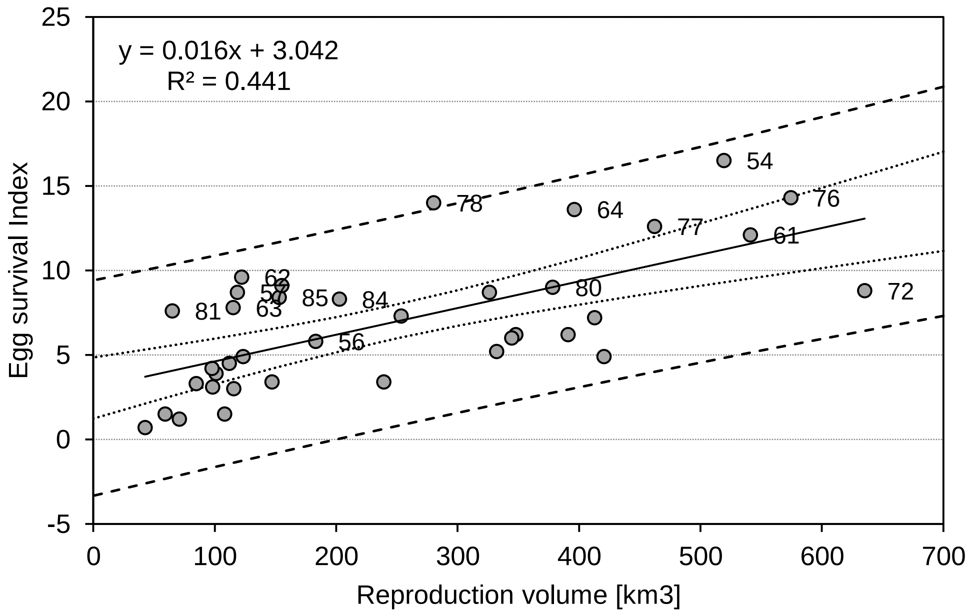

Figure 11. Egg survival (April-August) dependence from total reproduction volume of Eastern Baltic cod in peak spawning time in May; (·······) 95 % confidence limits, (**-----**) 95 % prediction limits. Individual labels indicate the year of the observation.

3.4. Reproduction volume relation to cod recruitment.

The relationship between cod recruit numbers at age 2 (ICES, 2013) and the RV of the respective spawning year was examined. The average RVs adjusted for cod spawning time were applied in this analysis (Fig. 12). The correlation is significant although lower than with egg survival index (p=0.0006, F=13.55, df=44, R^2 = 0.24). The most abundant cod year-classes (Kosior and Netzel, 1989; ICES, 2013) from stock assessment and research surveys were observed in 1972, 1976, 1977 and 1980 i.e. when maximum extension of the RV in the eastern spawning grounds occurred. Inspection of the relation indicates that in case of large RV year class strength is above average, but in case of small volume variation of recruitment is much higher and even abundant year-classes can be observed, as e.g. in years 1971, 1975, 1978, 1979 and 1981. It should be mentioned that these year-classes was formed one year before or after strong ones.

Analysis of residuals shows that there is a certain prevalence of positive residuals during regular inflow events till 1980 and negative afterwards, with exception of recent inflows in 1993 and 2003 (Fig.13). This indicates that we underestimated recruitments in earlier aeration years and overestimated recruitment in stagnation years. Moreover, there is a negative trend of residuals by spawning stock biomass revealing that in case of high stock abundance (> 300 thousand tons) estimation of recruits based on reproduction volume is underestimated (Fig.14).

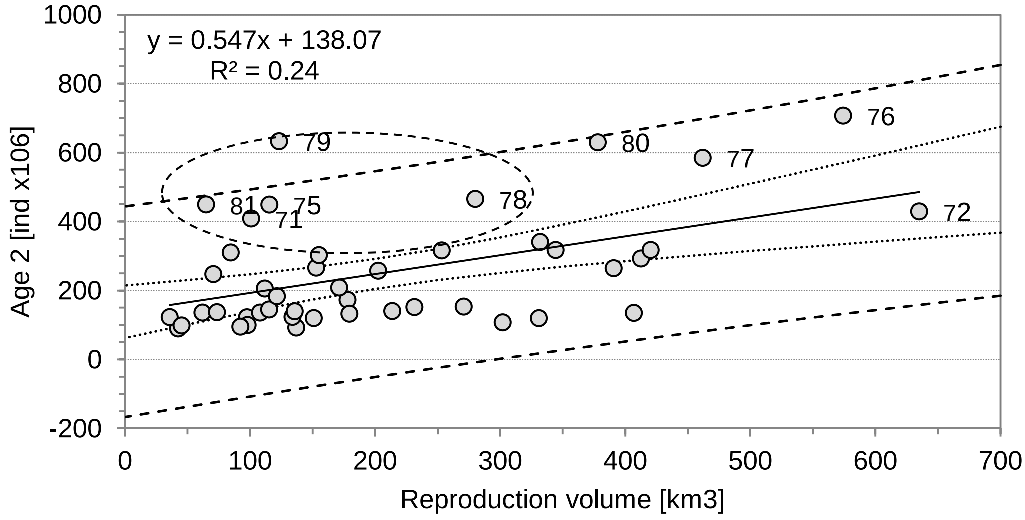

Figure 12. Dependence of Eastern Baltic cod recruitment at age 2 from Reproduction volume adjusted for spawning time; (┈┈)95 % confidence limits, (**-----**) 95 % prediction limits. Individual value labels indicate the year-class.

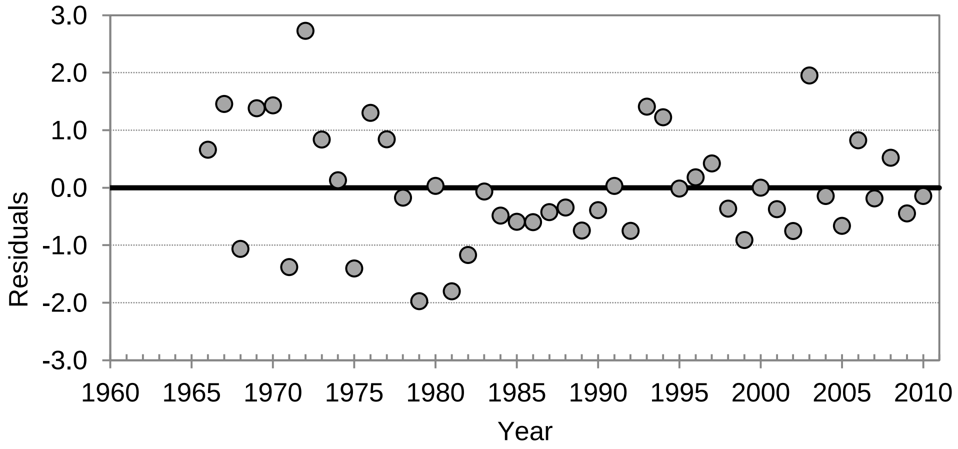

Figure 13. Residuals of recruit at age two dependency from RV by years.

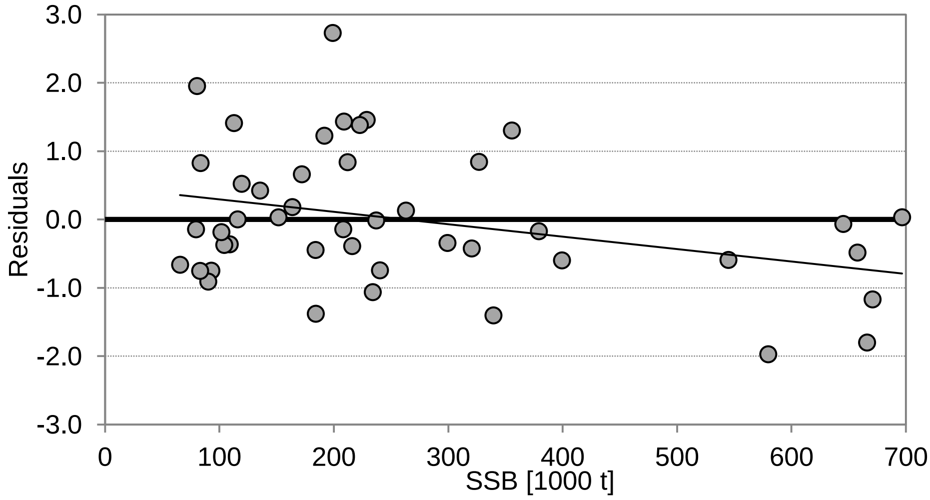

Figure 14. Residuals of recruit at age two dependency from RV by spawning stock biomass.

There is certain difference of importance of RV on cod stock –recruitment relationships by different Baltic subdivisions (**IV**). In total 25 different models were tested.

The only sensible statistical model for SD25 (Bornholm Basin) derived by the exploratory analyses is a multiple linear regression including potential egg production corrected for egg consumption ($p = 0.085$) and the oxygen content in the reproductive volume ($p = 0.062$) as independent variables. The model explained 31% of the variance in the larval abundance. The potential quantity of spawned eggs (predicted by its proxy, the SSB) as such does not play important role. For Eastern Baltic spawning grounds (SD26 and SD28), the larval abundance per unit of potential egg production was significantly related to the reproductive volumes (SD26 - $R^2 = 0.58$; SD 28 - $R^2 = 0.41$). Although these relationships show high variability in the survival to the larval stage, intermediate to high reproductive volumes obviously have an impact on survival until the larval stage. An anomalous situation was encountered in 1994, as no larvae were observed in either area, despite the existence of a fairly high reproductive volume due to major Baltic inflow.

3.5. Mechanism of reproduction volume formation in the Gotland Basin and its influence on recruitment

The formation of the RV in the Gotland Deep mainly is related to strong or major Baltic inflows. This formation is schematically presented in Figure 15. During periods of advection of saline and aerated water masses from the Kattegat into the Gotland Basin, salinity below the halocline increases while oxygen only increases in near bottom layers and decreases in intermediate layers. This is caused by the vertical displacement of less dense ‘old’ water masses. Such dynamical pattern results in formation of suitable conditions for egg survival, i.e. RV, in two distinct layers: the upper RV and the lower RV. Depending on the amount of the inflowing Kattegat water mass penetrating into the Gotland Basin and on its density, more or less expressed deviations from the presented pattern may occur - either in the particular areas or in the whole basin (**V**).

During the stagnation periods, the isooxygen 2ml l^{-1} usually is located above the isohaline 11 psu thus creating in traditional cod spawning depths the volume where successful cod egg development is impossible. This volume, we named ‘unsuitable reproduction habitat’ (UV), varies by years depending on the duration of stagnation period. Taking into account water mass heterogeneity it could be suggested that if the UV volume is smaller the possibility of cod eggs survival and production of viable larvae is higher. Such assumption also allowed us to construct continuous time series of quantitative parameters of environmental conditions for Gotland Basin where RV is observed only in several years.

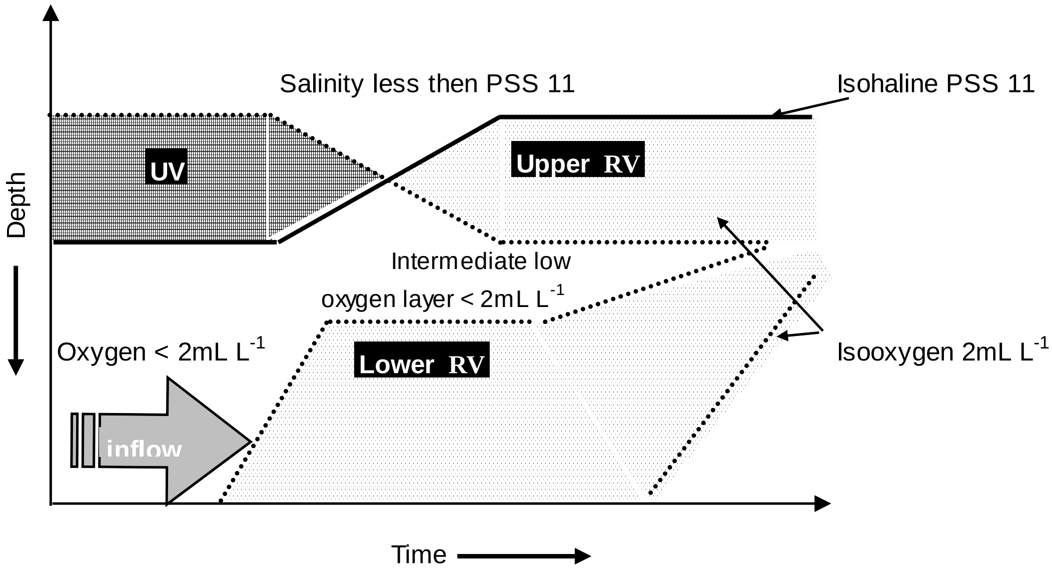

Figure 15. Schematic formation of the RV of cod in the Gotland Basin during inflow events; RV – reproduction volume; UV – unsuitable reproduction volume.

A historical overview of the RV dynamics as well as of UV volumes revealed different trends within different areas of the Gotland Basin (Fig. 16). In the Southern Gotland Basin RV volumes were observed more frequently and for longer time periods. Usually it extended from the 90 m depths down to the bottom (120 m). This spatial pattern maintained until the mid of the 1980s. The frequency of the occurrence of the RV decreased from the southern basin towards the north where it was observed registered very seldom. It can be clearly seen that periods of RV existence in the southern Gotland Basin coincide with Kattegat water advection into the Baltic (Matthäus and Franck, 1992, Matthäus and Nausch, 2003). Only strong or major inflows (such as in 1964, 1970, 1976, 1977 and 1993) were able to significantly improve the hydrological situation by providing favourable conditions for cod spawning in the Central Gotland Basin. In the Southern Gotland Basin UV develops mainly during stagnation periods, while in the Central Gotland Basin it was observed almost during all the years. Usually UVs were recorded in depths from 65 to 110 m but the exceptionally long stagnation periods after the mid of the 80-ies led to an extension of UV zones from 90 m to the deepest part of the basins in the early 90-ies.

The recent major inflow of 1993 (Matthäus and Lass, 1995) reached the Gotland Basin in 1994 and significantly influenced the hydrological regime there. In the Central Gotland Basin an increased reproduction volume was generated from approximately 130 m depth down to the bottom (Fig.16). Similar situation was observed only in the beginning of 1950'ies. In respect of the RV concept, it is very important to understand if this potential volume could be important for successful egg development, i.e. in which layers the cod eggs do really float. Available information from the Gdansk and Gotland Basins (Makarchouk and Hinrichsen, 1998) shows that the highest abundances of cod eggs were observed in density ranges from 1008.0 to 1009.9 kg/m^3. Density profiles reveal that only in the Southern Gotland Basin vertical egg distribution coincides with sufficient salinity and oxygen conditions while the potential RV occurring below 130 m should be excluded from later stock recruitment relationship inspection because egg neutral buoyancy not allow them to reach these depths.

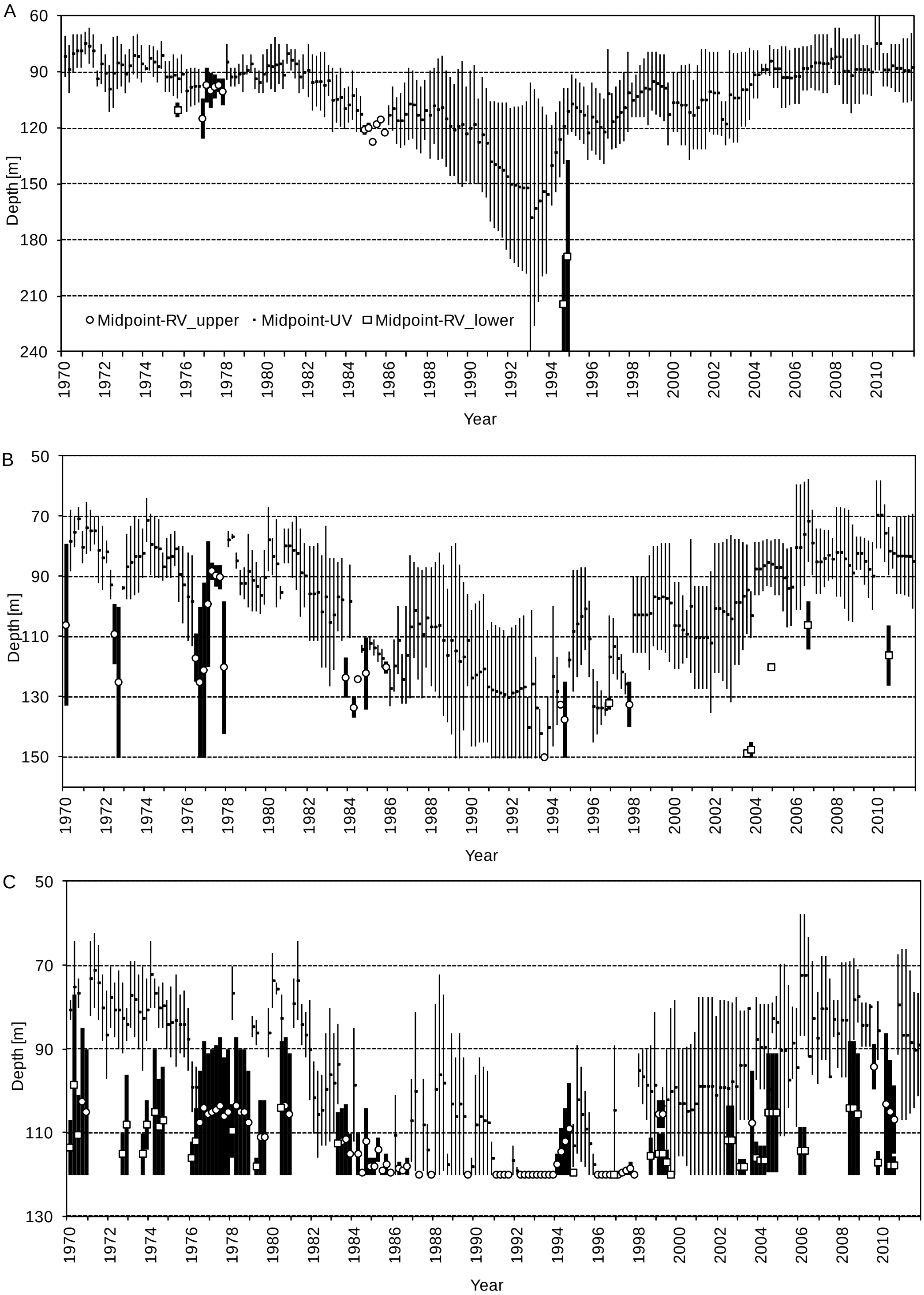

Figure 16. Vertical distribution of unsuitable habitat and reproduction volumes in the Gotland basin (February-August): A - Central Gotland Basin, station BY-15A;
B - Central Gotland Basin - station 43; C - Southern Gotland basin - station BY9A.
Bars: ——— UV ▬▬▬ RV

The estimated recruitment abundance (age 1) in the Gotland Basin was highly variable in late 1970s and during 2002-2007 (Fig.17). Higher abundance and variations were recorded in years when conditions in the Southern Gotland basin were appropriate for successful egg development. The environmental factors identified and described above, were incorporated into stock recruitment relationship analyses. The following factors were included in the analyses: RV (1) and UV (2) as average of May and August, as well as oxygen content at salinity of 11 psu in the Southern Gotland (4) and stock abundance index from research surveys in March-April (5). The relation and factor significance was explored by multiple linear regression analysis. Stock abundance in all trial runs appeared to be insignificant and therefore was excluded from the model. In statistical model for the whole time series (1975-2011) in the Central Gotland Basin only RV in May-August proved to be a significant factor (*p* value of model 0.031). In the Southern Gotland Basin RV and UV average of May-August has significance (*p* value of model 0.028). Oxygen saturation at 11psu is significant only for the period 1986-2011 in the Southern Gotland Basin

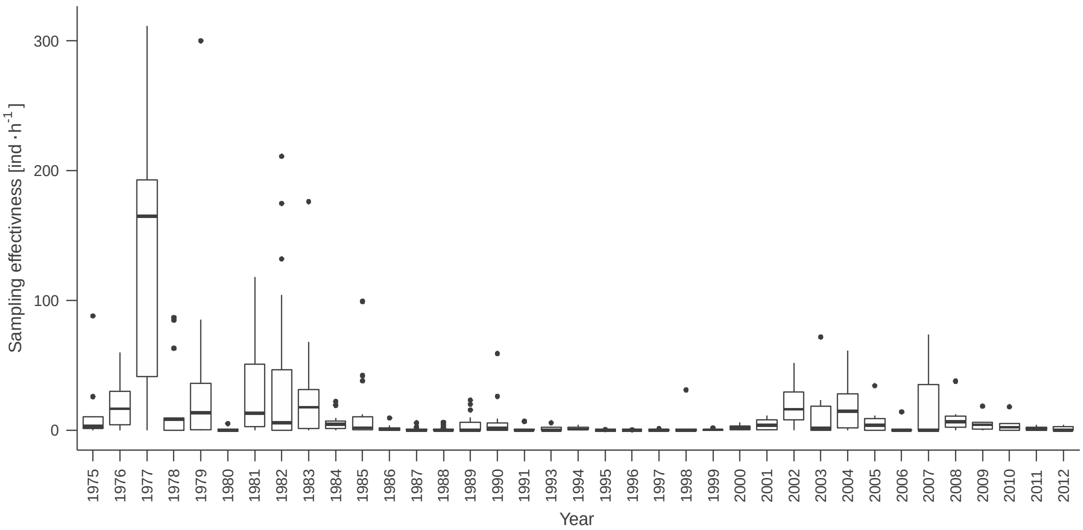

Figure 17. Average number of age group1cod from research surveys in the Gotland Basin.

3.6. Incorporation of Reproduction volume as an environmental variable in Ricker stock –recruitment model

The size of the reproduction volume fluctuated strongly throughout the observation period. However, before 1980 it was on average much larger than thereafter, and it was developing in all principal Eastern Baltic spawning sites within intervals of no more than 1-2 years. After 1980 formation of RV in Eastern Baltic has become very seldom because of decrease of water exchange with North Sea/Kattegat. At the onset of this period around 80% of cod population was distributed in the Gdansk and Gotland areas (Sparholt et all 1991; Sparholt and Tomkiewich, 1998; Eero, 2000). In the following years the cod population in the Eastern areas strongly decreased while sufficient environmental conditions for their successful reproduction were observed only in the Southern Baltic.

The visual inspection of S/R relationship indicates two different levels with breaking point around 1981 (**I**). First period 1966-1981 is characterized by regular formation of RV in all spawning grounds and regular North Sea/Kattegat water inflows in the Baltic with interruptions not exceeding 1-2 years. In the second period the stagnation processes prevailed, cod was mainly distributed in the Southern Baltic and successful reproduction could occur only in the Bornholm spawning ground. This separation also can be adjusted by regime shift in Eastern Baltic cod reproduction (see Chapter 3.2). Therefore the S/R curves for these two periods were examined separately, corresponding to the shift in reproduction volume level (Fig.18). The applied regressions explained for whole time series explains 28% of variation

(Table 2). Model fit improves if we separating time series in two periods: 1966-1981 and 1982-2011. The new models explained 40 and 56% of variance for the time series, respectively. The estimated parameter and model diagnostics are consistent with previous analyses for period 1966-1994 (**I**).

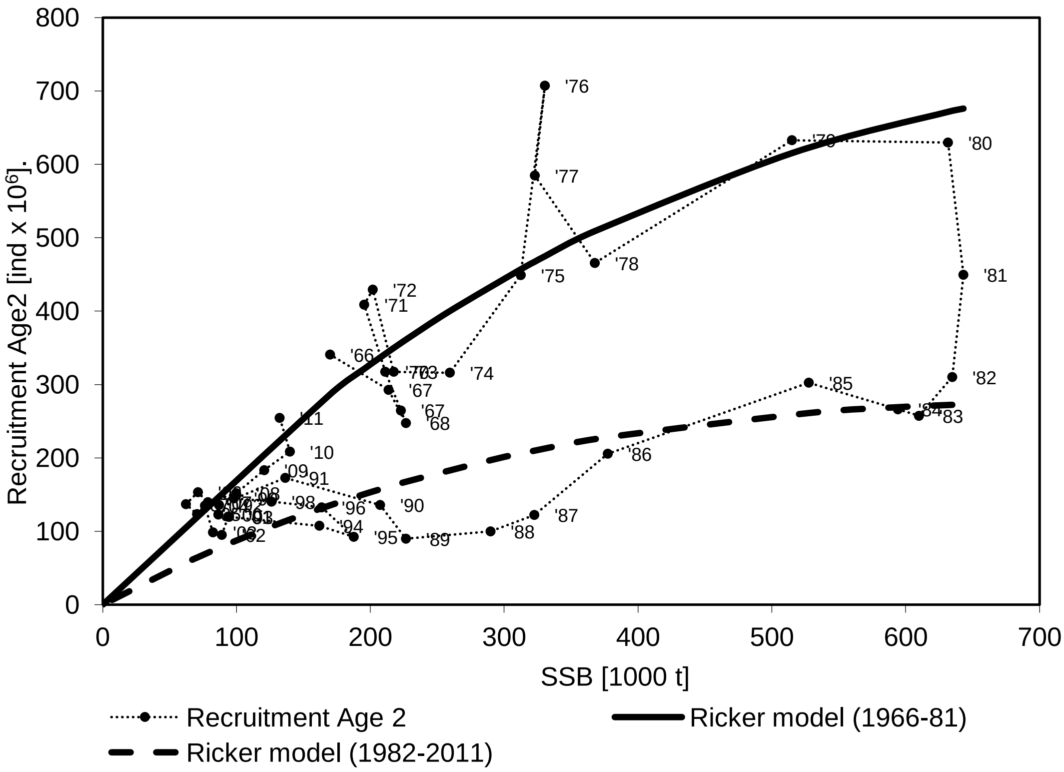

Figure 18. Recruitment of central Baltic cod at age 2 at different levels of parent stock size and fitted to the Ricker curve.

Table 2

Parameters estimates and diagnostics for the fitted model

Model	Period	ln(α)	β	*c*	R^2	*SE*	*F*	*df*	*p*
RM_1	1966-2011	0.510	-0.00169	na	0.281	0.457	18.61	46	<0.0001
RM_2	1966-1981	0.771	-0.00135	na	0.40	0.24	10.85	15	<0.005
RM_3	1982-2011	0.495	-0.00259	na	0.564	0.39	38.48	29	<0.0001
RME_1	1966-2011	0.215	-0.00171	0.00145	0.425	0.409	17.66	46	<0.0001
RME_2	1966-1981	0.498	-0.00113	0.000660	0.500	0.21	8.50	15	<0.004
RME_3	1982-2011	0.375	-0.00254	0.000733	0.560	0.39	19.50	29	<0.0001

RM – Ricker model; RME – Ricker model with environmental variable

An additional effort was made to incorporate RV as a variable into the Ricker stock-recruitment model (Haddon, 2001). The choice of a Ricker function in case of Baltic cod is justified by an assumption that recruitment actually should decline at large spawning stock biomass e.g. due to cannibalism or density dependent effects. The simulations performed using the modified Ricker function show significant increase of correspondence between the estimated and predicted recruitment level. . While the unmodified Ricker stock-recruitment model explains only 28% of the variation observed in the whole time series, including RV as factor improves explanation of variation to 42% for whole time series and even to 56 and 59% for the periods of 1966-1981 and 1982-2011 correspondingly (Fig. 19; Table 2). Besides Ricker function with environmental variable seems better capture the extreme generations, for example abundant ones in 1972, 1976, 1977 and 1980. The ANOVA test reveals that parameters estimated by Ricker model with environmental variable for whole time series and first period (1966-1981) is significantly better when classical Ricker model ($p<0.01$ and $p<0.1$ correspondingly) but for second period – insignificant. For latest period this is probably because there are no contrasting recruitment and SSB values.

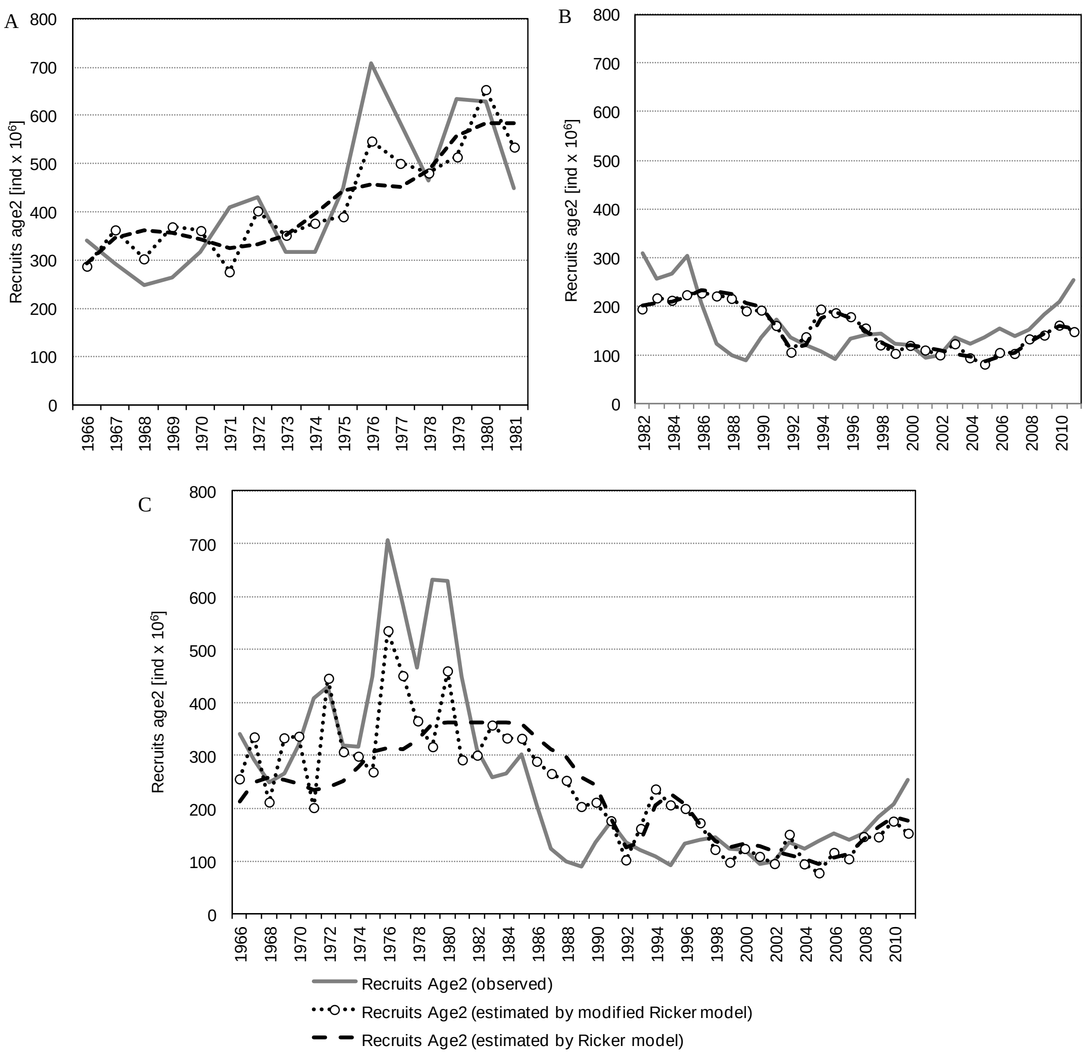

Figure 19. Observed (ICES, 2013) and estimated Eastern Baltic cod recruitment at age 2 by original and modified Ricker stock-recruitment relationships:
A - 1966-1981; B - 1982-2011; C - whole time series (1966-2011).

3.7. Cod cannibalism potential influence on cod recruitment abundance

In the Central Baltic during 1963–1990 cases of cod cannibalism were recorded in 300 stomachs (out of 69 346 examined) only (**III**). Conspecific food constituted 2.8% of the stomach content weight in stomachs where cod was as a prey. The mean frequency of occurrence of cod in stomachs was 0.93% and 1.05% in Subdivisions 28 and 26, respectively. Cannibalism was mainly observed in large cod (>35 cm) and was rare in the smaller size range (<35 cm). Both large and small cod preyed mainly on 0 and 1 age group cod (5–15 cm).

In Subdivision 28, cannibalism was more intense in coastal waters at depths of 40–80 m. In Subdivision 26, in stomachs cod was mainly found offshore at depths>80m (Fig.20). Cannibalism was mainly recorded in a few locations that correspond to established centres of juvenile cod distribution, i.e. where catch per unit of effort of 100–200 young cod/h^{-1} has been recorded. In addition, in certain localities of Subdivision 25 (Bornholm Basin), relatively high rates of cannibalism were observed during 1963–1976. However, there are no juvenile fish distribution from this area available.

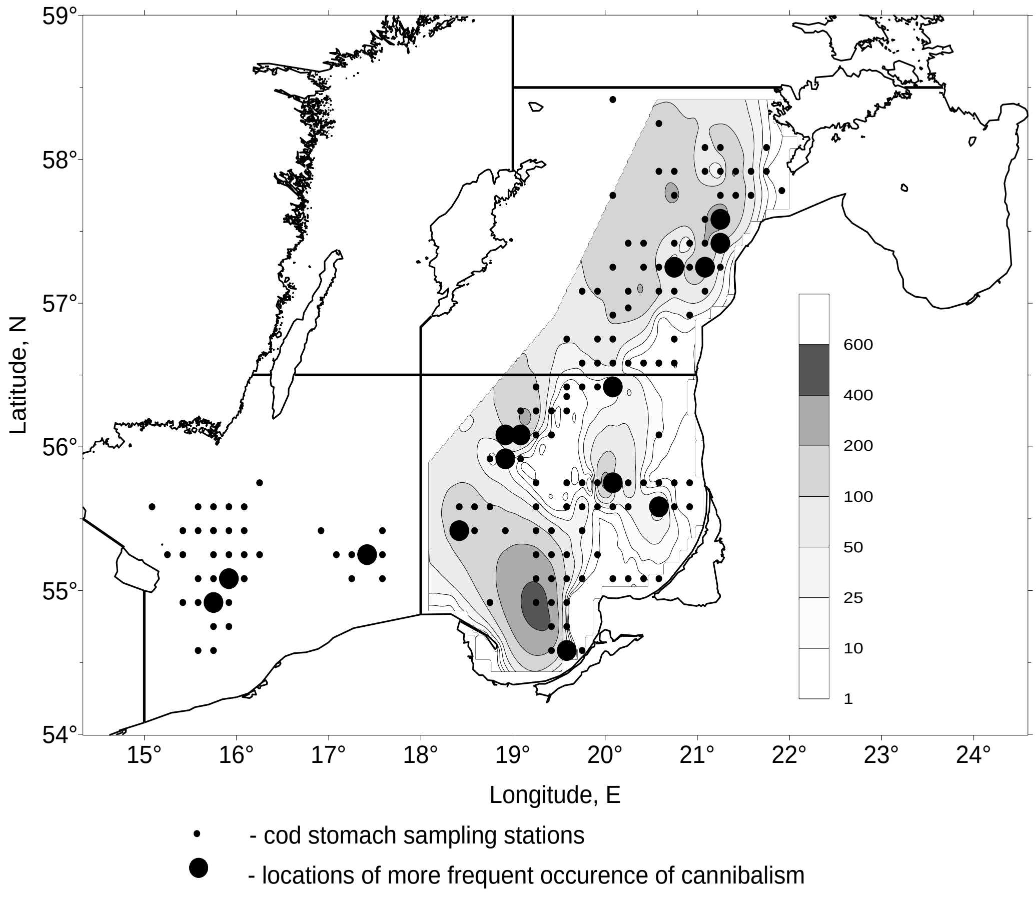

Figure 20. Cod stomach sampling stations (small dots) and stations where cannibalism was frequently observed (large dots) are shown in relation to the average spatial distribution of age-1 cod (catch per unit of effort [N h^{-1}], grey scale) during research surveys in March–April, 1977–1981.

As another measure of the frequency of cannibalism, we estimated the proportion of trawl catches in which cannibalism was observed and related this frequency to the catches of small cod (age-1) and large cod. In this analysis, data from all years within each of the three study periods were merged. During 1969–1975, cannibalism was observed in 15% of the sampled trawl catches, during 1976–1979 in 30%, and during 1980–1990 in 10%. The corresponding mean numbers of adult cod in these hauls were 83, 90, and 179 and the numbers of age-1 cod 51, 151, and 40, respectively. These figures suggest that a higher ratio of cannibalism is associated with high abundance of juveniles. Regression analysis of frequency of occurrence of cannibalism against age-1 cod abundance indices from research surveys indicates a significant positive trend (Fig. 21).

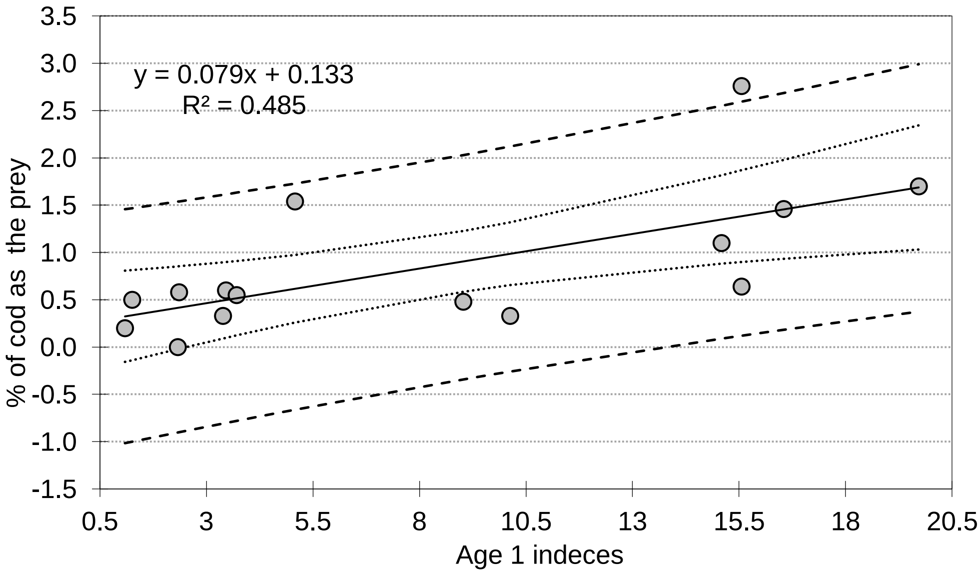

Figure.21. Relationship between frequency of occurrence of cod as prey in cod stomachs and the index of abundance of age-1 cod based on research vessel surveys in the Central Baltic, 1975–1990 (R^2=0.48, F=13.2, p< 0.003); (·······) 95 % confidence limits, (**-----**) 95 % prediction limits.

4. DISCUSSION

4.1. Reproduction volume importance for the dynamics of the Eastern cod stock

Recruitment variability of marine fish populations is enormous and is considered to depend on abiotic as well as biotic factors (Rothscshild, 1986). This is fully applicable for Eastern Baltic cod. Several authors have shown that variation in cod abundance is related to advection of the Kattegat and the North Sea waters to the Baltic Sea (Kändler, 1944, Kosior and Netzel, 1989). Without advection of the Kattegat waters it would not be possible for a permanent cod stock to survive in the Baltic Sea. The causes of the inflows are not totally clear but important determinants are global atmospheric circulation, westerly wind fields and sea level fluctuations in the Baltic Sea (Matthäus and Franck, 1992, Matthäus, 1993, Dickson et al., 1994).

The Baltic Sea is characterised by its spatial heterogeneity and the critical environmental factors determining reproductive success can differ between spawning grounds. In the Bornholm deep the occurrence of RV is mainly governed by the degree of depletion of oxygen in near-bottom layers. In the Gotland deep RV reduction or disappearance results from the decrease in salinity of the bottom water layers. Although, in the late 1980s major spawning concentrations of cod were observed in the Gotland area, reproductive success was negligible and till 2007 stock has declined to historically very low levels (ICES 2013).

Previous analysis of cod year-class dependence from environmental conditions showed that in the Bornholm deep oxygen content was the most important determinant (Berner et al., 1989, Koster et all 2001;Koster et al 2003) while in the Gotland area it was suggested that salinity is the most important parameter that limits successful reproduction (Lablaika et al., 1989). The hydrological changes in the Gotland Basin usually take place 6-9 months after the inflow was registered in the Bornholm Basin, respectively the impact of a winter inflow becomes apparent in the Gotland Basin during May–August. Oxygen is mainly renewed by inflows and is depleted due to biochemical processes (Kaleis, 1990).

Assuming RV hypothesis as a basic element that determines survival of spawned cod eggs our calculations and analyses of RV show that it is possible to quantify the volume of water in which cod eggs can successfully develop in the Baltic Sea. These volume estimates should be considered as approximations because they assume 100% and 0% egg survival at oxygen concentrations above and below 2 ml l^{-1}, respectively. In reality, laboratory experiments show that cod egg survival increases with increasing oxygen concentration in the range from 2 to 5 ml l^{-1}, and varies independently of oxygen concentration in the range 5 to 9 ml l^{-1} (Wieland et al. 1994). Hence, our estimates probably overestimate the true volumes which ensure cod egg survival in nature. Gobally there is no any other marine area where a similar reproduction habitat was defined and quantified. Obviously it is certain peculiarity of brackish Baltic Sea where marine species like cod has adopted and are reproducing. In other seas gadoid fish population year-class strength and population dynamics mainly is associated with temperature, atmospheric circulation or zooplankton abundance (Dickson and Brander, 1993; Dickson et al., 1974; Cushing, 1984; Ottersen et al., 1994).

Our analyses indicate that a carefully chosen monitoring site can represent conditions throughout an entire basin, at least for the purpose of estimating reproductive volumes. The locations of individual stations which produced the best correlation with the whole-grid volume estimates were those located in the central deep part of each basin.

Taking into account that the numerous factors that can influence cod recruitment until age 2 including cannibalism (Neuenfeldt and Köster, 2000), predation by sprat and herring on cod eggs (Köster and Möllmann, 2000), possible mortality caused by larvae starvation (Hinrichsen et al., 2002), it seems remarkable that a significant relationship was found between egg survival, recruits at age 2 and RV. This suggests that cod year class strength in the Baltic is determined to a large extent by events in the early stages of life.

The problem still remains as to what extent RV determines the year-class strength. A retrospective analysis indicates some important trends. Abundant generations in the Baltic were observed in 1954, 1964, 1972, 1976, 1977 and 1980 – the years in which RV was observed on all spawning grounds and cod reproduction was successful everywhere. During early the 1980'ies cod extended it distribution area and in high quantities entered the northern areas and Gulf of Riga significantly influencing the trophic interactions there (Casini et al., 2013). In some years however the analyses indicated a high abundance of recruits produced despite of a small RV: 1975, 1979 and 1981 (ICES., 2013). These anomalies occurred just before or after years of high RV; it is possible that misinterpretation of otolith age reading resulted in allocation of the recruits to the wrong year class (Reeves,.2003).

The largest RV was recorded at the beginning of the 1950s after the strongest inflow to the Baltic in this century (Matthäus and Franck, 1992). Although subsequent cod year classes were large with evidence of very high egg survival rates (Grauman, 1973) and an increase in catch per unit effort (CPUE) by the Baltic fishing fleets was recorded (Lablaika et al., 1991), the abundances of cod were significantly lower than in 1976 and 1977 (Eero, 2007). In the 1950s the parent spawning stock biomass was relatively low whereas in 1976 spawning was based on the abundant generation of 1972. Afurther factors are nutrient status and feeding conditions in the Baltic Sea. During the 1980s high abundances of zooplankton were observed (Kostrickina et al., 1988; Kornilovs et al., 2001; Möllmann et al., 2008) which coincided with the increase in nutrient concentration (HELCOM, 1990). Bagge et al. (1993) therefore concluded that nutrition is of major importance in production of extremely abundant generations.

Analyses of RV anomalies in whole Baltic and separately by principal cod spawning grounds suggest that regime change occurred around 1981. Baltic integrated assessment that is based on principal component analyses and take into account 52 environmental parameters (Möllman et all., 2009) identifys regime shift in the central Baltic around 1986. Obviously, Eastern Baltic cod reacted much earlier to the ecosystem changes that in great extent were associated with Baltic - North Sea water exchange. Thus it can be stated that cod recruitment and corresponding stock abundance decreased due to exclusion of the eastern spawning grounds from successful reproduction.

4.2. Reproduction volume and possible Eastern Baltic cod stock recovery

The concept that RV determines recruitment implies that there must always be a surplus of spawning adults available to fill the available reproduction habitat. Although the stock-recruitment relationships of gadoid fishes show abundant generations (even a recovery) in the years of low stock and *vice versa* (Laevastu, 1993), the role of the spawning stock must not be neglected. How effectively cod can utilise the potential RV will be dependent at first on spawning stock biomass (SSB) and secondly on the structure of that stock. It is well known that older fishes start spawning earlier, while younger age groups mature and spawn later in the season (Lishev and Lablaika, 1989, Kjesbu, 1994). World fisheries have numerous examples when even a complete fisheries moratorium for decades has not led to the stock recovery (Mayers et al., 1997, Martell and Walters, 2008). It is believed that stock fails to recover because the cod habitat is occupied by other species, not only predators but also pelagic species like herring that had drastic increase in abundance (McQuin, et al., 2009). In case of the Eastern Baltic cod, despite of the lack of major inflow events, the stock revealed an increasing trend in the recent 5 years (ICES, 2013).

The increase in stock size in such a short time obviously is related to significant reduction of fishing mortality. The main drivers of this are considered the introduction of cod multi-annual management plan by EU and several technical measures like increase of minimal landing size and the limitation of number of fishing days as well as significant elimination of illegal fishery (European Commission (EC), 2007; Eero et al, 2011). The recent recovery of the Eastern Baltic cod contrasts with other cod stocks, for example in the North-west Atlantic Canadian waters where reduction in fishing mortality has not led to stock recovery. We consider that Baltic ecosystem is much more 'simpler' with one main predator the habitat of which has not been occupied by any other predator species. Other top-predators in the Baltic Sea are seals and salmon. Although the seal abundance recently increase, seal predation on cod to have much lower impact on cod recovery compared to effects of exploitation and oceanographic regime change (MacKenzie et al., 2011). There is no recorded salmon predation on cod and due to relatively small salmon abundance, hence the possible predation and competition are not considered to have a major impact on cod stock (Hansson et al., 2001).

Oceanographic observations in the Gotland Basin in the recent years reveal that there is an increase of salinity and decrease of oxygen saturation in the intermediate water layers that allows the formation of small RV (Berzins, 2011). It is considered that these processes can be interaction between increase of biological productivity of the Baltic Sea (1), rise of temperature of inflowing Kattegat waters in the Baltic (2) and increase of speed of water mass transport to eastern Basins (3). As a result, the RV in the Gotland Basin is formed in the absence of major inflows.

4.3. Stock recruitment relationship and influence of reproduction volume on it

The relationship between spawning stock and recruitment is essential for providing predictions for the stock development and, consequently, for the fisheries management. Since the early works by Hjort (1914) recruitment variability has been in the focus of fisheries scientists' interests.

The choice of a Ricker model in our analyses is still discussible. Usually Ricker model is more appropriate when the case of the density dependence is cannibalism of the young by adults, or an increase in the time it takes for the young to grow through a vulnerable size range, or when there is a time-lag in the response of a predator or parasite to fish being attacked (Wooton, 1994) e.g. when there is clear evidence that recruitment actually declines in presence of large spawning stock biomass. However, in our case this is not well seen. An alternative approach is to use the classical Beverton-Holt stock recruitment relationship, which assumes that recruitment does not decline at high SSB levels. The Beveron-Holt curve is more appropriate if there is a maximum abundance imposed by food availability or space. Nevertheless we chose to apply the Ricker stock recruitment relationship that has been evaluated as a more appropriate and traditionally used for *Gadidae* fishes (Cushing and Harris, 1973; Rotshield, 1986).

Due to the variable environment of the Baltic Sea it seems that recruitment is linearly related to reproduction volume. Additionally it is confirmed by the fact that the stock – recruitment curve is divided into two distinct periods: 1966 – 1981 and 1982 -2011. Summing up these findings, there is also clear evidence that Eastern Baltic cod stock's recruitment benefits from increasing RV. However, the gradual increase in recruitment observed during the recent five years is not well explained by RV. The main reproduction area still remains in the Bornholm Basin and small improvement is observed also in the Southern Gotland. Evidently other factors may have also been rather important. It can be also proposed that there have been even 3 different regime periods – the last one taking place in 1989-2011 (ICES 2013). Choice of any time period based on spawning regime or climate change shifts would suggest changes in fishery management measures that ensure maximum sustainable yield and precautionary approach reference points (Koester et al. 2009).

There is a number of stocks for which environmental variables are already incorporated in the stock – recruitment relationships, e.g. Atlantic cod (Planque and Fredou, 1999), herring from the Strait of Georgia, British Columbia (Stocker et al., 1985), hake (Chen and Ware, 1999) and several others. Also for the Eastern Baltic cod the inclusion of RV into Ricker's stock – recruitment relationship improves model fit. However, application of the stock – recruitment relationship for long-term stock development simulations remains a challenge. So far, the prediction of RV development in the Baltic Sea has not been successful because its formation and volume depends not only from amount and nature of inflowing North Sea/Kattegat waters but seemingly also of other less explicit factors. Such factors could be the hypoxia (oxygen concentration <2 mg L^{-1}) in the Baltic Sea deep water layers, eutrophication and freshwater runoff. The area of hypoxia expanded in Bornholm and Gotland Basins from 5 000 km^2 to over 60 000 km^2 over the past 115 years. The anthropogenic nutrient discharges are the primary driving factor creating widespread hypoxic conditions (Carstensen, 2014). The nutrient loads have been increasing from the 1950s until peak value around 1980 followed by decrease up to present. The decrease is mainly due to a significant reduction in coastal point sources due to sewage treatment, while river loads have dropped by less than 10% (Gustafsson et al., 2012). This in combination with increasing temperature could prevent oxygen condition recovery in the Baltic Sea during recent decades. Additionally these processes are linked to river runoff that depends from wet and dry period alteration.

4.4. Eastern Baltic cod cannibalism as a population regulatory mechanism

Cannibalism is a feature of animals which has both the importance for its potential regulatory effect on population abundance and for its overall contribution to natural mortality (Smith and Reay, 1991). Ricker (1954), in his classic analysis of stock and recruitment, was the first to consider the likely importance of cannibalism in density-dependent population regulation that was expressed by his stock – recruitment curve. Functionally cannibalism appears as a very effective competitive strategy, increasing an individual's contribution of genes in the next generation through improved survival and reproductive success, while decreasing that of others (Smith and Reay, 1991). Consequently, if cannibalism is a significant factor affecting stock dynamics, it should be included in stock assessment. Cannibalism of the Eastern Baltic cod is taken into account in the Multispecies assessment where cod is represented also as a prey object.

The peak in cod cannibalism occurred in 1977–1978. After the appearance of extremely abundant year classes in the late 1970s, the population expanded. Cod distribution during that period was mainly regulated by population density and food availability. Competition for food increased in the areas where traditionally the main concentrations of cod were observed. Cod from the Central Baltic migrated to the Gulf of Riga, and northwards to the Gulf of Finland and the Bothnian Sea (Ojaveer et al., 1985; Aro, 1989). From the late 1980s the abundance of both juvenile and adult cod in the Baltic was reduced. Adult cod returned to their pelagic habitat, while young cod were distributed in the coastal regions of the Central Baltic. Cannibalism became very low because of low spatial overlap. Cod cannibalism in the Baltic appears to be controlled mainly by the abundance of juveniles and by the overlap of spatial distribution between juveniles and adults. The hypothesis that cannibalism increases in the years of high spawning stock biomass is not supported by the available data. In general the influence of cannibalism on recruitment success in the Central Baltic is negligible and cod stock dynamics in the area are mainly determined by the combined effects of variable oceanographic conditions and intensive fishing.

This conclusion contradicts the results of Multispecies stock assessment which estimated O-group cod removals during late the 1970s and the early 1980s of 32-60% from initial stock size. For age group 1 cannibalism accounted for 14-31% of the initial stock size (Neuenfeldt and Köster, 2000). After the mid-1980s estimated juvenile cod removals have decreased below 10% level. The possible explanation of the mentioned differences can be related to the very strong linear relationship between the cod stock abundance and consumed cod abundance (R^2=98%) assumed in multispecies stock assessment model and the average food suitability coefficient that is used for entire time period. This implies constant spatial distribution of predator and prey as well as permanent probability that the predator will catch the prey once encountered (Larsen and Gislason, 1992; Neuenfeldt and Köster, 2000).

In order to avoid this bias in the multispecies stock assessment, obviously it is necessary to estimate the magnitude of overlap between adult and juvenile cod. As shown by the survey data, the distribution of cod varies by years (Aro, 2000). Williamson's overlap index calculated from trawl survey data and estimated by years and by sub-divisions (Williamson, 1993) appears a good measure of such an overlap..

5. Conclusions

The reproduction volume is the primary and easily obtainable parameter for prediction of the success of reproduction and recruitment of the Baltic cod. Analyses of reproduction volume anomalies in the whole Baltic Sea and separately by principal cod spawning grounds suggest that the change of cod reproduction regime has occurred in 1981 when the water exchange between the Baltic Sea and the North sea/Kattegat significantly decreased.

In view of the numerous factors like cannibalism, predation of cod eggs by sprat and herring, possible mortality caused by larvae starvation and changes in the stock structure that can influence cod recruitment, it seems remarkable that a significant relationship was found between egg survival and abundance at age 2 and the reproduction volume. This suggests that cod year class strength in the Baltic is determined to a large extent by events in the early stages of life.

In the Bornholm deep the reproduction volume is mainly governed by the degree of oxygen depletion in the near-bottom layers while in the Gotland deep reduction or disappearance of reproduction volume depends of decrease in water salinity.

Abundant year classes of cod in the Baltic Sea can only be observed when the conditions for embryonic development are suitable in all principal spawning areas of cod in the Baltic.

A break into two separate periods of Ricker stock - recruitment relationship for the Eastern Baltic cod becomes understandable when the strong change in the level and spatial distribution of reproduction volume is taken into account. Moreover, our findings suggest that Baltic cod stock-recruitment relationship can be significantly improved by taking into account the environmental variables.

Hypothesis of reproduction volume relation to Eastern Baltic recruitment abundance that at first was tested in 1993 is still valid presently when stock abundance and oceanographic data sets are updated by more when 20 year observation.

Cod cannibalism in the eastern Baltic is dependent from juvenile cod abundance and distribution. The highest level of cannibalism is observed after appearance of abundant year-classes when juvenile cod extends its distribution area and probability of distribution overlap between juvenile and adult cod increases.

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7. References

Aro, E., 1989. A review of fish migration patterns in the Baltic. Rapp. P-v. Réun. Cons. Int. Expl. Mer., 190: 72–96.

Aro, E., 2000. The spatial and temporal distribution pattern of cod (Gadus morhua callarias L.) in the Baltic Sea and their dependence on environment variability – Implementations for Fishery management. Academic Dissertation, Helsinki University and Finnish Game and Fisheries Research Institute. Helsinki, Finland, 75p.

Bagge, O. and Steffensen, E., 1989. Stock identification of demersal fish in the Baltic. Rapp. P.-v. Réun. Cons. Int. Explor. Mer, 190: 3-16.

Bagge, O. and Thurow, F., 1994. The Baltic cod stock: fluctuations and possible causes. ICES Mar. Sci, Symp., 198: 254-267.

Bagge, O., Bay, J. and Steffensen, E., 1993. Fluctuations in Abundance of the Baltic Cod (Gadus morhua) Stock in Relation to Changes in the Environment and the Fishery. NAFO Sci. Coun. Studies, 18: 35-42.

Berner, M. and Vaske, B., 1985. Morphometric and meristic characters of cod stocks in the Baltic Sea. ICES C.M. 1985/J:11, 13 p.

Berner, M., Müller H. and Nehring D., 1989. The influence of environmental parameters on the recruitment of cod stock to the East and West of Bornholm described by regression equations. Rapp. P.-v. Réun. Cons. int. Explor. Mer, 190: 142-146.

Berzins, V., 2011. Dynamic of salinity and oxygen concentrations in the intermediate layers of central part of Gotland basin during recent 50 years. 69th scientific conference of Latvian University: 10-13 (in Latvian).

Bretherton, F.P., Davis R E, and Fandry C.B., 1976. A technique for objective analysis and design of oceanographic experiments applied to MODE-73. Deep-Sea Res, 23:559-582.

Carstensena,J., Andersen, J.H., Gustafsson, B.G., and Conley, D.G., 2014. Deoxygenation of the Baltic Sea during the last century. PNAS, 111(15):5628-5633.

Casini, M., Blenckner, T., Möllmann, C., Gårdmark, A., Lindegren, M., Llope, M., Kornilovs, G., Plikshs, M. and Stenseth N.C.,2012. Predator transitory spillover induces trophic cascades in ecological sinks. PNAS, 109(21):8185-8189.

Chen, D.G. and Ware, D.M., 1999.A neural network model for forecasting fish stock recruitment. Can. J. Fish. Aquat. Sci., 56:2385-2396.

Cushing, D. H. and Harris, J. G. K. 1973. Stock and recruitment and the problem of density dependence. Rapp. P.-v. Réun. Cons. int. Explor. Mer, 164: 142–155.

Cushing, D. H., 1984. The gadoid outburst in the North Sea. J.Cons.int.Explor.Mer, 41: 159-166.

Cushing, D. H., 1990. Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. Advances in Marine Biology (eds) JHS Blaxter and AJ Southward. Academic Press Limited, San Diego, CA.: 250-313.

Dickinson, R.R., Pope. J.G. and Holden, M.J., 1974. Environmental influences on the survival of North sea cod. In: The early life history of fish. Ed. By J.H.S. Blaxter: 69-80.

Dickson, R.R. and Brander, K.M., 1993. Effects of a changing windfield on cod stocks of the North Atlantic. Fish. Oceanogr., 2(3/4): 124-153.

Eero, M., Köster, F. W. and Vinther, M., 2011. Why is the Eastern Baltic cod recovering? Mar.Pol.,doi.org/10.1016/j.marpol.2011.05.010.

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 J. Mar. Sci., 64: 1257–1271.

Ehlin, U., 1981. Hydrology of the Baltic Sea. In: The Baltic Sea (Ed by A. Voipio). Elsevier Oceanography Series, 30: 123-133.

European Commission (EC), 2007. Regulation no. No 1098/2007 of 18 September 2007 establishing a multiannual plan for the cod stocks in the Baltic Sea and the fisheries exploiting those stocks, amending Regulation (EEC) No 2847/93 and repealing Regulation (EC) No 779/97.

Glowinska, A., 1963. Hydrologic conditions in the Southern Baltic in the years 1951-1960. Prace MIR, 12/A: 23-85 (In Polish).

Grauman, G.B., 1973. Investigations of factors influencing fluctuations in abundance of Baltic Cod. Rapp. P.-v. Réun. Cons. int. Explor. Mer, 164: 73-76.

Grauman, G.B., 1984. Ichthyoplankton. In: Review of Baltic Sea bioproductivity. Moscow, 3: 259-428pp (In Russ.).

Gunderson, D. R., 1993. Surveys of Fisheries Resources. Jon Wiley & Sons, Inc. 248 pp.

Gustafsson, B.G., Schenk, F., Blenckner, T., Eilola, K., Meier, H. E. M. Müller-Karulis, B., Neumann, T., Ruoho-Airola, T., Savchuk, O.P. and Zorita, E., 2012. Reconstructing the development of Baltic sea eutrophication 1850–2006. Ambio, 41(6):534–548.

Haddon, M., 2001. Modelling and quantitative methods in fisheries. London: Chapman & Hall/CRC ,406p.

Hansson, S., Karlsson, L., Ikonen, E., Christensen, O., Mitans, A., Uzars, D., Petersson, E. and Ragnarsson B., 2001. Stomach analyses of Baltic salmon from 1959–1962 and 1994–1997: possible relations between diet and yolk-sac-fry mortality (M74). J Fish Biol., 58(6): 1730–1745.

HELCOM, 1990. Second Periodic Assessment of State of the marine Environment of the Baltic Sea, 1984-1988; Background Document. Baltic Sea Environment Proceedings 35B. Baltic Marine Environment Protection Commission - Helsinki Commission: 153-210.

Hinrichsen, H.-H., St. John, M,. Aro, E., Grønkjær, P. and Voss R., 2001. Testing the larval drift hypothesis in the Baltic Sea: retention versus dispersion caused by wind-driven circulation. ICES J. Mar. Sci. 58: 973–984. doi:10.1006/jmsc.2001.1090.

Hinrichsen, H.-H. and Wieland, K., 1996. Reproduction volume of Baltic cod in the Bornholm Basin estimated from single point measurements. ICES CM, 1996/C+J:7.

Hinrichsen, H.-H., Möllmann, C., Voss, R., Köster, F.W. and Kornilovs, G., 2002. Biophysical modeling of larval Baltic cod (Gadus morhua) growth and survival. Can. J. Fish. Aquat. Sci. 59: 1858–1873.

Hjort, J., 1919. Fluctuations in the great fisheres of north Europe viewed in the light biological research. Rapp. P.-v. Réun. Cons. int. Explor. Mer, 20: 228p.

ICES, 2013. Report of the Baltic Fisheries Assessment Working Group (WGBFAS). ICES Headquarters, 10–17 April 2013. ICES CM 2013/ACOM:10.

Ignatius ,H., Axberg, S., Niemistö, L. and Winterhalter, B., 1981. Quaternary geology of the Baltic Sea. In: The Baltic Sea (Ed by A. Voipio). Elsevier Oceanography Series, 30: 54:104.

Jamieson, A. and Otterlind, G., 1971. The use of cod blood protein polymorphisms in the Belt Sea, the Sound and the Baltic Sea. Rapp. P.-v. Réun. Cons. int. Explor. Mer, 161: 55-59.

Kaleis, M.V., 1977. The peculiarities of Kattegat water advection in the deep layer of the Baltic Sea. Ambio Spec.Rep., 5:201-204.

Kändler, R. 1944. Untersuchungen über den Ostseedorsch während der Forschungsahrten mit dem R.F.D. "Poseidon" in den Jahren 1925-1938. Ber. dt. wiss. Kommn Meeresforsch. 11(2): 137-245.

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

Kjesbu, O.S., Solemdal, J., Bratland,P. and Fonn, M., 1996. Variation in annual egg production in individual captive Atlantic cod (Gadus morhua). Can.J.Fish.Aquat.Sci. 48:2333-2343.

Kornilovs, G., Sidrevics, L. and Dippner, J. W. 2001. Fish and zooplankton interaction in the Central Baltic Sea. ICES ICES J.Mar. Sci. 58: 579–588.

Kosior, M. and Netzel, J. 1989. Eastern Baltic cod stock and environmental conditions. Rapp. P.-v. Réun. Cons. int. Explor. Mer, 190: 159-162.

Köster, F.W. and Möllmann, C., 2000. Trophodynamic control by clupeid predators on recruitment success in Baltic cod? ICES J.Mar. Sci. 57: 310–323.

Köster, F.W., Hinrichsen, H-H., Schnack, D., St.John, M.A., MacKenzie, B., Tomkiewicz, J., Möllmann, C., Kraus, G., Plikshs, M., Makarchouk, A. and Aro, E., 2003. Recruitment of Baltic Cod and sprat stocks: identification of critical life stages and incorporation of environmental variability into stock-recruitment relationships. Sci.Mar., 67(Supl.1):129-154.

Köster, F.W., Möllmann, C., Neuenfeldt, S., St.John, M.A., Plikshs, M. and Voss, R., 2001. Developing Baltic cod recruitment models I: Resolving spatial and temporal dynamics of spawning stock and recruitment for cod, herring and sprat. Canadian Journal of Fisheries and Aquatic Sciences. 58(8):1516-1533.

Köster, F.W., Vinther, M., MacKenzie, B.R., Eero, M. and Plikshs., M, 2009. Environmental Effects on Recruitment and Implications for Biological Reference Points of Eastern Baltic Cod (Gadus morhua). J. Northw. Atl. Fish. Sci., Vol. 41: 205–220.

Kostrichkina, E. M., Yurkovskis, A. and Kalejs, M., 1990. Zooplankton dynamics associated with changes of water regime in the Baltic Sea during the recent 40 years (1949-1989). In: Plenary report of VIII All-Union conference on fisheries oceanography. Moscow, VNIRO: 87-98.

Kraus, G., Tomkiewicz, J. and Köster, F.W., 2002. Egg production of Baltic cod (Gadus morhua) in relation to variable sex ratio, maturity, and fecundity. Can. J. Fish. Aquat. Sci. 59: 1908–1920.

Lablaika, I. and Lishev, M. N. 1964. Possibilities of forecasting the distribution of stock and efficiency of fishing for Baltic cod during Pre-spawning and spawning period. ICES CM, Nr.90.

Lablaika, I., Hoziosky, S. and Kaleis , M., 1989. Abundance dynamics of Eastern Baltic cod stocks and related factors. Rapp. P.-v. Réun. Cons. int. Explor. Mer, 190: 163-165.

Laevastu, T., 1993. Marine climate, weather and fisheries: the effects of weather and climatic changes on fisheries and ocean resources. Fishing News Books Ltd. 204 p.

Larsen, J. R. and Gislason, H., 1992. MSVPA and prey/predator switching. ICES CM, G:42.

Lishev M. N., and Lablaika, I., 1989. Distribution of eastern-baltic cod stock. In: Main tendencies of ecosystem evolution. Project "Baltic" Problems of investigations and mathematical modelling on the Baltic Sea ecosystem (eds. Davidan, I.N. and Savchuk, O.P.). Leningrad, Gidrometeoizdat: 222-228pp (in Russ.).

MacKenzie, B.R., Eero, M. and Ojaveer, H., 2011. Could Seals Prevent Cod Recovery in the Baltic Sea? PLoS ONE 6(5): e18998. doi:10.1371/journal.pone.0018998.

Makarchouk A. and Hinrichsen, H.-H., 1998. The vertical distribution of ichthyoplankton in relation to the hydrographic conditions in the Eastern Baltic. ICES CM, 1998/R:11.

Marshall, G.T., Kjesbu, O.S., Yaragina, . N. A., Solemdal, P. and Ulltang Ø., 1998. Is spawner biomass a sensitive measure of the reproductive and recruitment potential of Northeast Arctic cod? Can. J. Fish. Aquat. Sci. 55: 1766-1783.

Martell, S.J. and Walters, C.J., 2008. Experimental policies for rebuilding depleted stocks. Can. J. Fish. Aquat. Sci., 65:1601-1609.

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

Matthäus, W. and Naush, G., 2003. Hydrographyc-hydrochemical variability in the Baltic Sea during the 1990.s in relation to changes during the 20th century. ICES Marine Science Symposia, 219: 132-143.

Matthäus, W., 1993. Major inflows of highly saline water into the Baltic sea - A Review. ICES CM, 1993/C:52.

Matthäus, W., 2006. The history of investigations of salt water inflows into the Baltic Sea—from the early beginning to recent results. Meereswissenschaftliche Berichte, 65, 73p.

Mayers, R.A., Huchings, J.A. and Barrowman, N.J., 1997. Why do fish stocks collapse? The example of cod in Atlantic Canada. Ecological applications, 7(1):91-106.

McQuin, I.H., 2009. Pelagic fish outburst or suprabenthic habitat occupation: legacy of Atlantic cod (Gadus morhua) collapse in eastern Canada. Can. J. Fish. Aquat. Sci. 66: 2256-2262.

Möllmann, C., Dieckmann, R., Müller-Karulis, B., Kornilovs, G., Plikshs, M. and Axe, P. 2009. Reorganization of a large marine ecosystem due to atmospheric and anthropogenic pressure: a discontinuous regime shift in the Central Baltic Sea. Global Change Biology, 15:1377-1393.

Möllmann, C., Müller-Karulis, B., Kornilovs, G. and St John, M. A. 2008. Effects of climate and overfishing on zooplankton dynamics and ecosystem structure: regime shifts, trophic cascade, and feedback loops in a simple ecosystem. ICES J.Mar.Sci., 65: 302–310.

Neuenfeldt, S. and Köster, F. W., 2000. Trophodynamic control on recruitment success in Baltic cod: the influence of cannibalism. – ICES J.Mar.Sci., 57: 300–309.

Neuenfeldt, S., Andersen, K. H. and Hinrichsen, H.-H., 2009. Some Atlantic cod Gadus morhua in the Baltic Sea visit hypoxic water briefly but often. J.Fish Biol., 75:290–294.

Nielsen, E.E., Grønkjær, P., Meldrup, D. and Paulsen, H., 2005. Retention of juveniles within a hybrid zone between North Sea and Baltic Sea Atlantic cod (Gadus morhua). Can. J. Fish.Aquat.Sci., 62(10): 2219-2225.

Nielsen, E.E., Hansen, M.M., Ruzzante, D.E., Meldrup, D. and Grønkjær, P., 2003. Evidence of a hybrid-zone in Atlantic cod (Gadus morhua) in the Baltic and the Danish Belt Sea, revealed by individual admixture analysis. Mol. Ecol. 12(6): 1497-1508.

Nikolsky, G., 1965. Theory of Fish Population. Nauka, Moscow: 245-253pp (in Russ).

Nissling A. and Westin L. 1991a. Egg buoyancy of Baltic cod (Gadus morhua) and its implications for cod stock fluctuations in the Baltic. Marine Biology, 111:33-35.

Nissling A. and Westin L. 1991b. Egg mortality and hatching rate of Baltic cod (Gadus morhua) in different salinities. Mar.Biol., 111: 29-32.

Nissling A. and Westin L., 1997. Salinity requirements for successful spawning of Baltic and Belt Sea cod and potential for cod stock interactions in the Baltic Sea. Mar.Ecol.Prog.Ser., 152 (1-3):261-271.

Nissling, A., Kryvi, H. and Vallin, L., 1994. Variation in egg buoyancy of Baltic cod Gadus morhua and its implications for egg survival in prevailing conditions in the Baltic Sea. Mar.Ecol.Prog.Ser, 110:67-74.

Ojaveer, E., Kalejs, M., Aps, R., Lablaika, I. and Vitinsh, M.,1985. The impact of recent environmental changes on the main commercial fish stocks in the Gulf of Finland. Finnish Fisheries Research, 6: 1–14.

Ottersen, G., Loeng, H., and Raknes, A. 1994. Influence of temperature variability on recruitment of cod in the Barents Sea. ICES Mar. Sci. Symp. 198: 471–481.

Planque, B. and Fredou, T. 1999. Temperature and the recruitment of Atlantic cod (Gadus morhua). Can. J. Fish. Aquat. Sci. 56:2069–2077.

Pliksh, M. and Kaleis, M., 1990. Cod distribution during the spawning period in the eastern Baltic in 1986-1988. Fischerei-Forschung, 28(2): 39-43 (In Russ.).

Plikshs, M., Kalejs, M. and Grauman, G., 1993. The influence of environmental conditions and spawning stock size on the year-class strength of the eastern Baltic cod. ICES-CM-1993/J:22.

R Core Team 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL: http://www.R-project.org/.

Reeves, S.A., 2003. A simulation study of the implications of age-reading errors for stock assessment and management advice ICES J. Mar. Sci., 60(2): 314-328.

Ricker, W.E., 1958. - Handbook of computation for biological statistics of Fish populations. Fish. Res. Board of Canada, Bulletin 119;

Rothscshild, B.J., 1986. Dynamics of Marine Populations. Harvard University Press, Cambridge, USA, 277p.

SAS, 1989. SAS/STAT User’s Guide. SAS Institute Inc., Version 6, fourth edition, 846p.

Schaber, M., Hinrichsen H-H. and Gröger, J., 2011. Seasonal changes in vertical distribution patterns of cod (Gadus morhua) in the Bornholm Basin, central Baltic Sea. Fish. Oceanogr. doi:10.1111/j.1365-2419.2011.00607.x.

Smith, C. and Reay, P., 1991. Cannibalism in teleost fish. Reviews in Fish Biology and Fisheries, 1: 41-64.

Sparholt, H. and Tomkiewich, J., 1998. A robust way of compiling trawl survey data for the use in the Central Baltic cod stock assessment. ICES CM, 1998/BB:1, 35p.

Sparholt, H., 1996. Causal correlation between recruitment and spawning stock size of central Baltic cod? ICES J. Mar. Sci., 53:771-779.

Sparholt, H., Aro, E. and Modin, J., 1991. The spatial distribution of cod (Gadus morhua L.) in the Baltic Sea, Dana, 9:45-56.

Stigebrandt, A. and Wulff, F., 1987. A model for the dynamics of nutrients and oxygen in the Baltic proper. J Mar Res 45:729-757.

Stigebrandt, A., 1987. A model for the vertical circulation of the Baltic deepwater. Am Meteorol Soc 17:1772-1785.

Stocker, M., Haist, V. and Fournier, D., 1985. Environmental variation and recruitment of Pacific herring in the Strait of Georgia. Can. J. Fish. Aquat. Sci. 42(Suppl.): 174–180.

Svetovidov, A.N., 1986. Gadidae. In: P.J.P Whitehead, M.-L. Bauchot, J.-C. Hureau, J. Neilsen and E. Tortense. Fishes of the North-eastern Atlantic and the Mediterranean. UNESCO. 680-710 pp.

Tomkiewicz, J., Lehmann, K. M. and St. John, M. A. 1998. Oceanographic influences on the distribution of spawning aggregations of Baltic cod (Gadus morhua) in the Bornholm Basin, Baltic Sea. Fish. Oceanogr. 7: 48–62.

Uzars, D., Plikshs, M., Grauman, G., Kalejs, M. and Baranova, T. 1991. Cod distribution and spawning in the Gotland Basin in the 1980-ies. ICES CM, 1991/J:15.

Voss, R., Hinrichsen, H-H. and StJohn, M., 1999. Variations in the drift of larval cod (Gadus morhua L.) in the Baltic Sea: combining field observations and modeling. Fish.Oceanogr. 8(3)3:199-211.

Voss, R., Hinrichsen, H-H. and Wieland, K., 2001. Model-supported estimation of mortality rates in Baltic cod (Gadus morhua callarias L.) larvae: the varying impact of 'critical periods'. BMC Ecology, 1:4, http://www.biomedcentral.com/1472-6785/1/4.

Westin, L. and Nissling, A., 1991. Effect of salinity on spermatozoa motility, percentage of fertilized eggs and egg development of Baltic cod (Gadus morhua) and implications for cod stock fluctuations in the Baltic. Marine Biology, 108: 5-9.

Wieland, K., Waller, U. and Schnack, D., 1994. Development of Baltic cod eggs at different levels of temperature and oxygen content. Dana 10:163-177.

Wieland, K., Jarre-Teichmann, A. and Horbowa, K., 2000. Changes in the timing of spawning of Baltic cod: possible causes and implications for recruitment. ICES J. Mar. Sci., 57: 452-464.

Williamson, C.E., 1993. Linking predation risk models with behavioural mechanisms: identifying population bottlenecks. Ecology, 75:320–331.

Wooton, R.J., 1994. Ecology of Teleost fishes. Chapman &Hall, London, 204p.