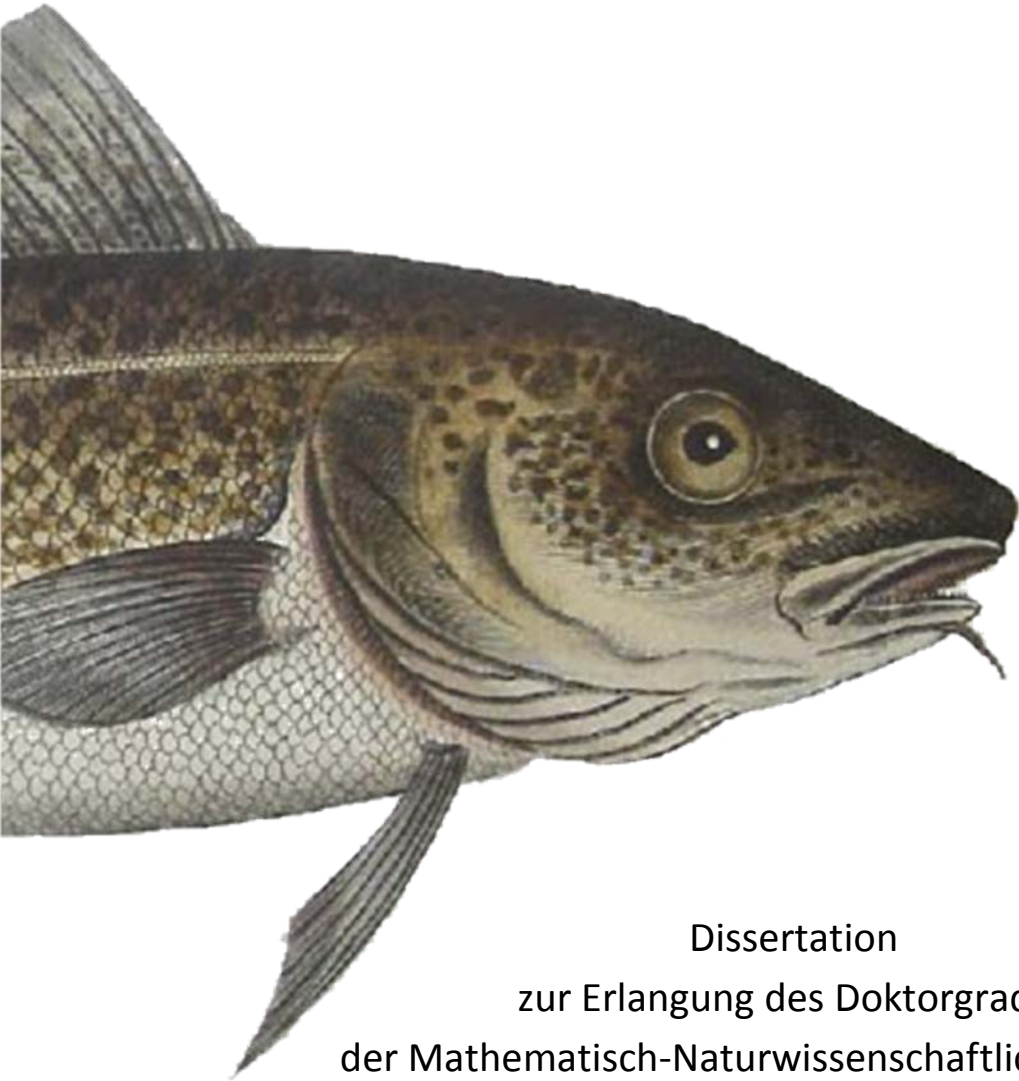


Small to meso-scale distribution of Baltic cod
(*Gadus morhua* L.) as resolved by hydroacoustics:
Habitat preferences, environmental limits, and
resulting implications for stock development



Dissertation
zur Erlangung des Doktorgrades
der Mathematisch-Naturwissenschaftlichen Fakultät
der Christian-Albrechts Universität
zu Kiel

vorgelegt von

Matthias Schaber

Kiel, August 2011

Cover artwork:

Bloch ME (1783) Oeconomische Naturgeschichte der Fische Deutschlands. Mit fünf und dreissig Kupfertafeln nach Originalen. Zweeter Theil, Berlin, pp [1-11] 1-197

Source: AnimalBase team/ Uni Göttingen

Referent: Prof. Dr. D. Schnack

Korreferent: Prof. Dr. J. Gröger

Tag der mündlichen Prüfung: 30.09.2011

Zum Druck genehmigt: 30.09.2011



If ever there was a fish made to endure, it is the Atlantic cod – the common fish. But it has among its predators man, an openmouthed species greedier than cod.

(Mark Kurlansky, COD – A BIOGRAPHY OF THE FISH THAT CHANGED THE WORLD, 1997)



Cod – a species of fish too well known to require any description. It is amazingly prolific. Leewenhoek counted 9.384.000 eggs in a cod-fish of a middling size – a number that will baffle all the efforts of man to exterminate.

(J. Smith Homands & J. Smith Homands Jr. (Eds.), CYCLOPEDIA OF COMMERCE AND COMMERCIAL NAVIGATION, New York, 1858)



ZUSAMMENFASSUNG

Dorsche (*Gadus morhua*) werden in der zentralen Ostsee mit speziellen hydrographischen Bedingungen in Form starker vertikaler Salzgehalts- und Sauerstoffschichtungen konfrontiert. Diese Bedingungen wirken sich direkt und indirekt auf Fortpflanzung, Eientwicklung, Sterblichkeit früher Entwicklungsstadien, Rekrutierung und auch auf die Verteilung von Eiern, Larven, juvenilen und adulten Dorsche aus. Die physischen und physiologischen Effekte dieser ozeanographischen Bedingungen sind relativ gut erforscht. Ihr Einfluss auf Verteilungsmuster adulter Dorsche wurde ebenfalls untersucht. Die hierfür angewandten Methoden waren jedoch entweder zeitlich und räumlich nicht hochauflösend genug, um Schlussfolgerungen für klein- oder mesoskalige Verteilungsmuster zu erlauben, oder beruhten auf einem kleinen Probenumfang.

Das Ziel dieser Arbeit war deswegen, kleinskalige Vertikalverteilungsmuster, Habitatpräferenzen und –limits für Ostseedorsche in ihrem Hauptlaichgebiet, dem Bornholmbecken, mit ausreichend hoher Auflösung zu untersuchen. Die Studie basiert auf hydroakustischen Messungen, welche die *in-situ* Identifizierung einzelner Dorsche im Wasserkörper und die individuelle Zuordnung ozeanographischer Umgebungsparameter erlaubt. Zusätzlich wurden, basierend auf Verteilungsmustern, mögliche Auswirkungen von klimabedingten Langzeitveränderungen der abiotischen Bedingungen auf den östlichen Dorschbestand evaluiert.

In **Kapitel I** wurde die Anwendbarkeit der hydroakustischen Einzelzielverfolgung überprüft. Dies geschah durch Vergleiche mit Verteilungsdaten aus zeitgleich in anderen Studien durchgeführten Markierungsexperimenten mit elektronischen Datenrekordern. Es konnte gezeigt werden, dass hydroakustische Methoden die aus diesen Markierungsexperimenten abgeleiteten Datensätze verbessern können, um vom Individual- auf einen Populationslevel zu skalieren. Verteilungsmuster wurden während der Hauptlaichzeit in zwei Jahren mit kontrastierenden hydrographischen Bedingungen (Einstrom und Stagnation) untersucht. In beiden Jahren wurde die Vertikalverteilung von Dorschen und damit das geeignete und präferierte Habitat durch Salzgehalt (obere Grenze) und Sauerstoffkonzentration (untere Grenze, v.a. in Stagnationsphasen) kontrolliert. Temperatur zeigte keine Auswirkung auf die Vertikalverteilung von Dorschen. Laichende Dorsche vermieden in beiden Jahren Salzgehalte <11 psu und Sauerstoff-Zehrschichten. Ein kleiner Anteil der Dorsche hielt sich in Bereichen mit weniger als 17 % Sauerstoffsättigung auf. Es wird angenommen, dass diese Dorsche kurze Beutezüge in tiefere Schichten unternahmen, in denen sich ihre Beute (Clupeiden, die eine höhere Toleranz gegenüber Sauerstoffzehrung aufweisen) aufhielt.

In **Kapitel II** wurden saisonale Veränderungen in der Vertikalverteilung von Dorschen untersucht und mit hydrographischen Umgebungsbedingungen verglichen, um zugrundeliegende Ursachen zu identifizieren. Hierzu wurden im April, Juni und August

der Jahre 2006-2009 Messungen auf Hydroakustiktransekten im Bornholmbecken durchgeführt. In allen Jahren führten schlechter werdende Sauerstoffbedingungen in tiefen Schichten zu einem Habitatverlust für Dorsche. Dies führte zu einer saisonalen Verringerung der Aufenthaltstiefe der Dorsche. Die obere Verteilungsgrenze (obere Schichten der permanenten Halokline) blieb annähernd konstant. Eine biologische Effektmodellierung (GLM) zeigte, dass neben einem signifikanten Jahres/Monats-Effekt vor allem Salzgehalt und Sauerstoffkonzentration die Haupt-Einflussfaktoren auf die Vertikalverteilung von Dorschen darstellen. Die zunehmend pelagische Verteilung wird bisher nicht in Surveys, die zur Bestandsabschätzung beitragen, berücksichtigt. Indices aus Grundschleppnetzsurveys könnten deswegen einen systematischen Fehler enthalten.

In **Kapitel III** wurden klimagesteuerte Langzeittrends in den Sauerstoffkonzentrationen der Ostsee und deren mögliche Konsequenzen für den östlichen Dorschbestand untersucht. Hierzu wurden die Auswirkungen eines beobachteten Rückgangs der Sauerstoffkonzentrationen in der zentralen Ostsee von 1951-2007 analysiert. Basierend auf Verteilungsdaten verschiedener Stadien und auf Laborexperimenten konnte gezeigt werden, dass negative Auswirkungen fortschreitender Sauerstoffzehrung alle Lebensstadien des Ostseedorsches betreffen. Dorscheier werden möglicherweise weiterhin häufig tödlichem Sauerstoffmangel ausgesetzt. Larven aus Eiern, die tiefer in der Wassersäule schweben, werden eventuell nicht die Vertikalwanderung durchführen können, die zum Erreichen der Wasserschichten mit ausreichend hohen Konzentrationen an Beutetieren erforderlich ist. Geeignete Ansiedlungsgebiete für juvenile Dorsche zeigten während der Untersuchungsperiode einen Flächenverlust von 25 %. Basierend auf Verteilungsdaten adulter Dorsche und deren abiotischer Umgebung wurde eine sauerstoffbedingte Verringerung der Magenentleerungsrate offensichtlich, die zu verringerter Kondition der Tiere führte. Generell sind durch die beobachteten Trends negative Auswirkungen auf alle sauerstoffabhängigen Prozesse bei verschiedenen Lebensstadien der Dorsche zu erwarten.



SUMMARY

Cod (*Gadus morhua*) in the central Baltic Sea face specific hydrographic conditions, characterized especially by strong vertical thermohaline and oxygen stratifications that significantly affect directly and indirectly reproduction, development, early life stage mortality, recruitment and distribution of eggs, larvae, juveniles and adults. The physical and physiological effects of these hydrographic conditions are comparatively well understood. Also the influence on the distribution pattern of adult cod has been studied. The methods applied however either did not resolve the temporal or spatial scale sufficiently to allow for conclusions on small- or meso-scale distribution patterns, or were based on a comparatively low number of samples.

Thus, the aim of this thesis is to study with sufficiently high resolution the small-scale vertical distribution patterns, habitat preferences and limits for Baltic cod in its major spawning area, the Bornholm Basin. The study is based on hydroacoustic single-target measurements and fish tracking algorithms, which allow to identify individual cod in their environment and to allocate hydrographic parameters to each individual. Additionally, distribution patterns were evaluated to identify the possible influence of climate driven long term trends in abiotic conditions on the Eastern Baltic cod stock.

In **Chapter I**, the applicability of the hydroacoustic single-fish tracking method was confirmed by comparing the results with *in-situ* distribution data obtained concurrently in other studies from data-storage-tags (DST) attached to cod. It could be shown that hydroacoustics can enhance the datasets provided by DST when it comes to scaling of individual data to population level. Distribution patterns were analyzed for the peak spawning period in two years with contrasting hydrographic conditions (post inflow and stagnation). In both years, vertical distribution of cod was controlled by salinity as upper and oxygen concentration (during stagnation) as lower boundary level, marking suitable and preferred habitat. Temperature had no significant effect on vertical distribution. Spawning cod in both years avoided salinities <11 psu and oxygen depleted layers. A small fraction of cod was distributed in oxygen concentrations of less than 1 ml l⁻¹. It is assumed that these cod undertake short feeding excursions into deeper layers where their prey organisms (clupeids, which show a higher tolerance towards oxygen depletion) are distributed.

In **Chapter II**, seasonal changes in vertical cod distribution were analyzed and related to ambient hydrographic conditions to identify the driving mechanisms. Longitudinal hydroacoustic transects covering the Bornholm Basin were sampled in April, June and August 2006-2009. In all years observed, cod experienced a loss of suitable habitat with deteriorating oxygen conditions in deep layers during the course of the year. This induced an upward movement of cod. The upper distribution boundary in the upper layers of the halocline remained nearly constant. A GLM model revealed that apart from

a significant year-month effect, salinity and oxygen concentrations were the most significant factors affecting cod vertical distribution. This increasingly pelagic distribution is not taken into account in surveys contributing to stock assessment of (Eastern) Baltic cod. Thus, indices derived from bottom trawl surveys in the area might be biased.

In **Chapter III**, climate driven long-term trends in Baltic Sea oxygen concentrations and potential consequences for the Eastern Baltic cod stock were evaluated. Effects of an observed decline in ambient oxygen concentrations in the central Baltic were studied for all life stages of cod from 1951-2007. Based on field distribution data of different life stages and on laboratory experiments it could be shown that negative effects of proceeding oxygen depletion affect all life stages. Cod eggs were and possibly will continue to be frequently exposed to lethal oxygen conditions. Larvae hatching from deeper floating eggs will possibly not be able to undertake vertical migration activities required for initiation of first feeding. Potential settling areas for juveniles deteriorated over 25 % in size during the time the series is representative for. Based on distribution patterns of adult cod and their corresponding abiotic environment, an oxygen induced reduction in gastric evacuation rates was evident leading to reduced overall conditions. Generally, the expected trend in long-term oxygen development will negatively affect all life stages of cod.



TABLE OF CONTENTS

ZUSAMMENFASSUNG	5
SUMMARY	7
TABLE OF CONTENTS.....	9
GENERAL INTRODUCTION.....	11
THE BALTIC SEA	11
THE PELAGIC BALTIC SEA ECOSYSTEM.....	14
COD (<i>GADUS MORHUA</i>) IN THE BALTIC SEA	15
GENERAL: STUDYING DISTRIBUTION PATTERNS OF FISHES.....	19
HYDROACOUSTICS	21
RATIONALE OF THIS THESIS	22
AIM AND OUTLINE OF THIS THESIS.....	25
IN A NUTSHELL: GENERAL MATERIAL AND METHODS.....	27
HYDROACOUSTIC DATA.....	27
ENVIRONMENTAL DATA.....	28
DATA ANALYSIS	28
Chapter I. Hydroacoustic resolution of small-scale vertical distribution of Baltic cod (<i>Gadus morhua</i> L.) – habitat choice and limits during spawning	31
Chapter II. Seasonal changes in vertical distribution patterns of cod (<i>Gadus morhua</i>) in the Bornholm Basin, central Baltic Sea.....	51
Chapter III. Climate driven long-term trends in Baltic Sea oxygen concentrations, and the potential consequences for eastern Baltic cod (<i>Gadus morhua</i>)	69
REFERENCES.....	95
ANNEX I: LIST OF FIGURES.....	113
ANNEX II: LIST OF TABLES	115
ANNEX III: LIST OF ABBREVIATIONS.....	117
CONTRIBUTIONS OF AUTHORS	119
ACKNOWLEDGEMENTS	121
<i>CURRICULUM VITAE</i>	123
ERKLÄRUNG	127

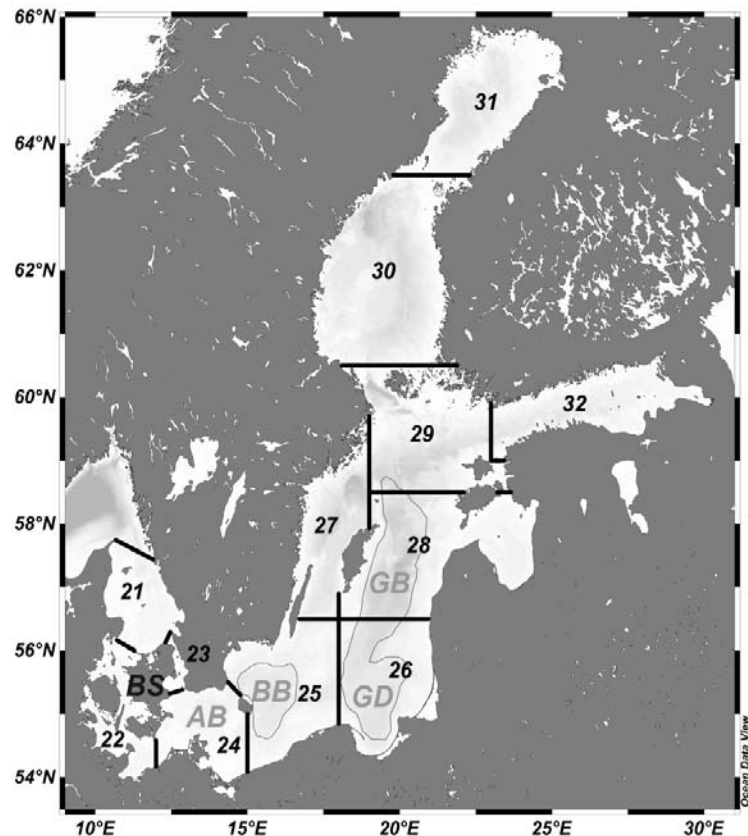


GENERAL INTRODUCTION

THE BALTIC SEA

The semi-enclosed Baltic Sea (Fig. 1) is one of the world's largest brackish water systems. A positive freshwater balance due to river inflows and precipitation leads to a permanent outflow of low saline surface waters through the narrow Danish straits of the Belt Sea. A compensatory inflow of water with higher salinity and density from adjacent North Sea areas via the Belt Sea leads to a distinct salinity gradient in surface water layers towards the northeastern Baltic Sea. There, surface salinity is as low as around 2 psu in contrast to around 15 psu near the Danish straits (e.g. Antonov et al. 2009) (Fig. 2).

Figure 1: The Baltic Sea. Black lines and numbers indicate ICES Subdivisions employed for fish stock assessment in the Baltic Sea. Grey areas indicate deep basins of the central and northeastern Baltic Sea. AB – Arkona Basin, BB – Bornholm Basin, BS – Belt Sea/Danish Straits, GD – Gdansk Deep, GB – Gotland Basin.



The deep basins of the Baltic Sea (Bornholm Basin, Gdansk Deep and Gotland Basin) are characterized by strong and stable temperature and salinity gradients between surface and deeper layers. In summer, heating of the upper water layers leads to a seasonal thermal stratification (Møller & Hansen 1994). A permanent halocline in 50-75 m depth separates the low-saline upper water layers from deep water layers with higher salinity (Fig. 3). Especially in the deep basins, this stable stratification inhibits vertical mixing and thus prevents transportation of oxygen rich surface waters into deeper layers. During so-

called stagnation periods, a bacterial breakdown of organic matter together with the lack of vertical mixing of oxygenated waters towards the deeper zones leads to oxygen depletion and anoxic zones in these layers (Fig. 3). A renewal of bottom waters and thus an improvement of oxygen conditions is only achieved during irregular inflow events of high saline, oxygen rich waters from adjacent North Sea regions.

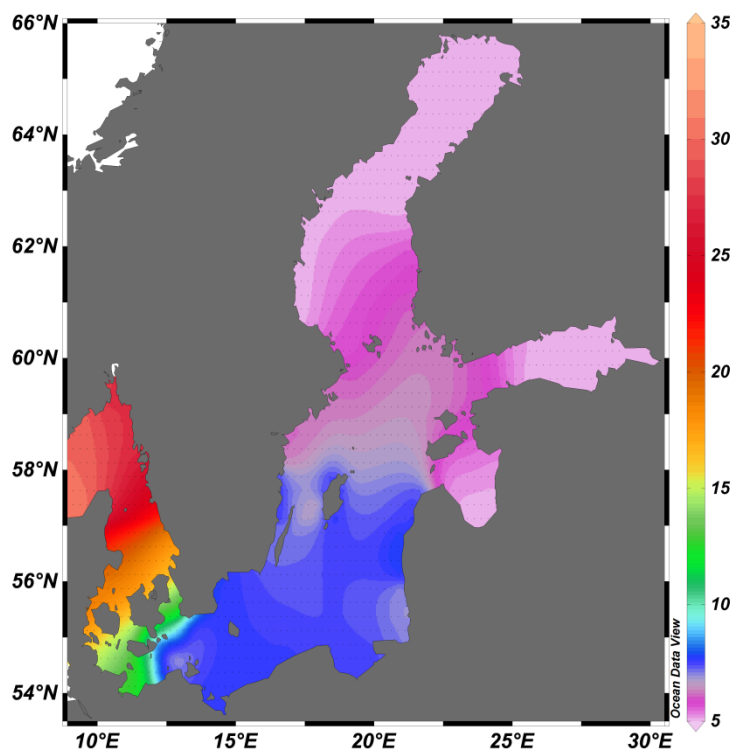


Figure 2: Mean summer sea surface salinity (psu) in the Baltic Sea. A distinct decrease in salinity from the Skagerrak and Kattegat via the Belt Sea towards the northeastern Baltic Sea is evident (data from World Ocean Atlas 2009, Antonov et al. 2009).

The temperature of the inflow water is also of importance as it affects oxygen solubility (Hinrichsen et al. 2002a) and oxygen consumption rates of biological processes (MacKenzie et al. 1996a). Inflow events are strongly dependent on atmospheric forcing conditions and coupled to the North Atlantic Oscillation (NAO) (Matthäus & Franck 1992, Matthäus & Schincke 1994, Fonselius & Valderrama 2003). Due to the topography of the southern and central Baltic Sea characterized by a series of deep basins and shallow sills, the intrusion of inflow water proceeds via the Arkona Basin and the westernmost (Bornholm Basin) to the easternmost (Gotland Basin) of the deep basins. However, the magnitude of an inflow event is often not sufficiently high to replenish the deep water masses of the more easterly Basins (Gdansk Deep and Gotland Basin) (e.g. Matthäus & Franck 1992). Therefore, minor inflows mostly only affect the westernmost Bornholm Basin, whereas a substantial improvement of bottom water oxygen conditions is rarely detectable in the more easterly basins.

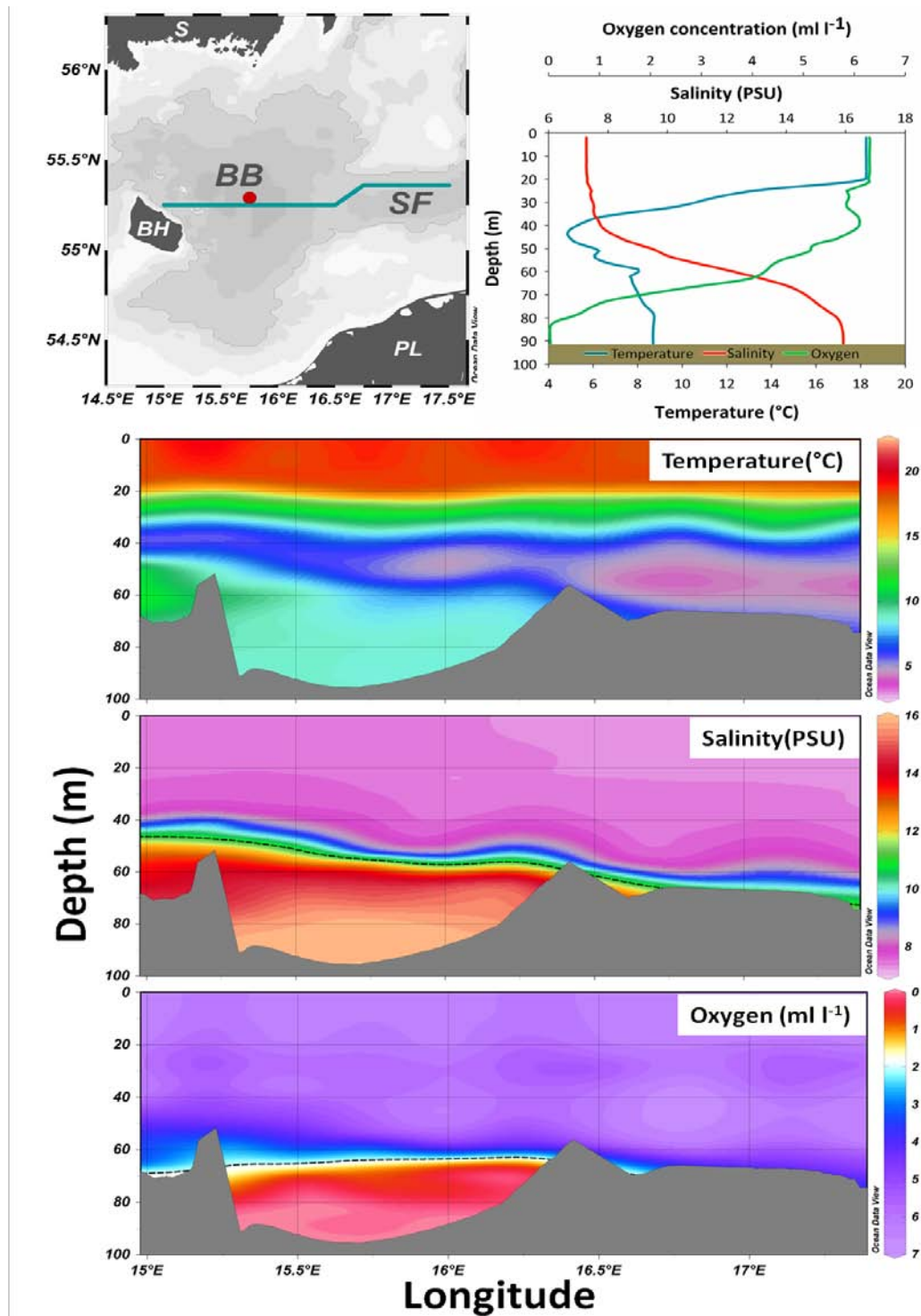


Figure 3: Hydrography profiles from the Bornholm Basin and adjacent areas in summer 2009. Top left: Survey area: Bornholm Basin (BB) and Slupsk Furrow (SF). Blue line indicates longitudinal hydrography transect depicted in the panels below. Red dot indicates hydrography station in central BB depicted in top right panel. S- Sweden, BH – Bornholm, PL – Poland. Top right: Typical vertical summer hydrography profile from the central BB. Note the distinct thermohaline stratification, the extended halocline below ca. 50 m depth and the oxygen deficit in deep layers. Lower panels: Longitudinal profiles of temperature, salinity and oxygen. Dashed lines indicate the 11 psu halocline and the 2 ml l⁻¹ oxycline respectively. Refer to text for further explanations.

In the 20th century major inflow events occurred in comparatively short intervals (e.g. Matthäus 2006). Since the 1980s however, the frequency of these events significantly declined due to changes in atmospheric circulation patterns (Matthäus & Schincke 1994). In the last decades, only few “major” inflow events took place (1983, 1993, 2003) (Feistel et al. 2008). The last significant inflow in January 2003 entirely replenished the oxygen-depleted water masses below the halocline in the Bornholm Basin. By summer 2003 oxygen concentrations near the seafloor had again distinctly decreased (Hinrichsen et al. 2007). The peculiar complexity of the hydrographic regime directly affects the pelagic ecosystem of the central Baltic Sea and all of its components.

THE PELAGIC BALTIC SEA ECOSYSTEM

Due to the overall reduced salinity, the species diversity in the brackish Baltic Sea with its pronounced horizontal and vertical salinity gradients is reduced in relation to adjacent, fully marine ecosystems (e.g. Remane 1934, Arndt 1996). The fish community consists of ca. 100 species which comprise 70 marine and 30-40 freshwater species which are adapted to the brackish conditions (HELCOM 2006). Following the salinity gradient from the western to the eastern Baltic, a distinct decrease in fully marine species is evident, whereas freshwater species become dominant in the northeastern Baltic (Nellen & Thiel 1995). Altogether, the peculiar hydrography of the system strongly affects the distribution of the corresponding species, with their tolerance towards reduced salinity (marine species) or increased salinity (freshwater species) determining their range (Remane 1934). The pelagic Baltic ecosystem also comprises a relatively low species diversity with comparatively simple trophic interactions (Rudstam et al. 1994, ICES 2006, Link et al. 2009). In the upper trophic levels, the clupeids sprat (*Sprattus sprattus*) and herring (*Clupea harengus*) are the by far most abundant and main planktivores in the Baltic proper. The main piscivore predatory fish are cod (*Gadus morhua*) and, to a far lesser extent, Salmon (*Salmo salar*) (Rudstam et al. 1994). As the impact of predatory marine mammals is negligible at present (ICES 1990, MacKenzie et al. 2002, Eero et al. 2011), cod is by far the most important marine predator remaining in the central Baltic Sea ecosystem. Baltic cod and sprat stock biomass are significantly connected through predator-prey interactions with a high cod stock generally keeping the sprat stock on a low level through predation (Rudstam et al. 1994). As planktivore sprat however may substantially prey upon cod eggs and, to a far lesser extent, on cod larvae, a bottom-up link of sprat and cod is also present (Köster & Möllmann 2000). These strong trophodynamic interactions and their impacts on the Baltic cod stock are described in the following chapters.

COD (*GADUS MORHUA*) IN THE BALTIC SEA

Generally, Atlantic cod is one of the economically and ecologically most important fish species with many stocks having collapsed due to combined effects of overfishing and climate driven factors (e. g. Hutchings 2000, Frank et al. 2005, Lilly et al. 2008). In the Baltic Sea, cod is also heavily affected by fishing pressure and a combination of climate-related direct and indirect effects on reproduction and recruitment (Lindegren et al. 2010). Despite showing a broad capacity to adapt to different thermal regimes (Righton et al. 2010), cod in the brackish Baltic Sea like other fully marine fishes live at the margin of their geographical distribution (e.g. Rechlin 1999) and, due to the reduced salinity and prevailing oxygen depletion, at their physiological limits (see below). All life stages and phases of Baltic cod, from egg to adult, from reproduction to distribution, are significantly affected by ambient hydrographic conditions and their irregular alteration.

COD STOCK DYNAMICS

Cod in the Baltic Sea is divided into two stocks, the Western Baltic cod stock (WBC) and the Eastern Baltic cod stock (EBC) which are separated according to morphometric characters, genetic variation and tagging experiments (Bagge et al. 1994 and references therein). The stocks are also managed separately and comprise ICES Subdivisions 22-24 (WBC) and ICES Subdivisions 25-32 (EBC) respectively (see Fig. 1). There is little indication of substantial overlap of both stocks, and the division between both stocks occurs immediately west of Bornholm island (Bagge et al. 1994). Despite a certain overlap of both stocks, especially in the border region SD 24 (Arkona Basin), the degree of this mixing has not been quantified (ICES 2010a). The focus of this thesis is the EBC stock. In terms of mean total stock biomass (TSB) and spawning stock biomass (SSB), the EBC stock in the last ten years is about 4 times bigger than the WBC stock (ICES 2010a).

Generally, there has been large fluctuation of both total and spawning stock biomass of the EBC, henceforth referred to as Baltic cod, during the last 40 years of assessment (see Fig. 4). After a mostly continuous increase from ca. 350 000 t since 1970, that most likely was caused by high recruitment due to favorable hydrographic conditions and good food availability for the larvae due to high plankton production (Bagge et al. 1994), total stock biomass peaked at record high levels of over 1 000 000 t in the early 1980s. After 1983 however, due to a combination of increased fishing pressure and reduced reproduction caused by unfavorable environmental conditions, a drastic decline in TSB and SSB took place until the long-term equilibrium level of the 1960s and 1970s. This trend however continued further until 1992. From then on until the first five years of the 21st century, TSB and SSB averaged on low levels of around 186 000 (120 000) t and reached an all-time low in 2005 with TSB and SSB minima of 118 000 and 64 000 t respectively (ICES 2011a). This decline in cod biomass together with favorable environmental conditions for sprat led to a significant increase in sprat biomass during that period with sprat SSB increasing more than fourfold from the early 1980s to record levels of 1 690 000 t in

1996 (Parmanne et al. 1994, ICES 2011a) (Fig. 5). Afterwards, a continuous decrease in sprat stock biomass occurred that from 2000 on averaged around 940 000 t. Since 2005, EBC stock shows signs of recovery with rapidly increasing TSB and SSB after above average year classes in 2006, 2007 and 2008 (ICES 2011a).

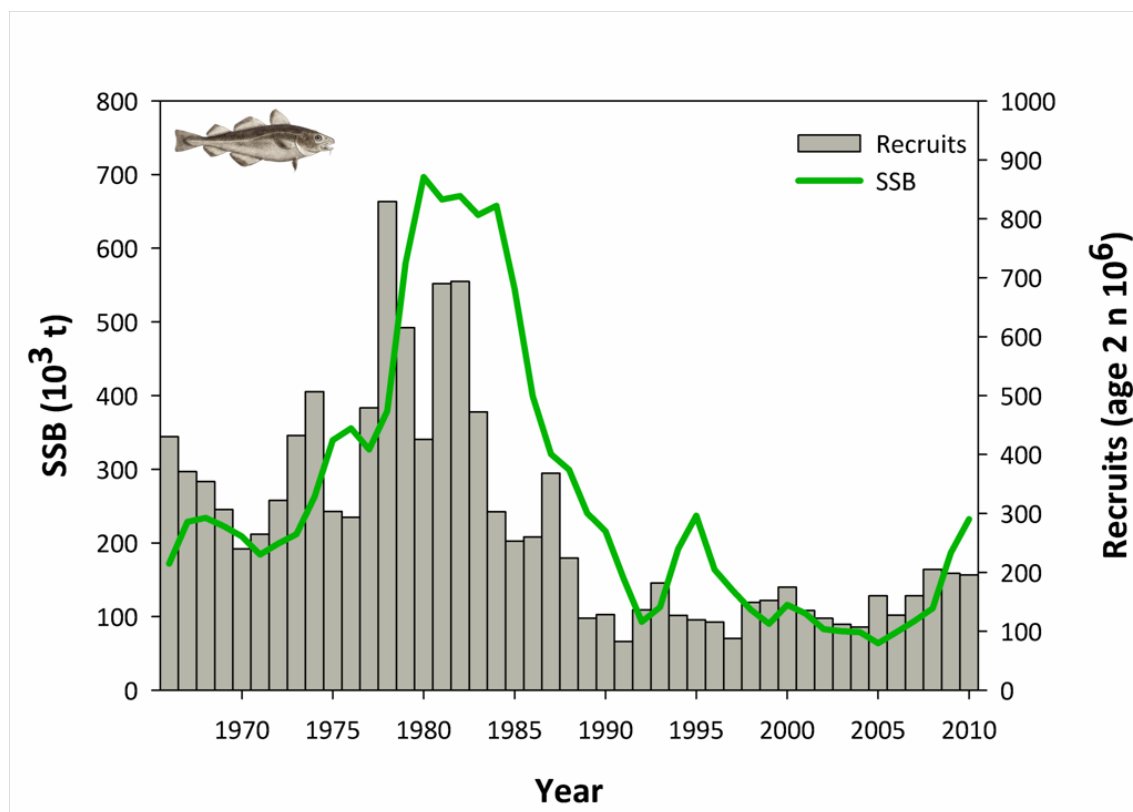


Figure 4: Development of Eastern Baltic cod (ICES SD 25-32) spawning stock biomass (SSB, green line) and recruitment (vertical bars) from 1966 to 2009 (ICES 2011a).

ENVIRONMENTAL LIMITS FOR BALTIC SEA COD

The main spawning period of EBC stock lasts from March to August (Bagge 1981). According to surveys carried out in the last century, cod eggs can be found in the central Baltic Sea from March until October, with annual peak spawning date changing considerably (Kändler 1949, MacKenzie et al. 1996b). While peak spawning used to occur in spring during the 1970s and 1980s a shift towards the summer months has taken place during the recent decade (Wieland et al. 2000). In recent years, there were indications for a back-shift of peak spawning towards the late spring months (e.g. Schaber et al. 2011). Unlike the western Baltic cod stock that is not significantly limited with regards to suitable spawning areas, the reproduction of EBC is confined to the deep basins (Bornholm Basin, Slupsk Furrow, Gdansk Deep and Gotland Basin) (Aro 1989, Bagge et al. 1994). Due to unfavorable hydrographic conditions in the Gdansk Deep and the Gotland Basin with vast anoxic zones resulting from a lack of major inflow events in the last decades, successful spawning of Baltic cod nowadays is mostly restricted to the Bornholm Basin (Bagge et al. 1994, MacKenzie et al. 2000).

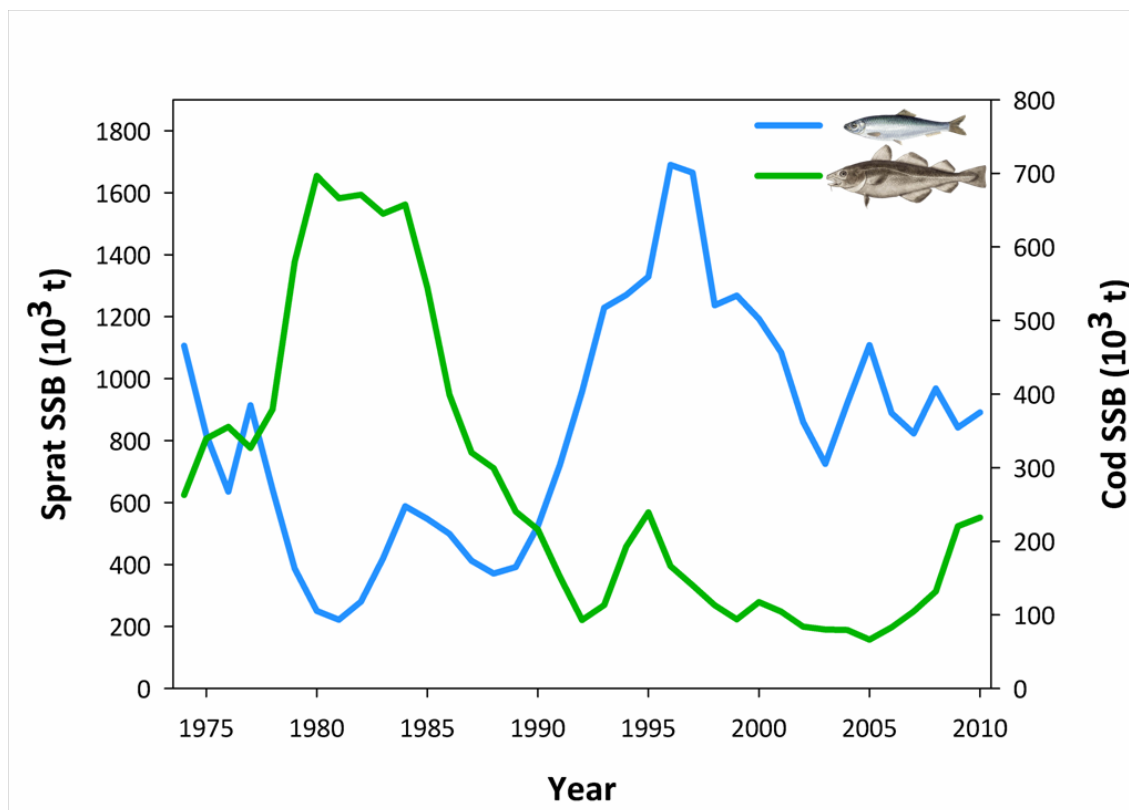


Figure 5: Inverse development of Eastern Baltic cod (*Gadus morhua*, green line) and sprat (*Sprattus sprattus*, blue line) spawning stock biomass (SSB) leading to a regime shift in the pelagic Baltic Sea ecosystem (ICES 2011a).

The limitation to the deep basins results from a minimum salinity of 11 psu that is required for fertilization success and neutral buoyancy of cod eggs (Westin & Nissling 1991). Owing to the peculiar hydrography, this salinity level is only prevalent in and below the permanent halocline of the deep basins of the central and eastern Baltic Sea. Therefore, during the spawning time, a peak abundance of eggs can be found in the region of the halocline with some quantities of viable eggs in deeper layers with higher salinity (Kändler 1944, Wieland & Jarre-Teichmann 1997). Due to a lack of regular inflows and a resulting decline in ambient oxygen concentration caused by restricted vertical mixing and biological degradation processes, oxygen concentrations in these layers may often be too low to allow for a successful cod egg development (Wieland et al. 1994). Ambient oxygen concentration has a non-linear effect on egg mortality, and the oxygen-related egg survival increases markedly above an oxygen concentration of $> 2 \text{ ml l}^{-1}$ with about 50 % viable hatch at 4 ml l^{-1} (Köster et al. 2005). Thus, especially in stagnation periods, a large quantity of cod eggs float in regions characterized by an ambient hydrographic conditions that do not sustain their survival and successful development. A combination of both salinity and oxygen thresholds led to the conceptual formulation of the so called “reproduction volume” (RV) (Plikshs et al. 1993, MacKenzie et al. 2000), which comprises the volume of water allowing for successful cod egg development. As the RV however only explains a part of the variance in cod

recruitment, other factors affecting the success of cod recruitment were identified: Amount and quality of eggs produced in relation to food availability (Kraus et al. 2002), low egg survival rates at slightly-above threshold oxygen levels (e.g. Wieland et al. 1994, Köster et al. 2005), food supply and accessibility for larvae and early juveniles (Rohlf 1999, Hinrichsen et al. 2002b, Huwer 2009), cannibalism on juveniles (Sparholt 1994) and predation on cod eggs by clupeids (Köster & Möllmann 2000).

Predation on cod eggs by clupeids sprat and herring, is of crucial importance as the decline of the EBC stock and an increase of the sprat stock co-occurred (Sparholt 1994). Despite an improvement of environmental reproduction conditions in the 1990s, cod stocks remained far below average (Köster & Möllmann 2000).

With Baltic cod and sprat stocks explicitly developing in an inverse manner, a considerable change from a cod-dominated to a sprat-dominated ecosystem occurred from the mid 1980s to the mid 1990s (Rudstam et al. 1994, Köster et al. 2009), mostly due to a recruitment failure of Baltic cod (Bagge et al. 1994). The underlying causes for the sharp decline in cod stock biomass in the 20th century, that has been referred to as regime shift (Alheit et al. 2005), and for the negative feedback-loops sustaining this altered regime have been allocated to climate driven effects in combination with overfishing. Namely, these were i) high egg mortality due to anoxic conditions in the spawning area, ii) high predation on cod eggs by clupeids due to high spatial overlap of clupeids and eggs and because of high stock numbers of sprat resulting from reduced fishing pressure and predation mortality by cod, and iii) increased larval mortality due to reduced abundance of key prey items (e.g. Köster & Möllmann 2000, Hinrichsen et al. 2002b, Köster et al. 2005, MacKenzie et al. 2007). Alternatively, Österblom et al. (2007) suggested human impacts, mostly fishing pressure and eutrophication, as main causes with climate effects possibly affecting magnitude, timing and persistence of the observed changes.

DISTRIBUTION OF ADULT COD

Apart from direct and indirect effects of ambient environmental conditions on early life stages of Baltic cod, adult cod are also affected by the distinct hydrographic features of the central Baltic Sea. This mostly applies to their spatial distribution.

Generally, cod are considered euryhaline and do not experience severe osmotic disturbances in salinities as low as 7 (Dutil et al. 1992, Claireaux et al. 1995). Additionally, the experimentally induced acclimation of cod from salinity levels of 28 to 7 psu did not affect their ability to tolerate low oxygen levels (Claireaux & Dutil 1992). However, cod faced with heterogeneous and unstable hydrographical conditions behaviorally maximize their scope for activity to reduce energy budgeting conflicts (Claireaux et al. 2000). Thus, cod generally avoid zones of low oxygen, but voluntarily enter oxygen depleted layers for short feeding excursions (Claireaux et al. 1995,

Neuenfeldt & Beyer 2006, Neuenfeldt et al. 2009). Outside their spawning period cod are obviously less dependent on ambient hydrography and disperse within their known distribution range in the central and northeastern Baltic Sea (Aro 1989, 2000). In their rather unstructured and undirected movements during the feeding period, cod cover extensive distances and are distributed in large areas (Bagge et al. 1974, Bagge et al. 1981). Cod in the southern central Baltic, i.e. in the Bornholm Basin, seem to be rather stationary, with migrations usually occurring from deeper parts to shallower areas in adjacent regions and back (Bagge et al. 1974, Netzel 1963, 1968, 1974). Despite showing a wider tolerance towards reduced salinity conditions and also being able to dwell in layers with low ambient oxygen concentrations, cod are still influenced by hydrography in a way that different tolerances of main prey species sprat and herring towards heterogeneous ambient hydrographic conditions lead to different, environmentally driven, spatial predator-prey overlaps (e.g. Neuenfeldt & Beyer 2003, 2006).

Like other major cod stocks, e.g. Icelandic cod (Jónsson 1982), Arcto-Norwegian cod (Bergstad et al. 1987), Faroese cod (Jakupsstovu & Reinert 1994) and Newfoundland cod (Hutchings et al. 1993, Lawson & Rose 2000a, b), Baltic cod also exert extensive spawning migrations to their spawning grounds, i.e. the Bornholm Basin (Aro 1989, Wieland et al. 2000, Neuenfeldt et al. 2007), where they accumulate prior to their spawning season (Aro 1989). During spawning, Baltic cod obviously tolerate less variability in salinity and prefer salinities between 11 and 15 psu below the permanent halocline, with their distribution generally being positively correlated with increasing salinity and oxygen levels (Tomkiewicz et al. 1998, Wieland et al. 2000).

GENERAL: STUDYING DISTRIBUTION PATTERNS OF FISHES

A sustainable marine, ecosystem-based management requires the knowledge of spatial distribution and abundance patterns of marine species. The understanding and predicting of such distribution patterns in heterogeneous environments lies at the very heart of ecology (Planque et al. 2011). Neither animal nor plant populations are distributed arbitrarily in space. All exhibit spatial patterns, with fish populations being no exception. Different factors, both external (e.g. environmental) and internal (density dependent processes, demographic structure), control the spatial distribution of fish populations (Fig. 6).

As many continental-shelf ecosystems underwent changes in community structure due to habitat destruction and overfishing (e.g. Jennings & Kaiser 1998, Myers & Worm 2003), much focus has been put on distributional characteristics of fishes in relation to habitat availability and habitat use (e.g. Morris & Ball 2006). One of the greatest barriers for mapping distribution data of marine species is the access to sampling data over a suitable spatial scale. Further complications arise when required spatial scales for mapping geographical distributions are larger than the stretch of individual surveys, the results of which sometimes base on different sampling gear and survey protocols

(Maxwell et al. 2009). Still, an increasing number of datasets from regularly conducted long-term scientific surveys facilitates studies on assemblage and distribution data of fishes (e.g. Maxwell et al. 2009, Bosman et al. 2011).

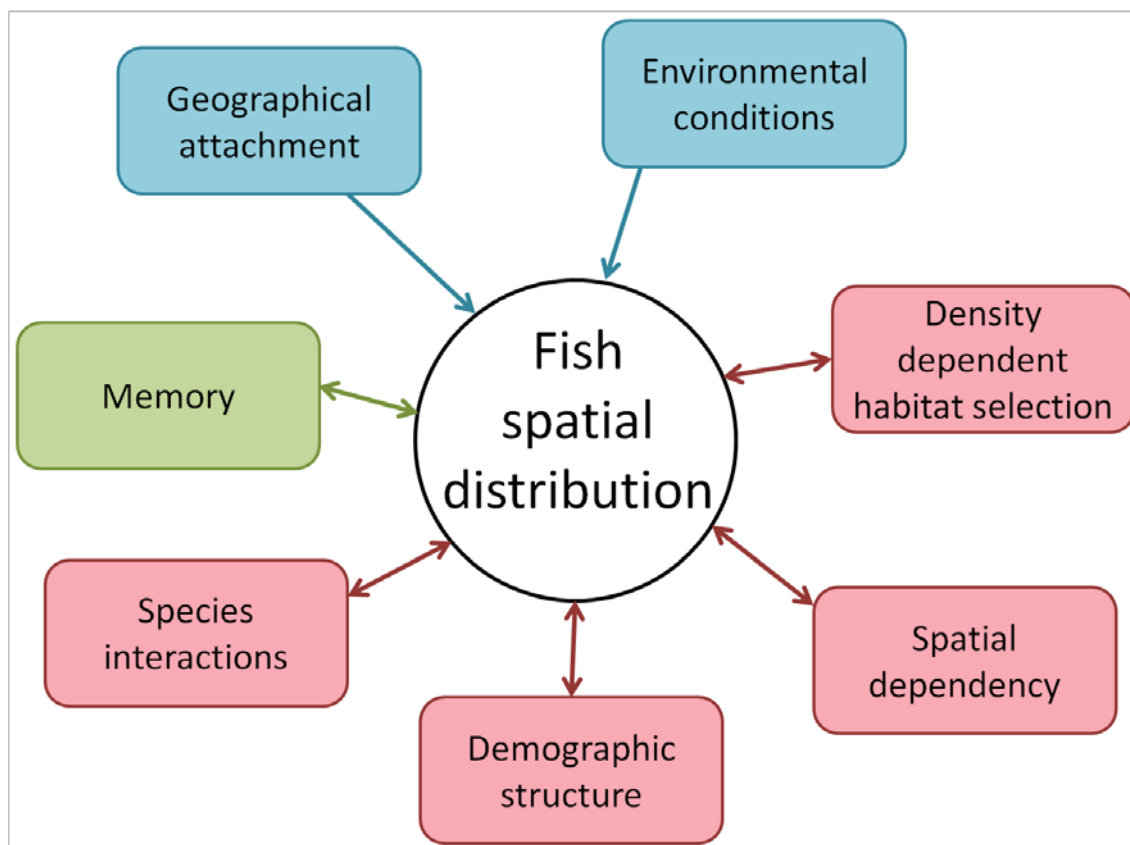


Figure 6: The main types of control of spatial fish distribution. Blue types are not dependent on the state of the population (external controls). Red types are dependent on the state of the population (internal controls). Green type is dependent on the current and past state of the population (after Planque et al. 2011).

Possible outcomes of corresponding studies for example can be temporally and spatially restricted closed areas (Marine Protected Areas, MPAs) (Apostolaki et al. 2002). A spatially explicit conservation measure that nevertheless is temporally restricted has been implemented since 1995 in the Bornholm Basin to protect and restore the spawning stock of Baltic cod: A summer-fishing ban on targeted cod fishery together with a specific spawning closure in a small area east of Bornholm Island with varying size over several years – both not leading to significant signs of recovery until 2009 (Kraus et al. 2009).

HYDROACOUSTICS

Whereas references to underwater sound can be traced back to medieval times (Urick 1983), the initial application of so-called “echosounders” is dated to the first decades of the 20th century (Simmonds & MacLennan 2005). It was not until 1929 before the first successful detection of fish via hydroacoustics was reported (Kimura 1929). Soon, first reports of the detection of schools of sprat (*Sprattus sprattus*) appeared (Anon 1934), and valuable scientific contributions were reported by Sund (1935) who revealed first insights on the distribution of cod (*Gadus morhua*) and their confinement to unexpectedly small water layers. After a rapid development of the method during the 2nd World War, the civil application of echosounders was enhanced, and first investigations on measuring fish abundance with hydroacoustics were conducted in the 1950s. This was initially accomplished by simply counting individual echoes (Mitson & Wood 1962), later echo amplitudes were summed up – which is basically the technique of echo integration remaining a fundamental principle of fish abundance estimation (Simmonds & MacLennan 2005). With the advent of dual-beam and split-beam echosounders, the target strength of individual fish in their environment could be measured. Until today, notable progress in the development of scientific echosounders has been made. In combination with multi-frequency analyses etc., hydroacoustics has become an invaluable tool in not only estimating fish abundance but also in determining distribution characteristics, habitat preferences, schooling behavior, community structure, etc. (see below).

After a paradigm shift leading to a growing consensus that single-species stock assessment is not sufficient to manage fisheries sustainably (Pikitch et al. 2004), an ecosystem based fishery management (EBFM) has been implemented aiming on a variety of effects of fishing on commercially exploited stocks, their predator, their prey, their competitors, their habitat, etc. (Koslow 2009). Acoustic methods, together with other oceanographic tools, are amongst the most promising to meet the requirements and scientific challenges of dynamic models explaining the interaction of fish and their environment (Koslow 2009). Hydroacoustic data can contribute to EBFM in a variety of applications and analyses.

Different fish species as well as e. g. zooplankton (mysids) etc. show specific frequency responses when ensonified with pulses from multiple echosounders operated at different frequencies (e. g. Korneliussen & Ona 2003). Thus, several methods can be applied to allow for species identification as well as an estimate on abundance, distribution patterns and behavior: Single target detection and fish tracking (e. g. Handegard et al. 2003), multi-frequency analyses for discrimination of species (e. g. Axenrot et al. 2009, Fernandes 2009, Korneliussen et al. 2009), or a combination of methods (e. g. Kaartvedt et al. 2005).

Further applications include investigation of target strength (e.g. Axenrot et al. 2009, Fernandes 2009, Korneliussen et al. 2009, Rose 2009), mapping of benthic habitat structure and characterization of pelagic community structure (e. g. Lebourges-Dhaussy et al. 2009), assessment of ecosystem dynamics in predator-prey interactions (e. g. Kaartvedt et al. 2005) and application of hydroacoustic methods to resolve the recruitment process of fishes (Koslow 2009 and references therein).

EBFM requires the knowledge of different ecological relationships between species as well as the ability to predict possible effects of climate variability and climate change (Koslow 2009). In conclusion, “no research tool is likely to prove as effective as acoustics in meeting these needs, if it is properly integrated into interdisciplinary research programmes involving ecology and oceanography, as well as fisheries” (Koslow 2009).

RATIONALE OF THIS THESIS

In the Baltic Sea, cod distribution and migration patterns have been assessed by trawl surveys (Neuenfeldt & Beyer 2003, 2006, Hjelm et al. 2004) or by tagging investigations (Aro 1989 and references therein). Tomkiewicz et al. (1998) used a combination of trawl catch results and hydroacoustic records to investigate the distribution of spawning cod in relation to external controls. Hinrichsen et al. (2007) employed the distribution of early egg stages as a proxy for spawning cod distribution and aggregation. In recent years, advanced electronic data-storage tags have been applied to reveal migration patterns and habitat preferences of adult cod (Neuenfeldt et al. 2007, 2009). It could be shown that outside their spawning period, EBC are distributed over large parts of the central and northeastern Baltic Sea and undertake rather undirected movements during the feeding period (Bagge et al. 1974, 1981; Aro 1989, 2000).

Based on trawl survey results conducted in ICES subdivisions 25-28, Hjelm et al. (2004) could show a positive correlation between oxygen concentration as well as salinity and cod distribution. An increased influence of external hydrographic controls on both horizontal and vertical distribution could be identified by Tomkiewicz et al. (1989) for spawning cod, with cod accumulating in areas and layers with oxygen concentration exceeding a certain threshold level. Additionally, Neuenfeldt & Beyer (2003, 2006) could show that these environmental influences also heavily affect the vertical and spatial overlap of cod and clupeids and thus determine both predation rates of cod on clupeids, but also of clupeids on cod eggs and larvae. Movements of cod tagged with data storage tags have been analyzed using geolocated positions derived from pressure, salinity and temperature measures of the tags (Neuenfeldt et al. 2007). Results also revealed that cod migrate into deeper layers of the Bornholm Basin when ambient oxygen concentration is high enough after inflows, but also showed that cod will migrate into hypoxic layers for short term feeding excursions (Neuenfeldt et al. 2009).

All of these investigations provided valuable data and information on distribution patterns of Baltic cod, showing that this species despite being known as euryhaline still faces environmentally induced habitat limitations affecting adult cod with a varying degree. However, the studies mentioned were either temporally or spatially restricted or characterized by method inherent shortcomings. Especially in the vertically stratified (central) Baltic Sea characterized by large hydrographic gradients on small vertical scales, trawl surveys due to the large vertical net opening of the gear employed often enough cannot sufficiently resolve the vertical distribution of cod to allow for a precise identification of external controls. Electronic data storage tags provide *in-situ* data allowing a precise measurement of the abiotic environment and a reconstruction of movement and migration patterns (e.g. Neuenfeldt et al. 2009), but due to the high costs of tags and due to the necessity to re-catch tagged individuals this method can only provide data for a low or restricted number of individuals.

Hydroacoustics, previously mainly applied to assess fish abundance (see section above) and also employed in some studies on cod distribution in the Baltic Sea, provide highly resolved real-time *in-situ* 3D field data containing quantitative information on density and size distributions of backscattering organisms (Koslow 2009). Another capacity of hydroacoustic data, the identification of single fish in their environment- could specifically be used to overcome the shortcomings of the combined studies mentioned above. Thus, additional information contributing to the present knowledge on cod distribution in the Baltic Sea can provide small-scale distribution data of cod that can be related to the physical environment of the fishes. This will facilitate to i) identify highly resolved external controls of EBC distribution, ii) scale the results from individual to population level and iii) allow for conclusions on the possible future development of EBC in light of large-scale changes of their abiotic environment.



AIM AND OUTLINE OF THIS THESIS

The general aim of this thesis is to identify distribution patterns of adult cod (*Gadus morhua*) in the Bornholm Basin, central Baltic Sea, during different phases of their annual cycle and to identify external driving mechanisms affecting those distribution patterns. To continue and expand previous studies on Baltic cod distribution (see previous chapter), highly resolving hydroacoustic methods are applied to identify single cod specimens and to further relate their *in-situ* distribution to ambient environmental influences.

Based on single-fish detection and fish-tracking algorithms applied and in combination with hydrodynamic models characterizing ambient environment, possible hydrographic influences on the distribution of adult cod in the environmentally heterogeneous pelagic central Baltic Sea ecosystem are identified. Implications of these findings for stock assessment as well as for future stock development in light of climate change are assessed and discussed in the corresponding chapters. Overall, the thesis is divided into the following chapters:

CHAPTER I

Hydroacoustic resolution of small-scale vertical distribution in Baltic cod *Gadus morhua* – habitat choice and limits during spawning

Matthias Schaber, Hans-Harald Hinrichsen, Stefan Neuenfeldt, Rüdiger Voss

In this study, the following hypothesis is tested: The distribution of cod is affected by abiotic factors, which also constitute habitat limits. Thus, several aspects of cod distribution in the central Baltic -methodical as well as seasonal and environmental- are addressed. One aspect is to validate the applicability of hydroacoustic single fish-tracking to identify distribution patterns of cod. This is addressed by comparing *in-situ* hydroacoustic data with cod distribution data recorded by archival electronic data-storage-tags. Another aspect of this study is to identify environmental influences on cod distribution during spawning and to compare these influences and corresponding distribution patterns between years with improved oxygen concentrations in the deep parts of the Bornholm Basin (post-inflow situation 2003) and years with extended oxygen depletion in these layers (stagnation situation 2005). Abiotic influences on cod distribution, cod habitat preferences and habitat thresholds are identified and tested with quotient rule analysis and non-parametric regression models (GAM).

CHAPTER II

Seasonal changes in vertical distribution patterns of cod (*Gadus morhua*) in the Bornholm Basin, central Baltic Sea

Matthias Schaber, Hans-Harald Hinrichsen, Joachim Gröger

In this study, the following hypothesis is tested: Long-term trends in distribution patterns of cod are affected by environmental factors. Therefore, long-term variations in seasonal distribution patterns of adult cod along longitudinal hydroacoustic transects covering the Bornholm Basin are investigated. The sampling period covers the years 2006 to 2009 and comprises surveys in April, June and August of each year to cover the total spawning period of eastern Baltic cod in the Bornholm Basin. Key parameters affecting the distribution patterns are identified using a GLM effect model. Results of the long-term investigation on distribution patterns are discussed in context with the sampling method hitherto applied in international trawl surveys for assessment of the Baltic cod stocks.

CHAPTER III

Climate driven long-term trends in Baltic Sea oxygen concentrations, and the potential consequences for eastern Baltic cod (*Gadus morhua*)

Hans-Harald Hinrichsen, Bastian Huwer, Andrejs Makarchouk, Christoph Petereit, Matthias Schaber, Rüdiger Voss

This study addresses the following hypothesis: Based on distribution data of different life stages of cod, negative long-term effects of environmental changes can be expected. To verify this hypothesis, long-term trends of progressive oxygen depletion in the Baltic Sea and resulting effects on Eastern Baltic cod are investigated. Analyses are based on published data, laboratory experiments and field data and cover all life-stages of cod – eggs, larvae, juveniles and adults. Experimentally derived results of oxygen driven processes are validated by field data. Field data, amongst others, are analyzed to assess the effects of declining ambient oxygen concentrations on e.g. adult cod. Therefore, hydroacoustically derived long-term distribution patterns of cod are related to corresponding ambient oxygen saturation and its effects on e.g. gastric evacuation rates and overall condition. Overall results are discussed in light of local effects of global warming and climate change and lead to a comprehensive picture of expected environmentally driven future cod stock development in the central Baltic Sea.



IN A NUTSHELL: GENERAL MATERIAL AND METHODS

HYDROACOUSTIC DATA

In all studies of this thesis, the following basic method was employed to identify individual cod (*Gadus morhua*) from echorecordings: Hydroacoustic distribution data were collected with a hull-mounted Simrad EK60 scientific echosounder operated at 38 kHz. After post-processing of the data with Echoview software (Sonardata 2007), a single fish detection algorithm and consecutively a fish-tracking algorithm were applied (Fig. 7). The former is mainly based on the target strength of individual echoes scattered by fish and the (angular) position of the corresponding echo-sources in the sound beam. The latter is used to identify and combine groups of single echoes that show a systematic pattern of movement, assuming that the echoes have been generated by a single object moving through space or repeatedly ensonified by the echosounder.



Figure 7: Identification of individual cod from hydroacoustic data from the Bornholm Basin. a) Hydroacoustic raw data as visible on echosounder screen at a threshold of -50 dB. Five typically shaped echotraces consisting of multiple echoes indicate presence of fish. Colors indicate different target strength of echoes. b) After application of a single target identification algorithm with a threshold of -37 dB, only the echoes that are attributed to a single backscattering target with predefined properties remain. Note that one individual fish can scatter multiple single echoes with different target strength. c) The application of a fish-tracking algorithm combines single targets with systematic movement and distribution patterns to a single object (Fish Track, FT) – in this case four individual cod (*Gadus morhua*).

Both algorithms combined allowed the detection of individual cod in the survey area, and further the allocation of an exact three-dimensional position to each cod in the water column. Amongst a multitude of derived parameters available for each single cod, longitudinal and latitudinal position data together with vertical position data were primarily used to determine the spatial position of the fish in the water column. Based on the position data, the corresponding date of detection and simultaneous (or near-time) oceanographic measurements, hydrodynamic models were used to assess ambient environmental conditions of each individual cod detected. Detailed information on survey design, transducer settings and data evaluation are given in the corresponding chapters of this thesis.

ENVIRONMENTAL DATA

To identify environmental conditions cod meet in their habitat, ambient temperature, salinity and oxygen concentration values were allocated to each individual cod, identified *in-situ* as described above. Attribution of environmental data was based on geographic position and depth of each cod. Oceanographic data were either recorded on a regular station grid with a stationary, vertically deployed ADM-CTD probe (**Chapter I & II**) or continuously recorded with a towed, undulating CTD probe (**Chapter II**). Depending on the sampling gear employed for recording of hydrographic data, the allocation of oceanographic data to individual cod was achieved in different ways. Data from the stationary, vertically deployed CTD probe were interpolated by employing a free-surface Bryan-Cox-Semtner hydrodynamic model (Killworth et al. 1991) adopted for the Baltic Sea (Lehmann 1995, Lehmann & Hinrichsen 2000). Data from the undulating, towed CTD probe were assigned to individual fish based on the horizontally nearest dataset and the corresponding depth stratum. Due to the restricted horizontal resolution of the model grid employed, the resolution of hydrographic data was lower than that of hydroacoustic data (regular station grid vs. continuous recording). As gradients in hydrographic parameters are distinctively more pronounced on the vertical than on the horizontal scale in the deep basins of the Baltic Sea (e. g. see Introduction Fig. 3), the method employed seems to be the best trade-off between requirement and availability of highly resolved oceanographic data. An overview of data sources and methods applied in studies contributing to this thesis is given in Fig. 8.

DATA ANALYSIS

To address the specific biological hypotheses outlined in the previous section, different testing and modeling approaches were followed. Additionally, different indices applicable to underline the specific hypotheses were implemented. A corresponding overview is given in Tab. 1. The reader is referred to the specific chapters for detailed descriptions of methods applied and approaches followed.

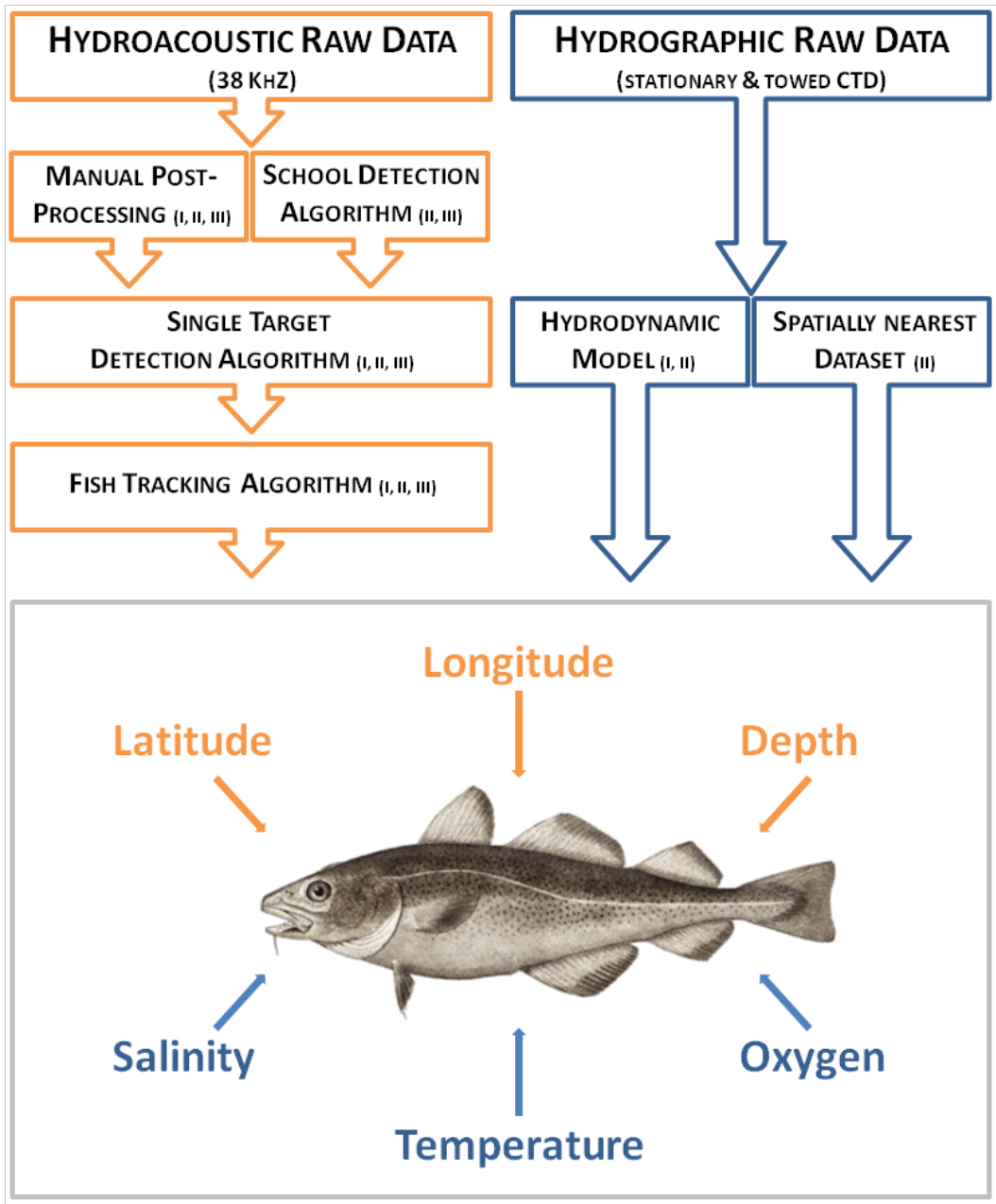


Figure 8: General data sources and methods applied in the studies contributing to this thesis. Hydroacoustic data sources, post-processing procedures and resulting parameters allocated to individual cod are depicted in orange. Hydrographic data sources and processing procedures as well as resulting parameters allocated to individual cod are depicted in blue. Numbers in brackets indicate the referring chapters the method was applied in.

Table 1: Hypotheses, null hypotheses and methodical approaches followed in the contributing chapters. Refer to specific chapters and Annex III (List of Abbreviations) for details.

CHAPTER	WORKING/BIOLOGICAL HYPOTHESIS	H0	INDICES/TESTS APPLIED
I	The distribution of cod is affected by biotic factors. Habitat preferences and thresholds exist.	Observed distribution patterns within an environmental category are arbitrary.	Quotient Rule Analysis GAM GCV
II	Long-term trends in distribution patterns are caused by environmental factors.	No significant influence of environmental parameters on seasonal depth distribution patterns of cod is evident.	GLM
III	Based on distribution data of different life stages of cod, negative long-term effects of environmental changes are evident.	Environmental- and distribution specific processes affecting different life stages of cod are not related to abiotic parameters.	OES LVMA Settling Area Size GER Fulton's K



I. Hydroacoustic resolution of small-scale vertical distribution of Baltic cod (*Gadus morhua* L.) – habitat choice and limits during spawning

Matthias Schaber ¹, Hans-Harald Hinrichsen ¹, Stefan Neuenfeldt ² and Rüdiger Voss³

¹ *Leibniz Institute of Marine Sciences, Düsternbrooker Weg 20, 24105 Kiel, Germany*

² *Technical University of Denmark, National Institute of Aquatic Resources,
Charlottenlund Castle, Jaegersborg Allé 1, 2920 Charlottenlund, Denmark*

³ *Sustainable Fisheries, Department of Economy, University of Kiel, Wilhelm-SeeligPlatz 1,
24118 Kiel, Germany*

ABSTRACT

Highly stratified marine ecosystems with dynamic features such as fronts or clines in salinity, temperature or oxygen concentration, challenge the individuals' ability to select suitable living conditions. Ultimately, environmental heterogeneity organizes the populations' spatial distributions and hence the ecosystems spatial structure. Our aim here is to present a method to resolve small-scale distribution on individual level, as needed for the behaviorally based prediction of habitat choice and limits. Focus was on the small-scale vertical distribution of cod (*Gadus morhua* L.) in the Bornholm Basin, central Baltic Sea, during spawning time in two years with different vertical thermohaline and oxygen stratifications. Individual cod were identified by echo-tracking of real-time *in-situ* hydroacoustic distribution data. In order to resolve and identify hydrographic preferences and limits, ambient parameters including temperature, salinity and oxygen concentration as well as expected egg-survival probability were individually allocated to each fish. The vertical distribution of hydroacoustically identified fish was compared to data simultaneously recorded by data-storage-tags attached to cod. Results showed a clear influence of ambient salinity and oxygen concentration on distribution pattern and distributional limitation of cod during spawning time, and also consistency of data-storage-tag derived distribution patterns with those based on individual echo-tracking. We consider this method therefore a useful tool to analyze individual behavior and its implications for the population's spatial distribution in stratified environments.

Keywords: Baltic Sea, cod, vertical distribution, hydroacoustic tracking, environmental parameters

INTRODUCTION

Much focus has recently been put on distributional and ecological characteristics of marine fish with special regards to habitat availability and habitat use (Austin 2002a, Morris & Ball 2006). Spatially explicit conservation measures such as closed areas (Apostolaki et al. 2002) as well as the assessment of predator-prey overlap (Neuenfeldt 2002, Neuenfeldt & Beyer 2003) necessitate measurements of individual fish occurrence in relation to biotic and abiotic environmental parameters during different conditions, as for example feeding or spawning.

Scientific echosounders provide real-time *in-situ* 3D field data (Massé & Gerlotto 2003) containing quantitative information on density and size distributions of backscattering organisms (Towler et al. 2003). Consequently hydroacoustic surveys have widely been applied for the analysis of fish abundance (see MacLennan & Simmonds 1992), diurnal and shoaling dynamics (e. g. Fréon et al. 1996, Orłowski 1999, Nilsson et al. 2003, Orłowski 2005), predation and avoidance behavior (e. g. Handegard & Tjøstheim 2005, Kaartvedt et al. 2005) as well as distribution and habitat association (e. g. Lawson & Rose 2000a, Lawson & Rose 2000b, Robichaud & Rose 2001, McKinstry et al. 2005). However, analyses based on echosounder data are often hampered because (i) the detection of individual targets is difficult and (ii) if identification of individual fish is possible, allocation of echoes to a certain fish species is difficult. Therefore, corresponding trawl hauls have to be carried out for species identification and abundance estimation – with the shortcoming that small-scale acoustic information collected from echosounders is transformed to the larger trawl scale, which often cannot resolve environmental gradients and thus distributional characteristics detailed enough.

In this paper we propose a novel method to overcome this problem by applying hydroacoustic fish track identification. To verify our method, we compare observed individual based small-scale vertical distribution patterns in relation to ambient hydrography to data from comparable hydrographic situations obtained from data-storage-tags (DST). Focus was put on cod (*Gadus morhua*) in the central Baltic Sea during peak spawning season.

Due to the semi-enclosed brackish water system characteristic of the Baltic, a strong vertical stratification of temperature, salinity and oxygen is established. A permanent halocline separates low saline water on the surface from high saline deep-water. Below that halocline salinity continuously increases whereas oxygen concentration decreases due to stable vertical stratification. Renewal of bottom waters and thus improvement of hydrographic conditions therefore is only achieved by major water intrusions from adjacent North Sea regions. These irregular inflow events are strongly dependent on atmospheric forcing conditions (Matthäus & Franck 1992, Matthäus & Schinke 1994, Fonselius & Valderrama 2003).

Cod reproduction in the central and eastern Baltic Sea is limited to the deep basins, as a minimum salinity of 11 psu is required for fertilization success and neutral buoyancy of eggs (Westin & Nissling 1991). Peak abundance of cod eggs occurs in the region of the halocline with some quantities of viable eggs in the more saline deep layer depending on oxygen levels (Kändler 1944, Wieland & Jarre-Teichmann 1997). However, due to a lack of regular major inflow events, oxygen concentrations in these layers may be often too low for cod eggs to survive (Wieland et al. 1994). Oxygen concentration has a non-linear effect on egg mortality. Ambient oxygen-related egg survival (OES) increases markedly above 2 ml l⁻¹ oxygen concentration with 50 % viable hatch at 4 ml l⁻¹ (Köster et al. 2005).

We studied the vertical distribution of cod in their spawning environment in the Bornholm Basin during spawning time in two years with contrasting abiotic (inflow vs. stagnation) conditions. Distributional characteristics were derived from single fish identified and tracked by hydroacoustic measurements. These individual based small-scale vertical distribution patterns of cod were related to ambient hydrography and ambient oxygen-related egg survival. Vertical distributions derived from electronically tagged individuals for the same specific period were used for verification of the echo-tracking.

MATERIAL & METHODS

Hydroacoustic data

Hydroacoustic data were continuously recorded during day- and nighttime on two research cruises of RV „Alkor“ in the central Baltic Sea in July/August 2003 and August 2005. Data sampling was carried out on a regular station grid (Fig. I-1) that was utilized for measuring corresponding ambient hydrographic and biological parameters.

A Simrad hull-mounted split-beam transducer ES38-B (beam width 6.86° along and 6.80° athwart) and a Simrad scientific Echosounder EK60 operated at 38 kHz by Simrad ER60-Software were used for collection of data. The echosounder and transducer had been calibrated with a 60 mm copper sphere prior to the survey according to the standard method described by Foote et al. (1986) and ICES (2001). Ambient sound speed was calculated from temperature and salinity recorded and applied in echosounder settings during measurements. Transducer settings used differed on the cruises in 2003 and 2005. In August 2003 the focus of echorecordings was on pelagic clupeid schools whereas a higher horizontal and vertical resolution was the main task in setting transducer parameters in August 2005. A detailed list of settings applied in the accordant cruises is given in Tab. I-1.

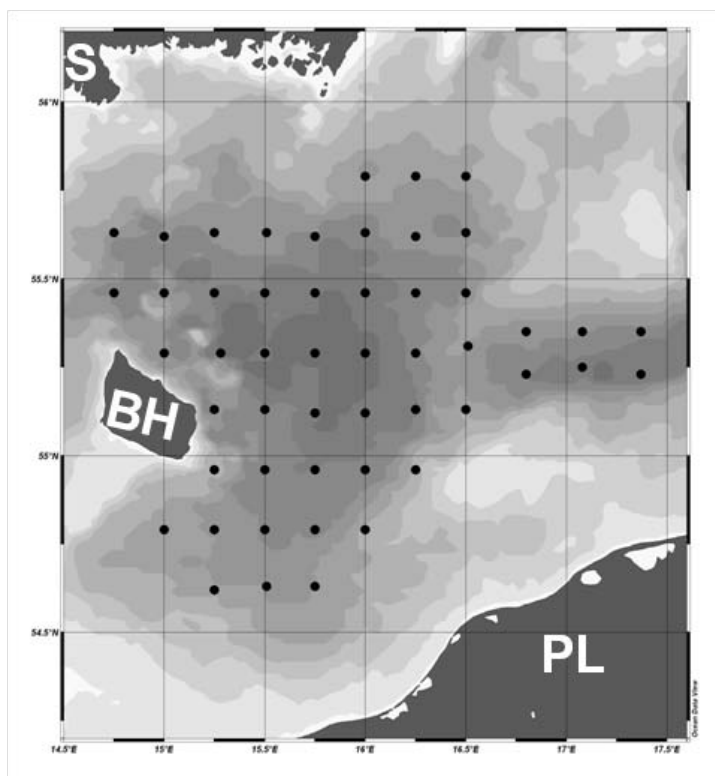


Figure I-1: Station grid utilized for measuring hydrographic and biological parameters in August 2003 and July 2005 (BH – Bornholm (DK), S – Sweden, PL – Poland). Map generated with ODV (Schlitzer 2007).

Table I-1: Transducer settings used in cruises AL226 (August 2003) and AL262 (July/August 2005).

	2003	2005
Sample interval (ms)	0.256	0.128
Frequency (kHz)	38	38
Pulse length (ms)	1.024	0.512
TS Gain (dB)	26.22	25.91

Post-processing of data was performed using Echoview software (Sonardata 2007; www.echoview.com). Echo detection of the bottom topography was corrected when necessary. Noise signals and scattering layers as well as clupeid schools were marked in the echograms and excluded from further processing, i.e. analyzing for single target echoes. Echoes located within the upper 10 m of the water column were neglected due to possible origin from artificial turbulent effects caused by ship operation.

Single target echoes were identified by applying Echoview's single target detection operator. Therefore, the split-beam single target identification method 2 based on target strength- and angular-position-data was adopted. Thus, echoes scattered by

single fish could be discerned from those scattered by shoals of fish. As target strength (TS) is a function of fish size (Foote 1987, Clay & Castonguay 1996, Ehrenberg & Torkelson 1996, Rose & Porter 1996, McQuinn & Winger 2003), a threshold of -50 dB was set for single cod identification in order to cover the size range derived from corresponding fishery hauls. The single target detection parameters used were: minimum normalized pulse length = 0.49, maximum normalized pulse length = 1.51, maximum beam compensation = 12.0 dB.

The resulting single target echoes were processed using Echoview's target tracking algorithm allowing the aggregation of single echoes to one track by allocating multiple consecutive echoes to one single fish and thus avoiding pseudo-replication of targets. The tracking algorithm chosen was based on range, angles and time. Due to a mean vessel speed of 10 knots between stations, the horizontal range for target acceptance between single targets was set higher than vertical and lateral range, i.e. the minor (longitudinal) axis was allocated 50 % weight in contrast to 30 % weight for the major (transversal) axis. The minimum number of single targets required for an accepted fish track and the minimum number of pings in one track were set to 3. This led to a reduction in the total number of fish tracks but also to an enhanced reliability of single tracks. In order to distinguish echotraces of densely aggregated multiple fish from interrupted echotraces left by a single fish, the fish tracks identified by the tracking algorithm were –when necessary- manually edited and corrected. This was accomplished using angle echograms displaying along and athwart angular position data derived from the split-beam transducer. Both angular echograms and the single target echogram were synchronized and thus allowed the interpretation of the relative position of tracked targets in the beam and the identification of previously allocated fish tracks that needed to be split (originating from multiple fish) or merged (interrupted track from one single fish) (Mueller, www.aquacoustics.com/AngleEchograms.pdf).

Mean geographical position, mean depth and mean target strength of the single fish identified then were exported for further analysis. As the sample interval was lower (i.e. less pings on a horizontal scale) and the pulse duration was longer (i.e. lower vertical resolution) in 2003 than in 2005 (see Tab. I-1), the number of resulting tracks was higher for 2005 (n=5471) than for 2003 (n=1875).

Hydrographic data

Ambient vertically resolved hydrographic variables such as temperature, salinity, oxygen concentration and saturation, etc. were recorded using an ADM-CTD probe deployed on the regular station grid in the Bornholm Basin (Fig. I-1). These hydrographic parameters were taken for the assignment to hydroacoustically located individual fish. The horizontal resolution of the hydrographic parameters can influence the prediction of the fish distribution. Thus, as a rule of thumb, the grid size should be fine enough to capture

the appropriate horizontal mixing processes (e.g. smaller than the internal Rossby radius; Hinrichsen et al. 2002). Horizontal maps were constructed by interpolating the physical property data onto a model grid with 5 km horizontal resolution using objective analysis (Bretherton et al. 1976). An isotropic covariance function

$$f(r) = \sigma^2 \exp(-r^2/R^2) \quad (1)$$

was used with $R = 25$ km, σ^2 the variance and r the distance between data points. It was assumed that the error variance due to measurement errors and small scale noise amounted to 15 % of the total variance of the fields, because in our field measurements the error variance did not exceed 15 % of the total variance. Correlation length and variance were obtained from fitting the data to a Gaussian function. It was also assumed that the hydrographic field observations taken prior to the hydroacoustic surveys were quasi-synoptic. Further linear interpolation of data between model grid points was used to assign quasi-realistic ambient variables to each single fish identified.

Data-storage-tags (DST)

Data from echorecordings were compared with ambient hydrographic and distribution data obtained from tagged cod. The *Star-Oddi* CTD (conductivity, temperature and depth) tags used recorded ambient pressure (depth), temperature and salinity every hour. Maximum recording period was set to 2 years. Accuracy of the according parameters after calibration was ± 0.5 for salinity, ± 0.1 °C for temperature and ± 0.2 dbar for depth. Data extracted from recovered tags was then used to reconstruct migration routes of individual cod by geolocation using a hydrodynamic model of the Baltic Sea (Lehmann 1995). Hydrodynamic model runs could result in increasing uncertainties in the simulated physical property fields, and hence in the assignment of environmental properties to tagged individual fish. To overcome at least some of these problems the utilization of assimilation techniques were used to improve the output of the model simulations. In order to initialize and to re-initialize the model, three-dimensional distributions of temperature, salinity and oxygen concentrations were taken from hydrographic surveys of Baltic cod covering different sub-areas of the Baltic Sea undertaken prior to the investigation periods. Both initialization and re-initialization of hydrographic properties prior to the beginning of the tagging period are an essential pre-requisite to keep the uncertainty of the modeled data relatively low. Further improvement was achieved through additional (4-6) re-initializations of the modeled fields during the tagging period. During the surveys the hydrographic property distributions in the western Baltic, the Arkona Basin, the Bornholm Basin, and the Stolpe Trench were recorded. Residuals obtained between physical parameters measured by the tags, and the corresponding values generated by the model were used for quality control. The histograms for all the parameters taken into consideration indicate that for all parameters (pressure, temperature and salinity) 66 % of the residuals were in the

range of 0-0.5. For detailed information on tags and methods applied, see Neuenfeldt et al. (2007). For comparison, only cod echoes and DST-recordings below the halocline (salinity >9 psu) were included (n = 111 DST records in 2003 and n = 117 DST records in 2005).

Cod habitat characterization

Distributional patterns of hydroacoustically identified cod in relation to ambient hydrography and available habitat frequencies were resolved. Relative available habitat distribution frequencies were calculated as relative frequency of a categorized parameter (temperature, salinity, oxygen concentration) based on numbers of all categories observed per parameter on the grid.

As distribution of cod was significantly limited to layers below the halocline, further results focused on distributional characteristics in habitats with a salinity higher than 9 psu. This led to a reduction of single cod tracks to 1730 in 2003 and 5241 in 2005 respectively.

Data collection in both years took place in peak spawning time of eastern Baltic cod (Wieland et al. 2000). Therefore, cod distribution also was related to ambient oxygen-related egg survival (OES). OES was calculated based on an oxygen-egg survival relationship by Köster et al. (2005) using a sigmoid function showing oxygen levels with a 50 % relative viable hatch at 4 ml l⁻¹. As a minimum salinity of 11 psu is required for fertilization success and neutral buoyancy of cod eggs (Westin & Nissling 1991), OES was focused upon in layers with a salinity >11 psu. This further reduced the absolute numbers of cod detections to 1584 (2003) and 5089 (2005) respectively.

To further identify and statistically evaluate preferred habitat of cod and environmental habitat limits the total hydroacoustic transects were classified in horizontal and vertical strata (observation-cells with a 10 km horizontal and 5 m vertical resolution). Quotient curves have been derived from hydroacoustically obtained cod abundance data and individual environmental variables within each stratum. The ratio (Q_c) of the percentage of total number of cod within each environmental parameter (%cod_c) and the percentage frequency of occurrence of each environmental parameter (%environmental parameter_c) was calculated.

$$Q_c = \%cod_c / \%environmental\ parameter_c \quad (2)$$

This analysis is based on the whole column below the halocline in each horizontal stratum with cod identified. Quotient values greater than 1 indicate positive selection of related categories, whereas quotient values less than 1 are considered to represent avoidance of those parameters (van der Lingen et al. 2001). Statistical evaluation was performed by applying the adapted R library “Shachar” (developed by M. Bernal, Instituto Español de Oceanografía, Centro Oceanográfico de Málaga, Apdo 285,

Puerto Pesquero s/n, 29640 Fuengirola, Spain) that includes a randomization test estimating the 95 % confidence limits for rejecting the null hypothesis of the observed quotient within a particular environmental category being obtained by pure chance alone.

To further isolate and statistically validate factors affecting cod abundance (CA) in the field, non-parametric regression models (i.e. GAMs) were used (e.g. Porter et al. 2005, Dingsoer et al. 2007). A GAM is a statistical model blending properties of multiple regressions (a special case of general linear model) with additive models. In a GAM the parameter terms b_i and x_i of a multiple regression are replaced with functions $f(x_i)$: The functions $f(x_i)$ are arbitrary and often nonparametric, thus providing the potential for better fits to data than other methods. A typical GAM might use a smoothing function such as a locally weighted mean for the $f(x_i)$. Thus, the priority of GAMs is predictive ability.

The following physical environmental variables were determined for each observation-cell and subsequently used as independent variables to explain adult cod abundance.

Latitude, Longitude: For each observation-cell the mean geographical position was recorded, giving information about adult position in relation to the basin topography.

Ambient temperature, salinity, oxygen content: Temperature profiles were measured on each CTD station and allocated to each cod identified. Mean temperature, salinity and oxygen content were calculated for each observation-cell to represent adult cod ambient conditions.

Vertical gradients in abiotic conditions: For each observation-cell the within-cell gradient of abiotic conditions, i.e. the change in conditions over a 5 m vertical scale, were calculated, as organisms have been shown to accumulate at clines or to use gradients for orientation.

Inflow/Stagnation: Hydrographic conditions in the Bornholm Basin have been shown to be very different comparing post-inflow situations to years after a longer time of stagnation. In January 2003, a major Baltic inflow occurred, which dominated the hydrographic conditions in July 2003. After 2 further years of stagnation, the situation in July 2005 can be seen as a typical stagnation scenario. Therefore, the year-effect was included as a factor variable with two levels.

Cod abundance: For each observation-cell a cod abundance (CA) of $n = 0-73$ adult cod were identified by single-fish detection and tracking algorithms. As the dependant variable CA was not normally distributed, a fourth-root data transformation was applied. Afterwards no significant deviation from the normal distribution occurred (David et al.-test, $p < 0.05$).

All environmental factors were initially included as covariates in an additive GAM model. The *Generalized Cross Validation* (GCV, Wood 2000) was used as the criterion for model selection: all combinations of covariates were tested, potentially excluding non-significant ($p > 0.05$) covariates and minimizing the GCV. The GCV is a measure of predictive error of the model and thus takes into account not only the fit, but also the model complexity. It therefore does penalize excessively complex models as a result of greater prediction error. All analyses were conducted using the R-software (version 2.2.0, www.r-project.org), specifically the package “mgcv”.

RESULTS

Hydrography

The hydrography in deeper water areas observed during the July/August cruise in 2003 was primarily determined by a strong inflow event in January 2003 (Fig. I-2a). This major Baltic inflow entirely replenished the old oxygen-depleted water masses below the permanent halocline. Salinities at the bottom exceeded 18 psu. From the cruise data it is obvious that the oxygen concentrations near and below the halocline quickly decreased from March to August from almost 6 to 3 ml l⁻¹ at the bottom (Hinrichsen et al. 2007).

In July 2005, after a lack of further inflows, the hydrographic conditions had deteriorated (Fig. I-2b). Hydrographic measurements identified the permanent halocline in the Bornholm Basin in the depth range 55-60 m increasing from east towards west. Within the deep water area, oxygen values were below 2 ml l⁻¹ with temperatures around 6 °C and salinities not exceeding 17 psu. Although there was an indication of a new inflow of highly saline water which had entered the Bornholm Basin in January 2005, the oxygen conditions in the deep part of the Bornholm Basin had only slightly improved.

Vertical distribution of cod in relation to mean hydrography

There was a marked difference in the vertical distribution pattern of identified echoes between July/August 2003 and August 2005 (Fig. I-2). The major part however was situated below the halocline in both years. Corresponding fishery hauls and data-storage-tag recordings (see below) showed that there were no cod situated above the halocline. Thus, echoes above the halocline were considered non-cod. In 2003 cod showed a broad distribution below the halocline. Comparison with mean hydrography showed that the vertical distribution of cod was strongly linked to ambient hydrographic parameters. Salinity seemed to constitute the upper distributional limit whereas oxygen concentration was the limiting factor in deeper water. In 2003 the whole water column was well oxygenated with average oxygen levels still close to 3 ml l⁻¹ down to the seafloor. Therefore, no distinct vertical limitation as well as a relatively even distribution of cod below the halocline was obvious. There was no clear effect of temperature on fish distribution visible.

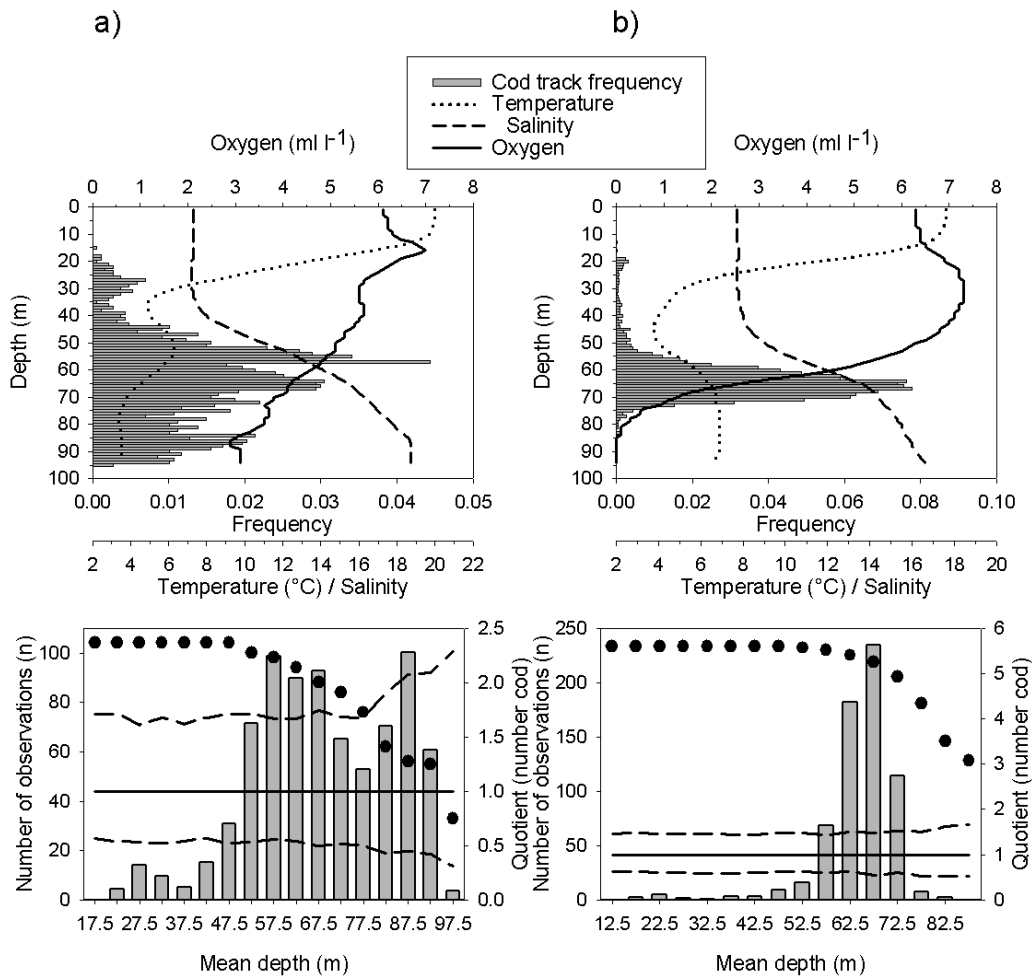


Figure I-2: Depth distribution of single fish echoes in August 2003 (a, n=1875) and July/August 2005 (b, n=5471) as derived from echo-tracking. Upper panel: Distribution in relation to mean ambient hydrography. Lower panel: Quotient rule analysis. Dots: number of observations of corresponding abiotic parameter. Bars: Single fish quotient curve. Dotted lines – 95 % confidence interval and quotient value 1 (marking random selection of habitat).

In 2005 upper distributional limits also were set by the halocline with 95 % of echoes identified being situated below a salinity of 10 psu (92 % below 11 psu). With regards to oxygen a clear depletion due to lack of inflow was measured in deeper waters. Oxygen concentration was below 1 ml l⁻¹ in 73 m depth and from 84 m downwards there was no oxygen detectable. Fish distribution markedly followed the oxycline with only a very small fraction (0.4 %) of identified echoes being distributed below 73 m. As in 2003, there was no clear effect of temperature on vertical cod distribution visible. Quotient analysis showed a significant avoidance of water layers shallower than 45 m and a clear preference of layers below the halocline (significant between 55 m and 70 m) in 2003, whereas in 2005 a clear and significant avoidance of layers above 55 m and below 75 m could be shown. Instead, cod significantly preferred depths between 55 m and 75 m.

Comparison of echodata and tags

In both years observed, there were –with the exception of one record in July 2005- no records from DS-tags attached to cod from above the halocline, i.e. all cod tagged almost exclusively dwelled below the halocline during the observation period.

In August 2003, cod echoes below the halocline ($n=1730$) were distributed between 41 m and 95 m with a distribution maximum at 57 m (Fig. I-3a). Two local distribution maxima were found in layers between 64 - 67 m and 86 - 87 m (>2 to >3 % each depth layer). Data from DS-Tags revealed a distribution between 58 m and 95 m during the period observed. Over 95 % of observations ($n=111$) were found between 60 m and 75 m with local accumulation maxima at 64 m and 73 m (9 – 11 %) and an absolute distribution maximum at 70 m (13 %). Only 4 observations were recorded in water layers deeper than 77 m.

In 2005 (Fig. I-3b), cod echoes below the halocline were observed between 45 m and 87 m ($n=5241$). The major part (91 %) was situated between 57 m and 72 m with a clear accumulation between 64 m and 67 m (32 %) and a distribution maximum at 67 m (8 %). Only 2 % of all cod observed were situated below 73 m. A comparison with data from DS-tags ($n=117$) revealed a similar distribution pattern of tagged cod during the period observed. Tag depth recordings ranged from 36 m to 73 m. Approximately 90 % of tagged cod dwelled in water layers below 60 m. A clear aggregation maximum corresponding to hydroacoustic data was observed between 63 m and 65 m (39 %) as well as a decrease in relative frequency below 70 m depth.

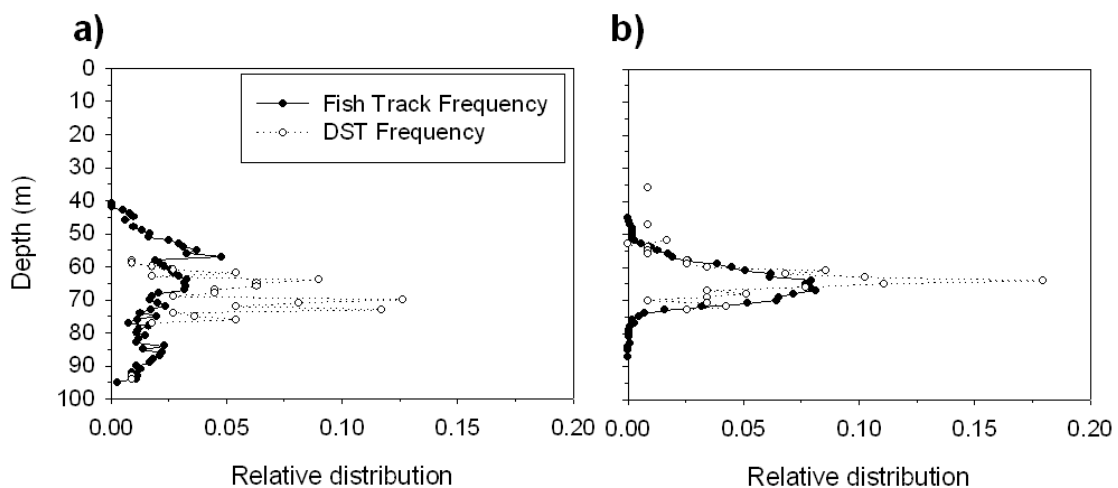


Figure I-3: *Gadus morhua*. Relative depth distribution below halocline (salinity >9) of echo tracks in comparison with depth distribution data obtained from data-storage-tags in 2003 (a, $n= 1730$ cod and $n=111$ tags) and 2005 (b, $n= 5241$ cod and $n= 117$ tags).

Habitat utilization – availability, choice and limits

Temperature

Observed habitat utilization below the halocline took place between 3.25 °C and 9.5 °C in 2003 (Fig. I-4a). More than 95 % of cod observed were distributed in temperatures between 3.25 °C and 6.25 °C with local maxima at 3.5 °C and 5.25 °C. Comparison with the frequency of available habitat in 2003 showed that cod did not use the whole temperature range available below the halocline. However, the temperature ranges with accumulations of cod also were present at higher frequencies in the available environment. Quotient analysis showed no clear pattern of preference or avoidance. Only temperatures higher than 7 °C were preferred with preference becoming significant above 8 °C.

In August 2005, after 2 years of stagnation, cod habitat utilization in relation to ambient temperature showed a different distribution pattern (Fig. I-4b). Except from temperatures of 8.5 - 8.75 °C the whole available temperature range below the halocline was used. However, clear accumulations at different temperatures were obvious: from 5 - 5.5 °C (24 %) and from 6 - 7 °C (56 %). Maximum abundance of cod was recorded at 6.5 - 6.75 °C (17 %). Available temperature habitat frequencies were almost evenly distributed below 6 °C, i.e. not explaining the accumulation of echoes at 5 - 5.5 °C by habitat availability. However, the layers with the highest cod frequencies also showed the highest habitat frequencies. Quotient analysis showed general avoidance of temperatures lower than 5 °C ($p < 0.05$) and a preference for higher temperatures.

Salinity

In 2003 cod were distributed throughout all observed salinity levels from downward of the halocline (Fig. I-5a). There were distributional accumulations and local maxima in layers with a salinity of 12 – 13 psu (20 %) and 18.75 – 19 psu (8 %). Comparison of cod distribution with the relative frequency of available habitat revealed no clear trend. All salinity levels higher than 9 psu were almost evenly present with only levels >17.5 psu appearing less frequent. Quotient analysis showed a clear avoidance of salinity levels lower than 10.7 psu ($p < 0.05$) and preference of layers with a salinity of 11.3 - 17.2 psu. Preference of these salinity levels was not significant as was the trend to avoid salinity levels >17.2 psu.

In 2005 the cod distribution in relation to ambient salinity showed a stronger limitation of layers used compared to habitat availability (Fig. I-5b). Most cod identified (96 %) were distributed in salinity levels between 11.25 and 14.5 psu. No cod were observed in salinity levels higher than 15.25 psu, although those were available as habitat. Quotient analysis revealed a clear and mostly significant avoidance of low salinities (<11.5 psu) as

well as high salinities (>14.3 psu). Salinity levels between 11.6 and 14.2 psu were characterized as preferred habitat (12 – 14 psu; $p < 0.05$).

Oxygen

In 2003, cod were observed between oxygen concentrations of 1.25 and 5.75 ml l⁻¹ (Fig. I-6a). The major part (81 %) was situated between 2.5 and 4.5 ml l⁻¹. A fraction of 11 % was detected at lowest observed oxygen levels of 1.25 - 2.5 ml l⁻¹. Due to the well-oxygenated environment, oxygen levels lower than 2.5 ml l⁻¹ only showed habitat frequencies of 1 %. Results of quotient analysis indicate a generally random distribution of cod in oxygen concentrations of less than 4 ml l⁻¹ and a significant selection of layers >4.5 ml l⁻¹.

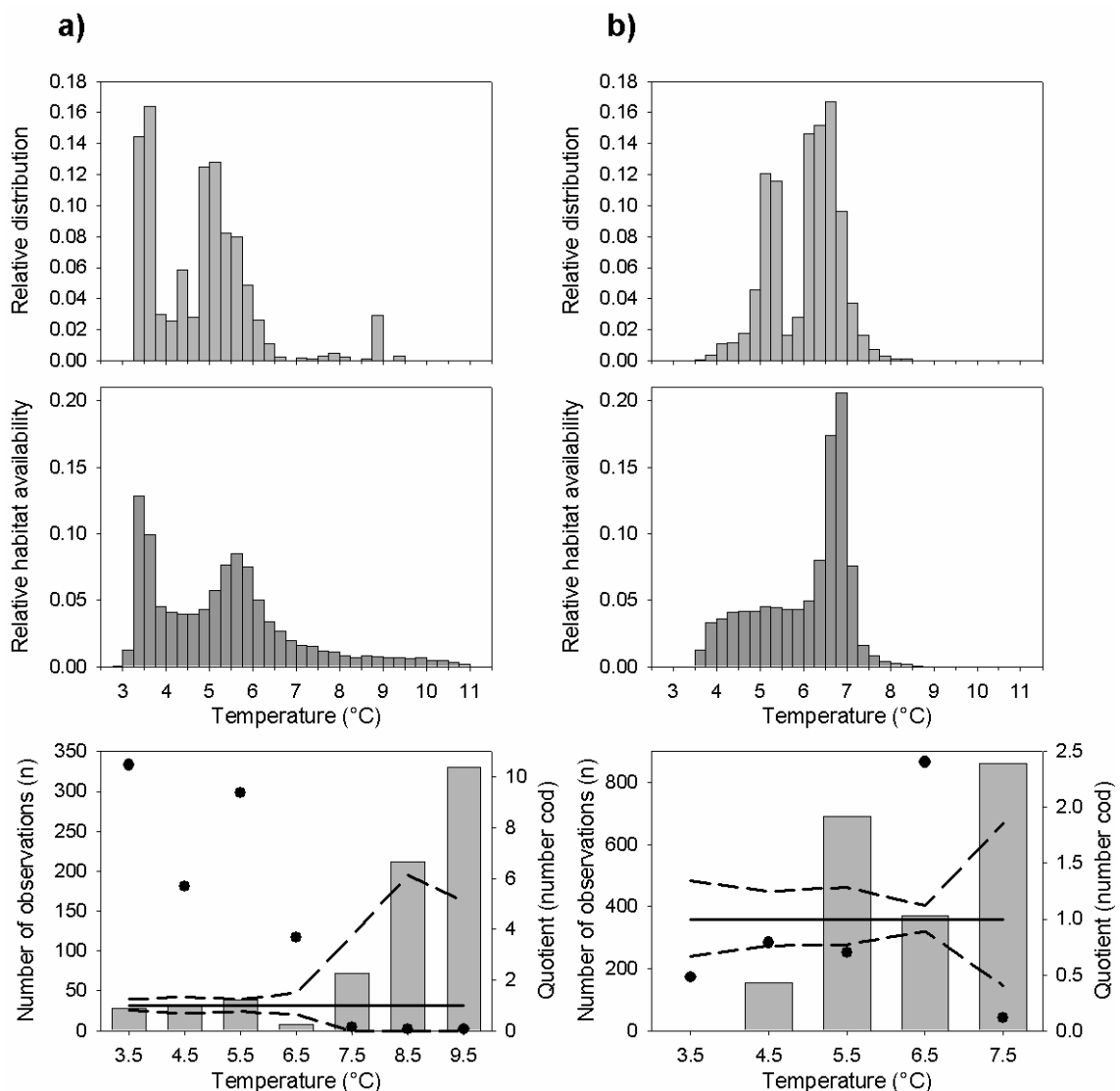


Figure I-4: *Gadus morhua*. Distribution of echoes below the halocline in August 2003 (a, n=1730) and July/August 2005 (b, n=5241) in relation to ambient temperature (upper panel) and relative availability of habitat in both years (middle panel). Lower panel: Quotient rule analysis. Dots: number of observations of corresponding abiotic parameter. Bars: Cod quotient curve. Dotted lines – 95 % confidence interval and quotient value 1 (marking random selection of habitat).

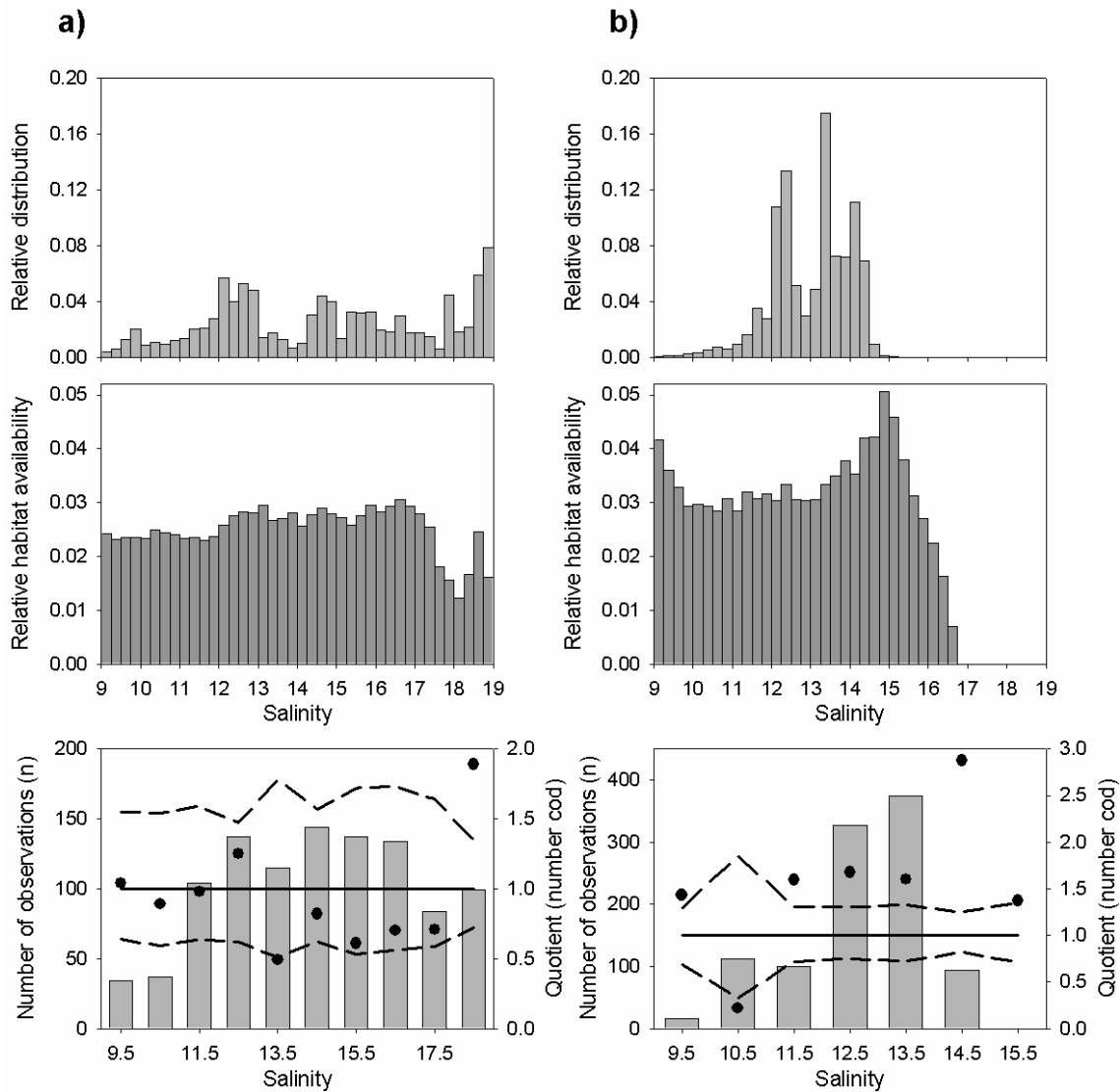


Figure I-5: *Gadus morhua*. Distribution of echoes below the halocline in August 2003 (a, n=1730) and July/August 2005 (b, n=5241) in relation to ambient salinity (upper panel) and relative availability of habitat in both years (middle panel). Lower panel: Quotient rule analysis. Dots: number of observations of corresponding abiotic parameter. Bars: Cod quotient curve. Dotted lines – 95 % confidence interval and quotient value 1 (marking random selection of habitat).

In August 2005, cod were distributed in oxygen concentrations between 0 and 6.75 ml l^{-1} (Fig. I-6b). The fraction of cod detected in layers with an oxygen concentration of less than 1 ml l^{-1} was very small. However, 38 % of cod identified dwelled at low oxygen levels between 1 and 2.5 ml l^{-1} . The preferred level of $3\text{-}3.5 \text{ ml l}^{-1}$ only contributed with $\sim 5 \%$ to the available habitat. Due to clear oxygen depletion below the halocline, oxygen levels of $0\text{-}1 \text{ ml l}^{-1}$ were present at a large extent. Quotient analysis revealed a clear and significant avoidance of oxygen concentrations lower than 1.5 ml l^{-1} ($<1.3 \text{ ml l}^{-1}$, $p < 0.05$), whereas oxygen concentrations between 1.5 ml l^{-1} and 4.5 ml l^{-1} were positively selected. Higher concentrations were present on a low number of stations and were selected or avoided mostly randomly.

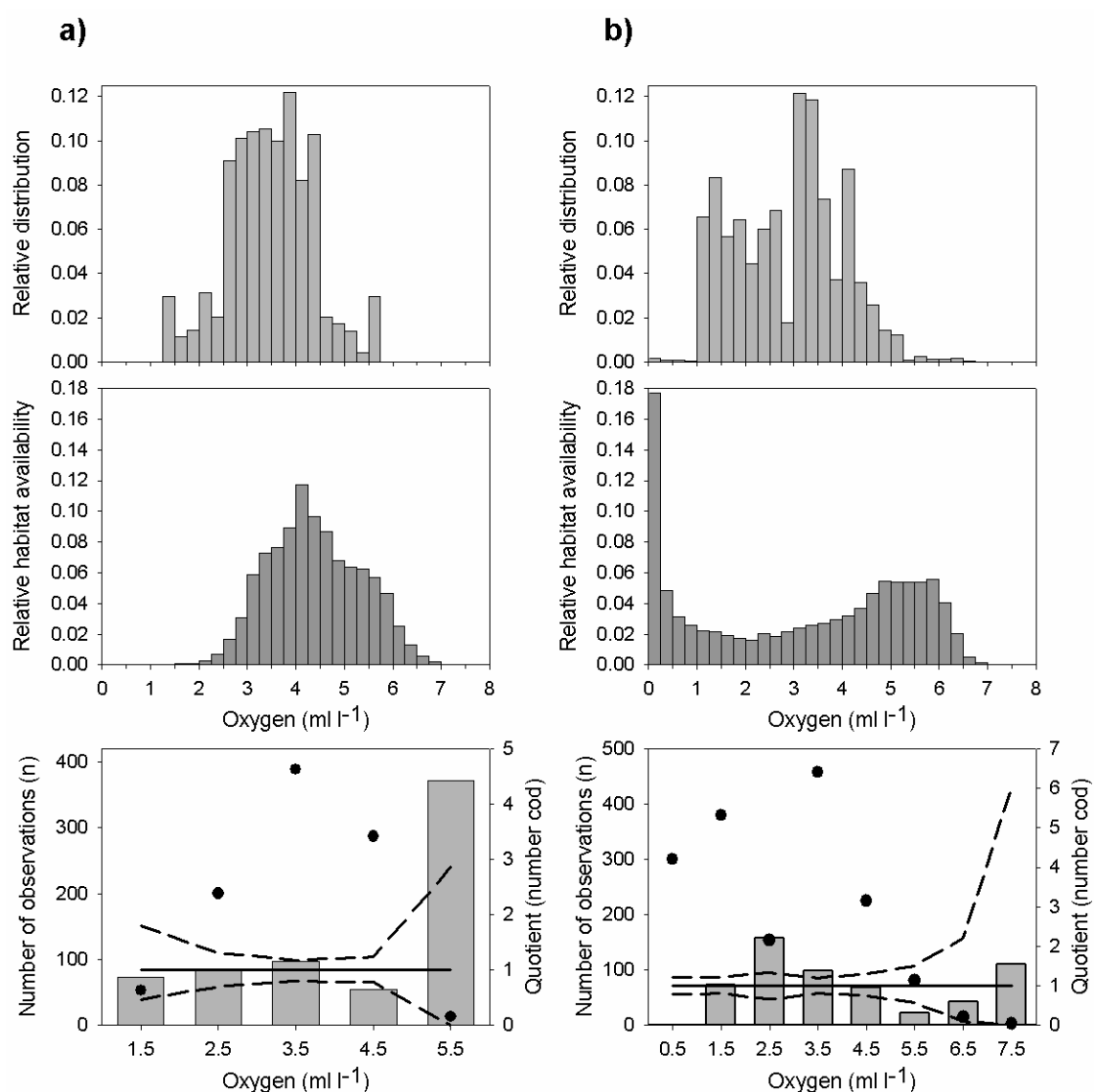


Figure I-6: *Gadus morhua*. Distribution of echoes below the halocline in August 2003 (a, n=1730) and July/August 2005 (b, n=5241) in relation to ambient oxygen concentration (upper panel) and relative availability of habitat in both years (middle panel). Lower panel: Quotient rule analysis. Dots: number of observations of corresponding abiotic parameter. Bars: Cod quotient curve. Dotted lines – 95 % confidence interval and quotient value 1 (marking random selection of habitat).

Oxygen-related egg survival

In 2003, cod were distributed in high saline (>11 psu) layers with a calculated oxygen-related egg survival (OES) of 0 - 0.85 (Fig. I-7a). The major part (67 %) was situated in layers with OES of 0.15 - 0.5, but a fraction >10 % was observed in regions with an OES of less than 0.1. Available habitat showed egg survival probabilities of 0 - 0.95. Only 0.6 % of habitat available showed an OES of less than 0.1.

In 2005 (Fig. I-7b), cod were observed in water layers with a similar range of OES rates as in 2003 (0 - 0.75). However, in contrast to 2003, the major part (25 %) was situated in

water masses with an egg survival probability of <0.1. Available habitat was dominantly characterized by egg survival probabilities of 0 - 0.05 (49 %). Only 25 % of ambient water body were characterized by an OES >0.5. Quotient analysis for 2003 and 2005 showed a significant negative selection of habitat with an OES <0.1 in both years.

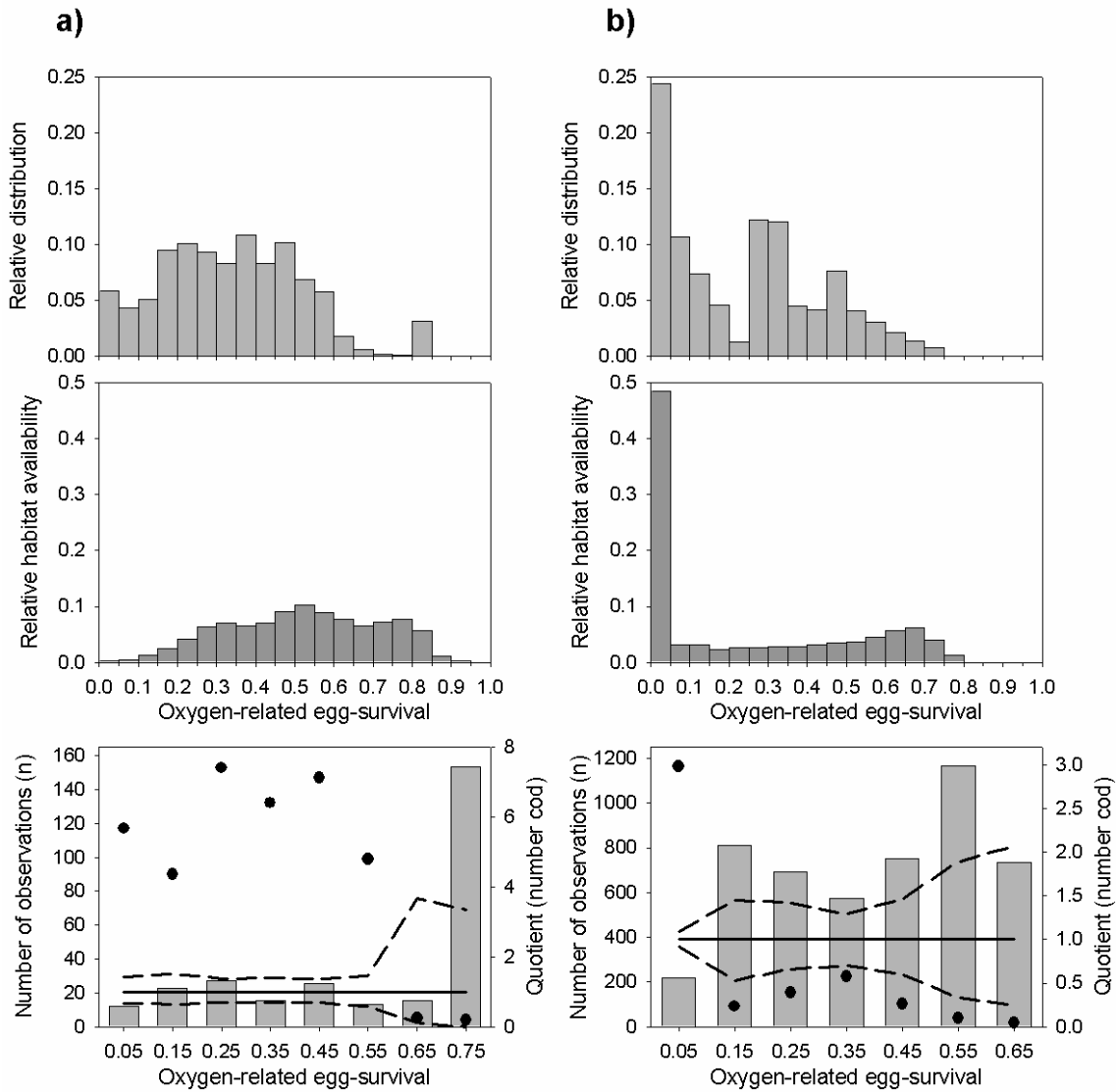


Figure I-7: *Gadus morhua*. Distribution of echoes within depth layers with a salinity >11 in August 2003 (a, n=1584) and July/August 2005 (b, n=5089) in relation to ambient Oxygen Related Egg-survival (upper panel) and relative availability of habitat with correspondent OES in both years (middle panel). Lower panel: Quotient rule analysis. Dots: number of observations of corresponding abiotic parameter. Bars: Cod quotient curve. Dotted lines – 95 % confidence interval and quotient value 1 (marking random selection of habitat).

GAM model results

According to the GAM, all inspected environmental factors had a significant ($p < 0.0001$) effect on adult cod abundance. The GCV score was 0.53197 and the model explained 47.4 % of the variance. The results from the quotient plot analysis with ambient

temperature and, to a higher extent, ambient salinity and oxygen influencing cod habitat were statistically validated. The model results showed a negative effect of temperature below 8.5° C and a positive effect above. Additionally, a slightly increasing influence of salinity on cod distribution with growing salinity levels was shown. Oxygen concentrations below 1 ml l⁻¹ had a significant negative effect on cod distribution.

DISCUSSION

Field-based, individual-level records of avoidance behavior at environmental limits are a necessary pre-requisite for the prediction of the population's dispersal under environmental changes (e. g. Guisan & Zimmermann 2000, Austin 2002b, Guisan & Thuiller 2005). Distribution data collected from trawl-catch often cannot be used to derive comparative small-scale spatial behavior. The net-opening is too wide and integrates a too far vertical range (Hjelm et al. 2004). Especially in highly stratified areas like the central Baltic Sea, small vertical movements of individual fish can result in massive changes in ambient hydrography experienced by the fish. The high resolution of hydroacoustics allows sampling on a much finer (vertical) scale and in much higher quantities. Spatially-explicit considerations can additionally improve the understanding of linkages between biological and physical processes (Mason & Brandt 1999). A high spatial resolution can help to identify the behavior of single cod towards their environment. Simultaneously, the high number of observations allows a quantitative assessment providing a good basis for the parameterization of future modeling. The high vertical and horizontal resolution of hydroacoustics thus can enhance the data basis for according models (e. g. Rose & Leggett 1990, Mason & Brandt 1996).

The method applied to interpolate ambient physical parameters has the advantage that in conjunction with data assimilation techniques a statistical measure (error variance) is provided to merge observed with modeled data in dependence on the error variance (see Neuenfeldt et al. 2007). The resolution of hydrographic data is on a km scale whereas the hydroacoustic data analyzed are usually on a meter scale. This difference in resolution can on the one hand be related to the lack of ship time available for measuring highly resolved hydrographic data. On the other hand, our method provides interpolated data on a scale that seems to be the best and only possible trade-off between requirement and availability of highly resolved hydrographic data.

As hydroacoustic devices alone cannot discriminate between individuals of different species, threshold levels have to be applied to minimize confusion with non-target species. Due to the relatively low biodiversity of fish species in the central Baltic pelagic ecosystem (ICES 2006) and derived from catch compositions of preceding investigations, the majority of echoes recorded can be allocated to either the clupeids sprat (*Sprattus sprattus*) and herring (*Clupea harengus*) or to cod. Catch data from corresponding

fishery hauls in both years investigated revealed that a certain proportion of fish caught from all species was in the same length range. Cod lengths ranged from 9 to 106 cm. Therefore, echoes from bigger sprat and herring could have mistakenly accounted for as small or juvenile cod using an identification threshold of -50 dB for TS measurements (Rose & Porter 1996, McQuinn & Winger 2003, Peltonen & Balk 2005). The threshold nevertheless was chosen in order to cover the whole observed size spectrum of cod. Due to the manual post-processing of the echograms and the identification of clupeid aggregations, the danger of misidentification was greatly reduced. Generally, this might have led to a reduction of total cod identified as cod dwelling within dense clupeid aggregations mistakenly were removed from the “tracking”. However, this would be a bias towards lesser cod identified that nevertheless guaranteed the reliability of the actually identified cod tracks and their ambient hydrography. Additionally, single fish echoes that were identified above the halocline could be regarded as originating from clupeids as corresponding fishery hauls and contemporary data-storage-tag recordings revealed that there were no cod distributed these layers.

Since the target tracking algorithm in Echoview is designed to avoid including multiple targets, the detected targets are, in general, within layers that have relatively low numerical densities, i.e., cod aggregation with higher numerical density may not give higher number of resolvable individual targets. As a result, the vertical distribution based on target tracking could provide a biased picture of cod vertical distribution. However, a comparison of the depth distribution of identified cod echoes with the total echo (NASC) depth distribution showed a consistency of both distributions, i.e. the peak cod abundances below the halocline were consistent with peak scattering values in the echograms.

The vertical distribution of cod during peak spawning period was controlled by salinity and oxygen concentration while an effect of temperature on vertical cod distribution was not obvious. This is probably not surprising. Although temperature is the single most important factor determining metabolic rates, the range of available temperatures during spawning period did not include previously reported critical limits for cod (North sea data; Lannig et al. 2004, Sartoris et al. 2003).

In both years observed, cod avoided salinities less than 11 psu. Non-spawning cod live in a wide salinity range in the largest parts of the Baltic Sea except for the Bothnian Bay and the easternmost parts of the Gulf of Finland (Aro 2000). Cod exposed to ambient salinities of 7 psu during experiments did not experience severe osmoregulatory disturbances (Dutil et al. 1992). Additionally, studies of Claireaux & Dutil (1992) showed no negative effects of acclimation of cod from salinity levels of 28 to 7 psu on their ability to tolerate low oxygen levels. During spawning time, adult cod prefer salinities of 11 to 15 psu with their distribution generally showing positive correlations to increasing salinity and oxygen levels (Tomkiewicz et al. 1998).

In 2005, a distinct oxygen depletion zone in deeper water layers marked the lower distributional boundary of cod. In contrast, ambient water was well-oxygenated throughout the whole water column in 2003. Cod were consequently distributed throughout the whole column below the halocline. However, even under the hypoxic conditions in 2005, a small fraction of cod was found in regions with a corresponding oxygen saturation of less than 17 %. This behavior has already been observed under laboratory conditions where cod generally avoided zones of low oxygen (< 50 % saturation at 5° C), but continued voluntarily to enter regions with values as low as 16 % saturation for short (~2 min, 5° C) excursions or if food was offered (Claireaux et al. 1995). Furthermore, also data from DS-tags showed that tagged cod entered oxygen-depleted layers for short periods (Neuenfeldt et al. 2009). This behavior can be related to feeding excursions. Sprat and herring are the main prey organisms of adult cod in the Bornholm Basin (Bagge 1989, Bagge et al. 1994) and obviously tolerate lower oxygen concentrations than cod (>0.5 ml l⁻¹ and 1.0 ml l⁻¹, Orlowksi 2005, Stepputtis 2006). In our data, the presence of clupeid schools on echograms and in corresponding fishery hauls in the referring depths indicates that in our case as well the cod could have entered the low oxygen levels for short feeding excursions.

Comparison of echorecordings and data-storage-tag recordings revealed similar distribution patterns with maximal frequencies in the same depth ranges in 2005. In 2003, echorecordings of cod were found in a broader depth spectrum than tagged cod. Echo tracks were rather randomly distributed below the halocline whereas tag-data were most abundant between 60 and 75 m. Keeping in mind that the lower, oxygen determined, distributional boundaries were consistent, the advantage of acoustic data for the purpose of monitoring population dispersal while still accounting for individual limitations becomes evident: an order of magnitude more fish tracks from hydroacoustic data were available as compared to sample size from DS-tags. The hydroacoustically derived data covered a much larger fraction of the distribution area of the corresponding cod population. The common distributional boundaries underline the viability of the echo-tracking.

The ambient habitat limits derived by the quotient plot analysis were validated by constructing a GAM model. Even when accounting for further significant abiotic parameters such as position within sampling area or depth, the model only accounted for 47.7 % of the total variability. This can be explained by a large value range of the according input variables. Further, behavioral traits of individuals or aggregations towards other factors (e.g. food availability, spawning behavior) could not be taken into consideration in the model. Nevertheless, the results showed that supplemental to the ability to identify limiting factors on cod distribution, the behavior of cod towards these factors under different scenarios has the potential to be modeled in the future.

Cod distribution in relation to crucial ambient abiotic parameters revealed by real-time *in-situ* echo-recording can enhance the data sets provided by data-storage-tags, especially when it comes to the scaling of DST derived data to population level. DS-tag based geolocation models use data from individuals for scaling results to population level (Neuenfeldt et al. 2007) whereas echorecordings represent a direct measure of the population characteristics.

Besides using single environmental parameters such as salinity, we also related individual vertical behavior to oxygen-related egg survival, which is a compound parameter that is difficult to integrate in experimental designs. Such compound environmental factors such as feeding success, competition, predation risk from larger predators (Grønkjær & Wieland 1997, Porter et al. 2005, Casini et al. 2006, Neuenfeldt & Beyer 2006) can effectively be tested only in the field, and echo-tracking appears to be a useful avenue to follow for adult fish, ultimately improving our perception of the variability in essential habitats.

ACKNOWLEDGEMENTS

We thank all the people involved in sampling and analyzing the data, especially Dr. Daniel Stepputtis. The study was carried out with financial support from the Commission of the European Communities, Agriculture and Fisheries (FAIR), Specific Targeted Research Projects 513670 (PROTECT) and 022717 (UNCOVER) and was partly funded by REX-I (the Danish ministry of food, agriculture and fishery). This paper does not necessarily reflect the view of the commission.



II. Seasonal changes in vertical distribution patterns of cod (*Gadus morhua*) in the Bornholm Basin, central Baltic Sea

Matthias Schaber¹, Hans-Harald Hinrichsen² and Joachim Gröger^{1,3}

¹ *Johann Heinrich von Thünen-Institute, Federal Research Institute for Rural Areas, Forestry and Fisheries, Institute of Sea Fisheries, Palmallee 9, 22767 Hamburg, Germany*

² *Leibniz Institute of Marine Sciences, IFM-GEOMAR, Düsterbrookweg 20, 24105 Kiel, Germany*

³ *Institute for Bio-Sciences, University of Rostock, Universitätsplatz 5, 18055 Rostock,, Germany*

ABSTRACT

Hydroacoustic single fish detection and corresponding hydrographic measurements were used to study seasonal changes in vertical distribution of adult cod (*Gadus morhua*) in relation to ambient environmental conditions in the Bornholm Basin, central Baltic Sea. Sampling was conducted in April, June and August covering the years 2006 to 2009. Vertical distribution of individual fish was resolved from hydroacoustic single-target detection in combination with a fish-tracking algorithm and related to ambient hydrographic conditions. Based on a GLM effect model, both salinity and oxygen concentration were identified as key parameters affecting cod vertical distribution. Results also showed a clear seasonal effect with a more shallow distribution as the spawning season progressed and oxygen concentrations in the deep parts of the basin deteriorated. The upper limit of the distributional range was mostly constituted by the halocline and remained rather constant, whereas increasing oxygen depletion in the deep water layers lifted the lower boundary of the vertical distribution leading to the observed upward shift in the overall distribution pattern. The results presented in this study highlight a significant shortcoming of the assessment survey design established for this species, as the observed shift in vertical distribution is not taken into account, thus introducing a potential bias into a data series used to tune the ICES standard stock assessment of this species.

Keywords: Vertical distribution, oxygen depletion, environmental thresholds, GLM, effect modeling

INTRODUCTION

In recent years, much attention has been put on distributional characteristics of adult cod in the central Baltic Sea in relation to ambient hydrographic conditions. The semi-enclosed brackish Baltic Sea is characterized by strong vertical thermohaline stratification with a permanent halocline separating low salinity surface waters from highly saline deep waters. Due to irregular inflow events of saline and oxygen rich water masses from adjacent North Sea regions and resulting stable stratification inhibiting mixing and thus transport of oxygen from upper to deeper layers, oxygen depletion is a common phenomenon, especially in the deep basins of the southern and eastern Baltic Sea (Matthäus & Franck 1992, Hinrichsen et al. 2002). Hinrichsen et al. (2002) showed a distinct decay of the so called “reproduction volume” (RV) for cod in the central Baltic sea, especially between quarters 2, 3 and 4. The RV is the volume of water with physical conditions favoring successful development of cod eggs (salinity >11 psu, oxygen concentration >2 ml l⁻¹, temperature >1.5° C; Wieland et al. 1994). As the depth of the oxygen depletion layer changes over the season due to oxygen consumption, vertical distribution patterns of adult cod in relation to ambient hydrographic conditions are most likely to change as well within the course of the year.

Spatial distribution patterns of cod in the Baltic Sea have previously, amongst others, been related to bottom depth and spawning behavior (Aro 1989, Sparholt et al. 1991, Bagge et al. 1994). The environmental influence on vertical distribution of cod in relation to clupeid prey was investigated by Neuenfeldt (2002) and Neuenfeldt & Beyer (2003). Further, oceanographic influences on the temporal and spatial distribution of cod outside their main spawning time were analyzed by Hjelm et al. (2004) based on trawl surveys. Tomkiewicz et al. (1998) investigated cod horizontal and vertical distribution during spawning time using a combination of trawl- and hydroacoustic data, whereas Hinrichsen et al. (2007) used early egg stages of cod as a proxy for adult distribution patterns during spawning. More recently, advanced tagging techniques have been applied to study cod distribution patterns. Neuenfeldt et al. (2009) identified vertical excursions of cod into hypoxic deep layers with data storage tags, recording *in-situ* ambient habitat conditions of individual cod. Schaber et al. (2009) applied hydroacoustic single fish tracking to identify environmental influences on habitat preferences and limits during spawning time in two years with contrasting hydrographic conditions. All these studies revealed that ambient hydrographic factors not only directly and indirectly affects early life stages, but also have a significant effect on the vertical and due to the basin geometry also horizontal distribution patterns of adult cod. Similar to early life stages, salinity and oxygen concentration have also been identified as key parameters by constituting the upper and lower boundaries of suitable habitat in the strongly stratified deep basins of the central Baltic Sea. Tomkiewicz et al. (1998) showed that cod in the central Baltic started to accumulate when ambient oxygen concentration exceeded 2.5 ml l⁻¹, whereas in water layers with lower oxygen concentrations cod was mostly absent.

Based on hydroacoustic data, providing high resolution information on the horizontal and vertical distribution, Schaber et al. (2009) have shown that spawning cod, even though partially distributed in layers outside their preferred habitat, generally avoid salinities < 11 psu and oxygen concentrations below 1.5 ml l⁻¹.

All of the studies mentioned were, however, restricted to observations at a single point in time (e.g. Tomkiewicz et al. 1998, Neuenfeldt & Beyer 2003), short time slot during main spawning activity (Schaber et al. 2009) or modeling approaches (Hinrichsen et al. 2007). Even more importantly, in some cases the sampling gear applied was not able to vertically resolve small-scale distribution patterns due to large vertical net-mouth openings of several meters (Tomkiewicz et al. 1989, Neuenfeldt 2002, Hjelm et al. 2004) or -in case data storage tags were used- sampling was limited to very few individuals (Neuenfeldt et al. 2007, Neuenfeldt et al. 2009).

Previous studies showed that applying hydroacoustic methods and especially single fish detection and tracking algorithms revealed reliable real-time and small-scale *in-situ* distribution characteristics of Baltic cod on a population level (Schaber et al. 2009). In the present study, we analyzed small-scale vertical distribution patterns of adult cod along transects within the Bornholm Basin during 2006-2009 over three months covering the second and third quarter of each year using the same methods. The main focus was to hydroacoustically identify the temporal and spatial course in small-scale (vertical) distribution patterns of cod on population level during large parts of their annual spawning cycle. To identify the underlying reasons for different distribution patterns, changes in ambient hydrographic conditions were related to the observed distribution of cod.

MATERIAL & METHODS

Hydroacoustic data

Hydroacoustic data were recorded on 10 research cruises of R/V “Alkor” in June and August 2006, April, June and August 2007 and 2008 and April and August 2009. No hydroacoustic data were available for April 2006 due to logistical restraints and for June 2009 due to unfavorable weather conditions. Hydroacoustic measurements were carried out mostly at nighttime on two parallel longitudinal transects covering the deep parts of the Bornholm Basin with a spacing of 30 nautical miles between transects. Longitudinal transect position was 15° 45’ 00” E and 16° 15’ 00” E (Fig. II-1). Data were collected with a Simrad hull-mounted split-beam transducer ES38-B and a Simrad scientific echosounder EK60 operated at 38 kHz by Simrad ER60-Software.

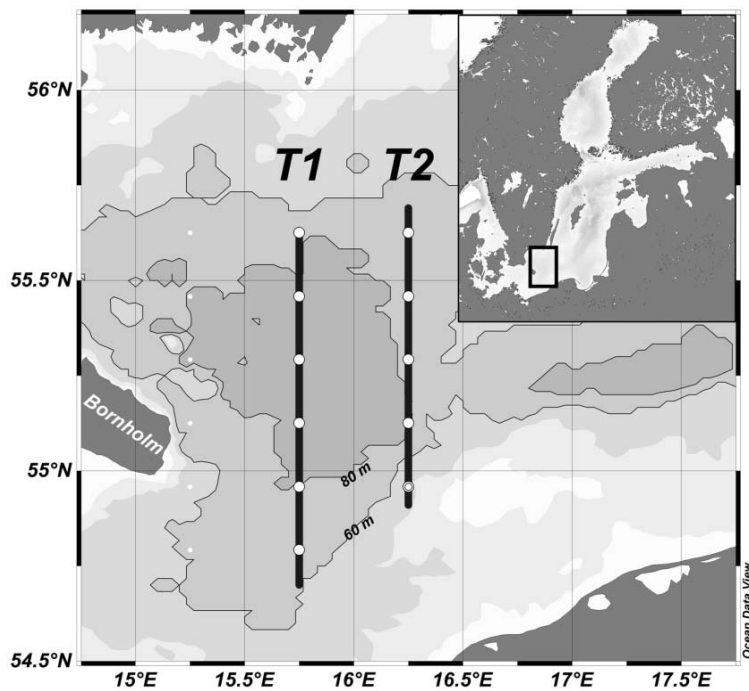


Figure II-1: Sampling area in the Bornholm Basin, central Baltic Sea. Longitudinal hydroacoustic transects T1 and T2 are indicated (black lines). White dots represent station grid for stationary hydrographic CTD measurements. Inlet marks location of sampling area in Baltic Sea.

To meet requirements for single fish tracking (see ICES 2007), a short pulse duration (0.256 ms; high vertical resolution) and high ping rate (high horizontal resolution) were set. Prior to the surveys, echosounder and transducer had been calibrated with the standard copper sphere method described by Foote et al. (1986) and ICES (2001). Ship speed at which the transects were covered was 10 knots (kn, 1 kn \sim 0.5 m s⁻¹) in 2006 and 5 kn in 2007-2009.

Echoview software (Sonardata 2007; www.echoview.com) was used for post-processing of hydroacoustic data. All echoes detected within the upper 10 m of the water column were not considered for analysis due to possible origin from turbulences caused by ship operation. Noise signals and scattering layers were manually marked in the echograms and excluded from further processing. In some cases hydroacoustic data were not exclusively recorded at nighttime but covered also dusk and dawn. Therefore, the detection of echoes scattered from clupeid schools could not be avoided as clupeids begin to vertically migrate upwards and disperse during dusk and vice versa during dawn (Nilsson et al. 2003). Therefore, a school detection algorithm (component of Echoview, settings see Nilsson et al. 2003) was applied to identify possible signals resulting from clupeid schools. Corresponding schools were excluded from further processing.

Echoview's single target detection operator was applied to identify single target echoes. Target strength (TS) is a function of fish size (e.g. Foote 1987, McQuinn & Winger 2003). In our study, a minimum threshold of -37 dB was set for acceptance of an echo as originating from (adult) cod. This restricted detections to fishes with a length of more than 30 cm but prevented inclusion of echoes scattered by clupeids sprat (*Sprattus sprattus*) and, more likely, herring (*Clupea harengus*) (McQuinn & Winger 2003,

Peltonen & Balk 2005, Fässler & Gorska 2009). Therefore, effects of hydrographic parameters on the distribution patterns of juvenile cod could not be observed.

The detection algorithm chosen was based on target strength and angular position data. Parameters used for detection of single targets were (minimum and maximum length of a single target pulse respectively) 0.49 and 1.51 times normalized pulse length (0.256 ms) and 12.0 dB for maximum beam compensation.

To avoid pseudo-replication of targets by processing several echoes scattered by one single fish, a target tracking algorithm was implemented on the data allowing an aggregation of several single echoes to one track and thus allocating multiple consecutive echoes to a single fish. Due to a continuous forward motion of the ship and thus the echo-recorder, the acceptance range for combining consecutive echoes to one fish was set higher on the horizontal than on both lateral and vertical axes. Therefore, the longitudinal axis was allocated 50 % weight. Due to different vessel velocity in 2006 and the consecutive years, the minimum targets and pings required for acceptance of a fish track were set to 3 (10 kn) and 5 (5 kn).

Relevant data recorded from resulting tracks of all identified fish included mean geographical position, mean depth, mean target strength and mean distance to seafloor.

Hydrographic data

Ambient hydrographic data were either measured on a regularly spaced 10 nautical mile station grid spatially complying with the transects (2006 – Jun 2007, Fig. II-1) or measured continuously along the transects during acquisition of hydroacoustic data (Aug 2007-2009). In the former case, a vertically deployed ADM-CTD probe was operated, in the latter case the probe was mounted on a towed frame and continuously operated in undulating oblique hauls to increase spatial and vertical resolution. Parameters recorded by the probe were temperature, salinity and oxygen concentration. To enhance the resolution of stationary CTD data and thus to allocate real-time ambient hydrography to each single fish detected by hydroacoustic measurements, a hydrodynamic model was applied. This model, based on the free surface Bryan-Cox-Semntner model (Killworth et al. 1991), has a horizontal resolution of 5 km and 60 specified vertical levels. Descriptions of modifications and adaptations of the model to Baltic Sea requirements can be found in Lehmann (1995) and Lehmann & Hinrichsen (2000). Physical properties simulated by the hydrodynamic model agree well with known circulation features and observed physical conditions in the Baltic (Lehmann, 1995, Hinrichsen *et al.*, 1997, Lehmann & Hinrichsen, 2000). Hydrographic data recorded by the undulating, towed CTD probe were allocated to individual fish by assigning the horizontally nearest dataset with measurements of referring depth strata to each fish.

Graphical mapping of both hydroacoustic and hydrographic data was performed using Ocean Data View software (Schlitzer 2007; <http://odv.awi.de>).

Statistical analyses and effect modeling

When studying the effect of environmental factors on the vertical depth of cod explorative investigations were begun by using symmetric Pearson-type correlation coefficients. Given the knowledge gained, the next step was to formulate the following ANCOVA-like general linear regression model (GLM):

$$Z = b_0 + \sum_i (b_i \times i) + \sum_j (c_j \times j) + \varepsilon \quad (1)$$

where Z is cod depth and ε is the associated error term being assumed variance homogenous, normally distributed, and white noise. Following the backward variable selection approach we started with the full model and initially included all linear combinations of the abiotic factors i available (such as oxygen, salinity, temperature) to reduce the risk of estimation bias through falsely excluding a non-redundant variable. Pre-analyses revealed a significant interactive year-month effect. Thus, linear combinations of all year-month effect level combinations j available were also included to avoid bias through ignoring these. The subscripts i and j behind the sum signs in equation (1) refer to the $i = 1, \dots, k$ linear combinations regarding the abiotic factors and $j = 1, \dots, l$ linear combinations regarding the year-month levels. To conversely avoid bias through multi-collinearity (redundant or overlapping information) each pair of abiotic factors included was orthogonalized, and the residual factors which *per se* are uncorrelated were used. Otherwise, the so-called variance-inflation factor would increase dramatically inflating the errors of the parameters estimated. This was accomplished by first fitting a linear calibration model between the variable pairs affected and then removing any linear trend (linear correlation) from them to give uncorrelated residuals which are then taken instead of the original variable itself. This treatment is similar to what is known as pre-whitening in Time Series Analysis. The model diagnostics included testing the null hypotheses of homoscedasticity of the final model's residuals, of non-significant parameters, of no factor interactions, and of normal residual distribution. The finally best model was selected using the coefficient of determination and was also based on the strength of positive correlation between predicted and observed cod depth values.

RESULTS

A total of 12760 cod were identified with hydroacoustics along the transects sampled in 2006 – 2009. Altogether, pronounced vertical patterns have been identified during the sampling period. These patterns are represented by an upward shift of the mean depths of cod from April to August in each year observed. Both between years and between months differences in depth distributions were highly significant ($\alpha=0.05$, Fig. II-2a, b). The overall mean (\pm SE) vertical distribution was deepest in April (74.69 ± 0.35 m) and significantly decreased by June (69.01 ± 0.22 m) and August (66.66 ± 0.24 m; Fig. II-2c).

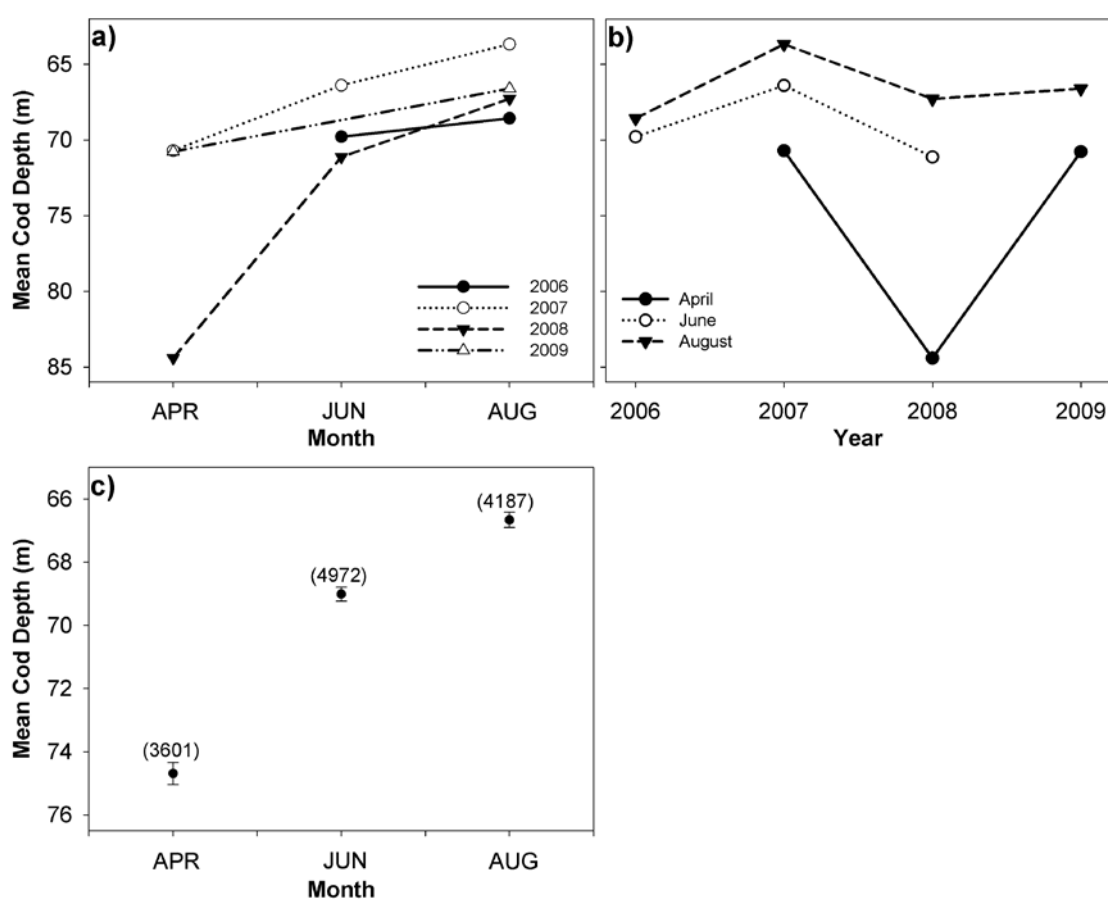


Figure II-2: Mean annual depth distribution of adult cod (*Gadus morhua*) per month (a) and mean monthly depth distribution per year (b) throughout the observation period ($n=12760$). (c) Overall mean (\pm SE) monthly depth distribution of cod. Numbers in brackets indicate number of cod identified. Missing values: see main text.

Figures II-3 and II-4 show exemplary seasonal distribution patterns along transect 1 in 2007 and 2008 in relation to ambient hydrographic parameters salinity and oxygen. In April 2007 (Fig. II-3), water layers below 75–80 m were characterized by oxygen depletion, and ambient oxygen concentration in these layers was lower than 1 ml l^{-1} . Hydroacoustically identified cod were distributed between 89 m and 55 m depth. North of 55° N , cod were almost exclusively distributed in the pelagial. More southerly,

demersal cod were observed dwelling slightly above the seafloor. By June oxygen depletion in the deep parts had progressed with layers below 70 m showing ambient oxygen concentrations of less than 1 ml l^{-1} . The overall distributional range of cod was between 23 m and 92 m depth with the largest fraction observed in layers >50 m depth with salinities exceeding 11.

A substantial part of all cod observed was distributed in depths below 70 m and thus in oxygen levels below 1 ml l^{-1} but the fraction of cod distributed directly above the seafloor had diminished compared to April. An upward shift in aggregate vertical distribution was most pronounced in August, when cod were observed between 30 m and 78 m depth. Again, the largest fraction was distributed in salinities >11 . The lower distribution boundary mostly followed the 1 ml l^{-1} oxycline and there were no more cod observed near the seafloor, with few exceptions in the very south of the transect in an area where the oxycline met the seafloor in ca. 70 m depth. The upward shift induced by oxygen depletion in the deep parts of the Basin was even more pronounced in 2008 (Fig. II-4). In April, the water body was well oxygenized with oxygen levels exceeding 2 ml l^{-1} in depths >90 m. Cod were observed from 44 m depth to the deepest parts of the Basin (99 m). The largest fraction was densely aggregated in the deep parts of the basin between 55.4° N and 55.0° N in depths below 80 m directly above the seafloor up to 10 m above.

Progressive oxygen depletion led to deterioration of oxygen concentration in the deep parts by June 2008. By then, water layers below 70 m near the northern and southern margins of the deep Basin and below 90 m in the central part were characterized by ambient oxygen concentration of less than 1 ml l^{-1} . While cod distribution covered a similar depth range as in April (40-95 m), the dense aggregations near the seafloor had decreased. North of 55° N , the largest part of cod observed was distributed in layers several meters above the seafloor with only a minor fraction dwelling close to the seafloor. South of that area, ambient oxygen concentration was well above 1 ml l^{-1} . There, cod densely aggregated at the seafloor, comparable to aggregations observed further north in April. In August, the 1 ml l^{-1} oxycline had shifted upwards to depths between ca. 70 m in the northern area of the Basin increasing in depth towards the south and meeting the seafloor in ca. 85 m depth slightly north of 55° N .

Cod distribution followed the salinity 11 psu halocline marking the upper and the 1 ml l^{-1} oxycline marking the lower boundary of the observed depth range (38 – 82 m) with only few individuals observed above the halocline and none observed in oxygen concentration levels below 1 ml l^{-1} . North of 55° N , distribution was restricted to pelagic layers well above the seafloor with distance to seafloor well exceeding 15 m in the northern area. In the southern part of the Bornholm Basin, oxygen concentrations exceeded 1 ml l^{-1} throughout the water column. There, cod were observed close to the seafloor. However, no clear aggregation patterns were found along the transect.

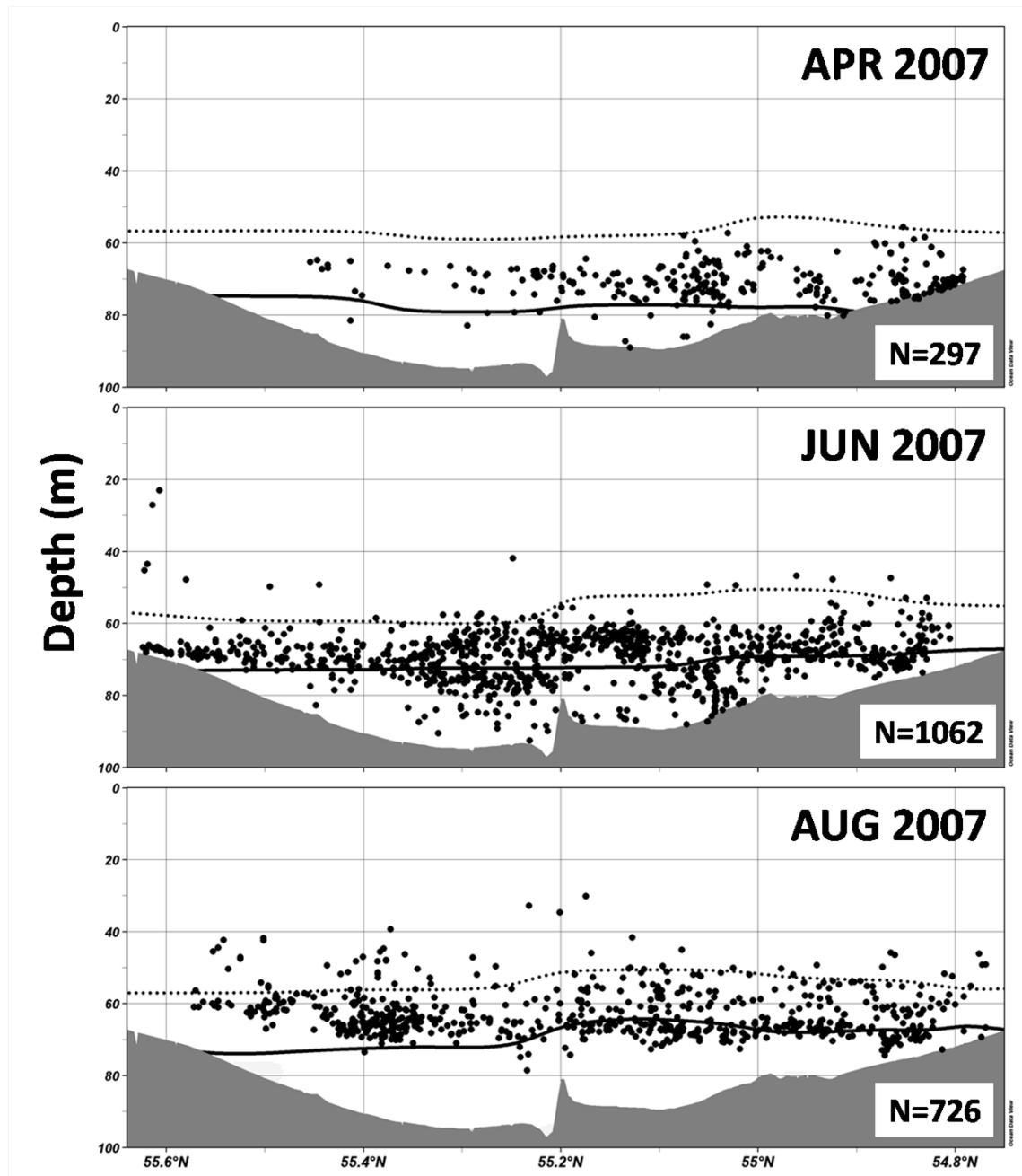


Figure II-3: Horizontal and vertical distribution patterns of adult cod (*Gadus morhua*) along hydroacoustic transect 1 (15° 45' 00" E) in the central Bornholm Basin in April (top panel), June (middle panel) and August (lower panel) 2007. Black dots represent individual cod identified by hydroacoustic single-fish tracking. Dotted line – salinity 11 psu halocline. Solid line – 1 ml l⁻¹ oxycline.

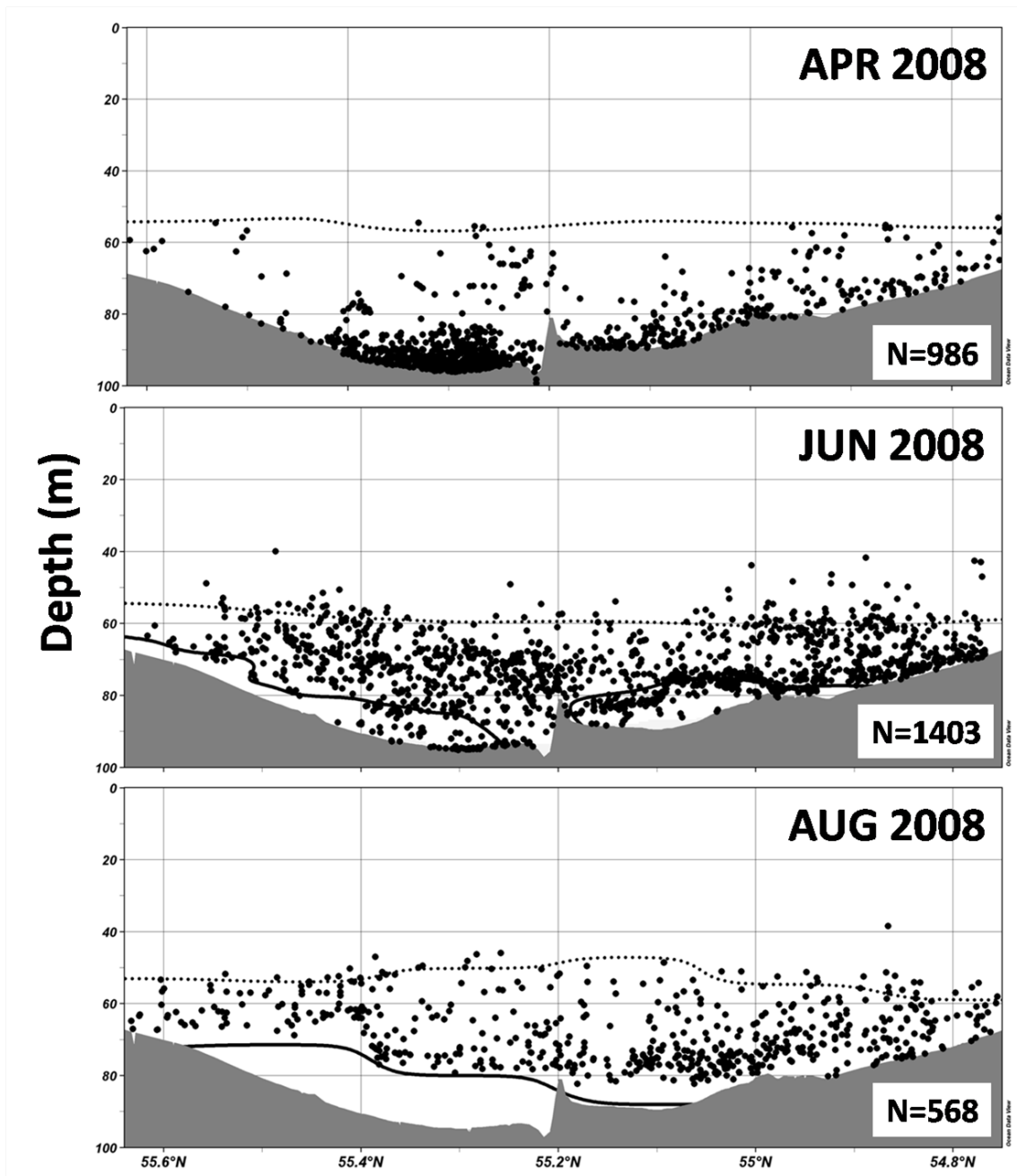


Figure II-4: Horizontal and vertical distribution patterns of adult cod (*Gadus morhua*) along hydroacoustic transect 1 (15° 45' 00" E) in the central Bornholm Basin in April (top panel), June (middle panel) and August (lower panel) 2008. Black dots represent individual cod identified by hydroacoustic single-fish tracking. Dotted line – salinity 11 psu halocline. Solid line – 1 ml l⁻¹ oxycline.

Results of the effect modeling are graphically presented in the correlation matrix in Fig. II-5. In all cases, significant correlations with $R > |0.44|$ ($p < 0.0001$) exist. However, the high correlations do not only occur between observed endogenous (vertical distribution of cod) and exogenous variables (abiotic factors such as temperature, salinity, oxygen) in the Bornholm Basin but also among the exogenous variables temperature, salinity, and oxygen. The latter observation requires careful variable selection and removing the correlation (trends) between those exogenous variables that are finally included into the model. From the shifting patterns of the colored dots in Fig. II-5 can be further inferred that the strength and type of correlation also depends on the month. A similar graphical pattern can be observed when using the years instead of the months while plotting the correlation matrix (not shown here). This obvious interaction between year and month is also confirmed by Fig. II-2: whilst Fig. II-2a shows that the lines for years 2006 and 2009 are inter-crossing, in Fig. II-2b the lines follow non-parallel tracks. Testing the year-month effect on the vertical distribution of cod either as a nested (or an interaction) term using an ANOVA-type approach also leads to significant results ($p < 0.0001$) indicating a strong interaction between both. Given all this, we ended up with the following ANCOVA-type GLM model for cod depth (Z) in relation to oxygen concentration (O), salinity (S) and year (Y) as well as month (M) sampled:

$$Z = b_0 + b_1 \times O + b_2 \times S^{(\text{calibrated})} + \sum_j c_j \times Y(M)_j^{(\text{nested})} \quad (2)$$

for the months April, June and August as well as years 2006 to 2009. To avoid multicollinearity between salinity and oxygen, in case of salinity we used the “calibrated” residuals which are trend removed instead of the original values, referred to as residual salinity in the following. This led to orthogonal factors with $R_{O \times S} = 0$ ($p = 1.0$). To include the year-month effect, the nested term version “ $Y(M)$ ” was used, although the result would be exactly the same when specifying the term as interaction version “ $Y \times M$ ”. It should be noted, that not only the entire model appears to be significant ($p < 0.0001$), but also the three factors oxygen, salinity plus the year-month interaction term ($p < 0.0001$). The model explains 76 % of the variation of the cod depth which is graphically confirmed when plotting observed and predicted cod depth values against each other (Fig. II-6a). Parameter estimates and p values are given in Tab. II-1. Figures II-6b and c indicate that the model’s residuals are normally distributed. However, Fig. II-6a also shows that a hidden factor may play some role as 24 % of residual variance is left unexplained.

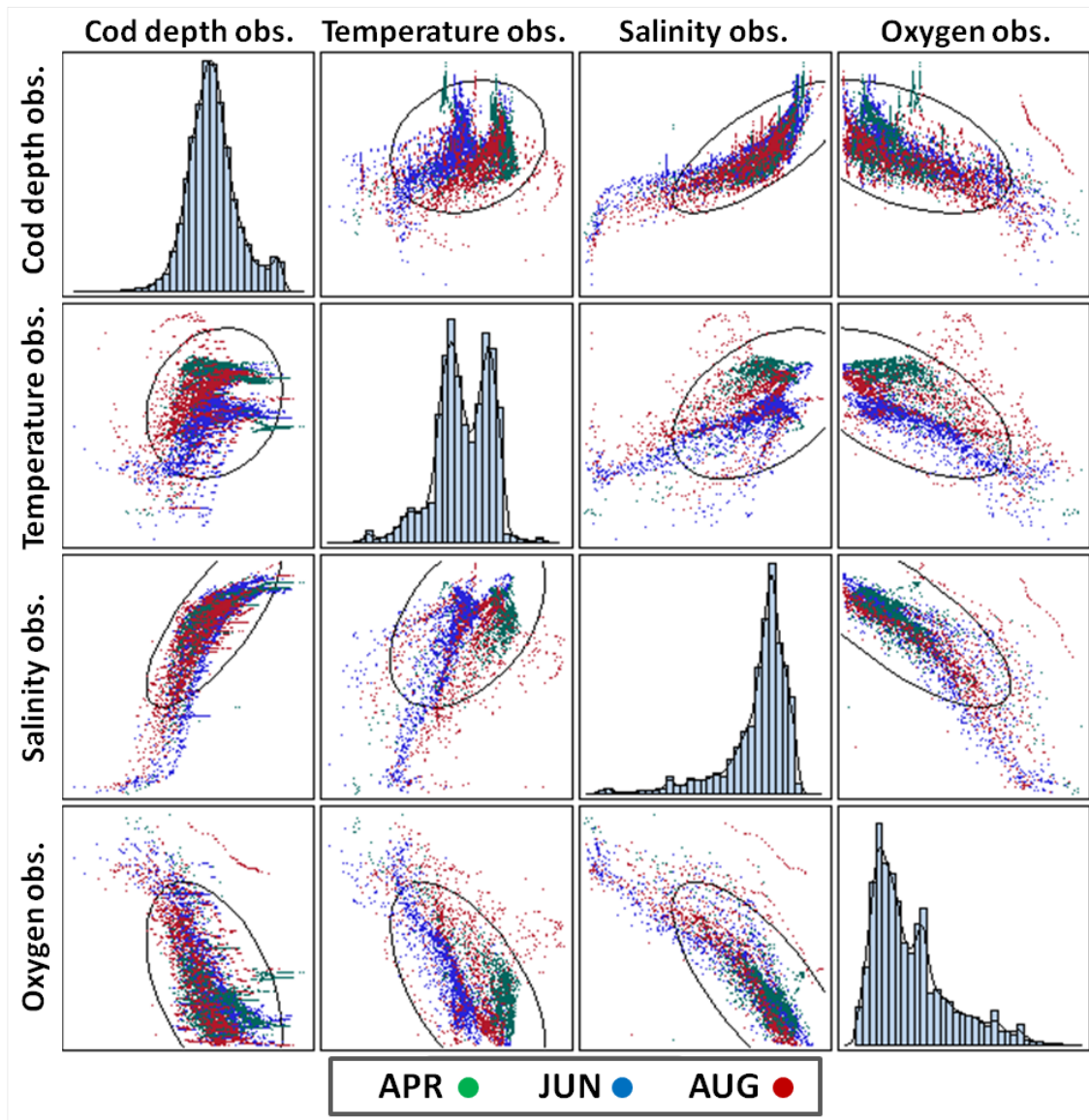


Figure II-5: Correlation matrix between observed endogenous (cod (*Gadus morhua*) vertical distribution) and exogenous variables in the Bornholm Basin. Ellipses indicate confidence of prediction around the center of the data cloud (95 %, $\alpha=0.05$) assuming a bi-variate normal distribution.

DISCUSSION

Based on *in-situ* spatial distribution data of cod (*Gadus morhua*) as well as corresponding hydrographic parameters, a GLM effect model explaining 76 % of cod depth variation was established. Apart from a significant year-month effect, salinity and oxygen concentration were identified as most significant factors influencing vertical distribution of cod.

The 24 % of variation in depth distribution of cod remaining unexplained by the model applied could either originate from a hidden factor (see below) or from deviations from linearity in the response of individuals to environmental stressors, which is indicated by

the inferior performance of the model for regions above the permanent halocline (i.e. above ca. 50 m depth, see Fig. II-6a). The transects sampled did not cover regions where bottom depth was shallower than halocline depth, i.e. where cod could have remained demersal in oxygenated layers of low salinity. Therefore it is possible that factors other than salinity determine vertical distribution patterns of cod in that area. As cod are physoclists, a swimbladder-defined limitation in free vertical range could be a possible factor. However, previous studies revealed that cod show a high plasticity in vertical movement and swimbladder capacity (Harden Jones & Scholes 1985, Righton et al. 2001) and in the Baltic Sea even do not display equilibration after capture and release but immediately return to the depth at which they were originally adapted (van der Kooij et al. 2007). Therefore, swimbladder related limitations in vertical range of cod are considered unlikely.

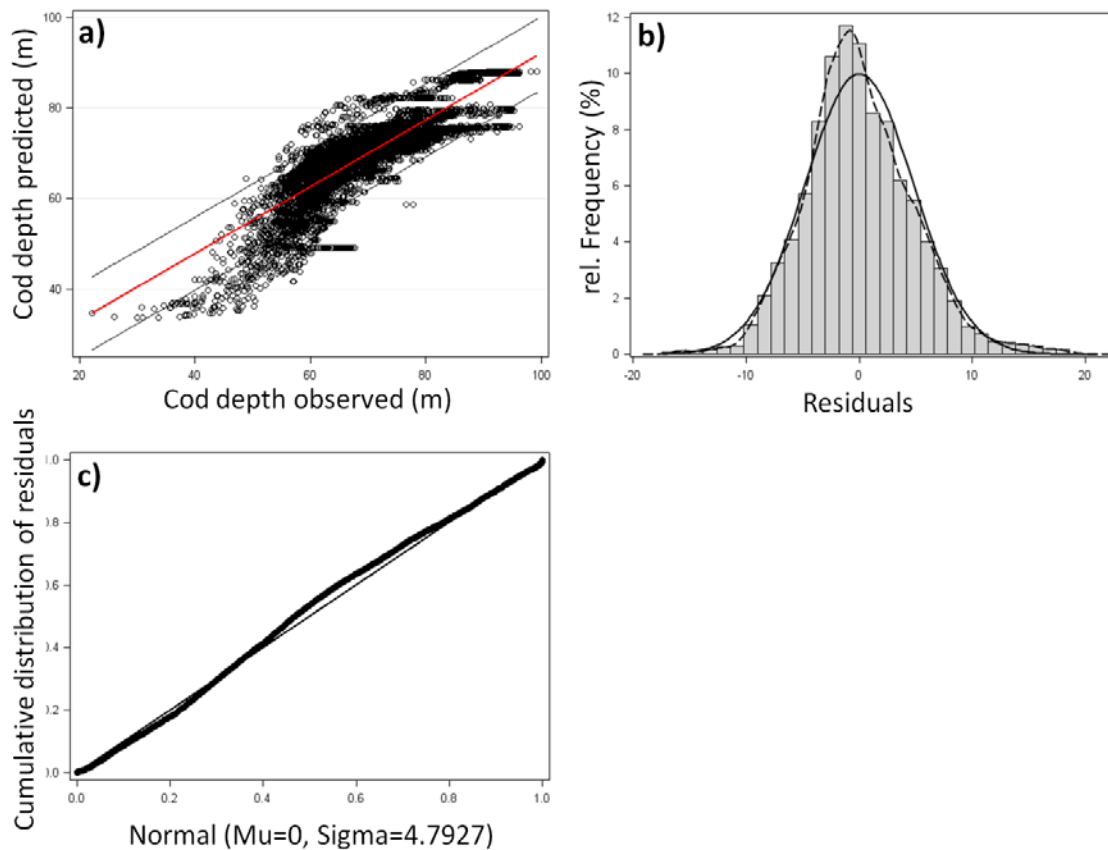


Figure II-6: Effect-modeling of cod (*Gadus morhua*) vertical distribution in the Bornholm Basin. (a) Plot of observed vs. predicted depth distribution of individual cod (circles) with correspondence line (middle solid line) plus 95 % confidence limits (outer solid lines). (b) Statistical distribution of the residuals: Histogram (vertical bars) with solid curve indicating the expected normal distribution and dashed curve representing the associated kernel distribution (normal kernel). (c) Probability-probability plot of the residuals.

Table II-1: Parameter estimates and p values from ANCOVA (GLM).

Type	Variable	Parameter	Estimate	Partial p value	Overall p value per factor
Intercept	Intercept	b_0	4.32279009	<0.0001	<0.0001
Hydrographical covariates	Oxygen	b_1	0.04715755	<0.0001	<0.0001
	residual Salinity	b_2	0.07968214	<0.0001	<0.0001
Year (Month) interaction	2007 (4)	C_{level1}	0.01890009	<0.0001	<0.0001
	2008 (4)	C_{level2}	0.11567843	<0.0001	
	2009 (4)	C_{level3}	0.00368297	0.0825	
	2006 (6)	C_{level4}	-0.0189703	<0.0001	
	2007 (6)	C_{level5}	0.03025222	<0.0001	
	2008 (6)	C_{level6}	0.05921711	<0.0001	
	2006 (8)	C_{level7}	0.02317519	<0.0001	
	2007 (8)	C_{level8}	0.05100519	<0.0001	
	2008 (8)	C_{level9}	0.02994956	<0.0001	
	2009 (8)	$C_{level10}$	0	.	

It has been shown that during the course of almost all years investigated, cod in the (central) Bornholm Basin obviously suffered from loss of favorable habitat due to deteriorating oxygen concentrations in the deep parts of the Basin. Progressive oxygen depletion induced an upward shift of cod distribution as characterized by a significant upward shift of mean cod depth. The upper boundary of overall vertical distribution remained nearly constant and was related to the upper layers of the permanent halocline. Cod generally concentrated near or at the seafloor, if oxygen concentrations allowed staying there and only migrated upward when oxygen near the seafloor decreased below acceptable conditions. This seasonal upward migration is consistent with observations of decreasing oxygen levels in the bottom layers of the Bornholm Basin in subsequent quarters of the year after the winter months due to a lack of atmospheric forcing events (Hinrichsen et al. 2002).

Echorecordings have been conducted almost exclusively during nighttime to avoid misidentification of echoes originating from clupeids. Irregular diurnal vertical migration behavior of cod has been observed in different regions and, amongst others, been related to prey availability and buoyancy equilibration (Godø & Michalsen 2000, Strand & Huse 2007). Vertical distribution patterns derived from data storage tags however indicated no specific diurnal migration behavior of cod in the central Baltic Sea (Neuenfeldt et al. 2007). Hence we consider our conclusions also valid for daytime distribution.

Vertical movements of cod and emerging vertical aggregation structures described as columns have been observed before and been related to spawning behavior (Rose 1993, Lawson & Rose 2000). The sampling conducted in this study was not capable of resolving small-scale individual vertical migration behavior. The extended vertical range observed during peak spawning time in June and August could at least partly be related to spawning and courtship activity. The reduced vertical range of the largest fraction of cod observed e.g. in April 2008 however rather indicates that hydrographic influences are the main cause with cod possibly having a natural preference for demersal residence if unrestricted by physical environment (e.g. van der Kooij et al. 2007). Additionally, spawning columns indicating instantaneous courtship and spawning behavior were not detected during night time hydroacoustic recording but in some instances detected in the area during dawn/daylight (Schaber, unpublished data).

Based on DST data, Neuenfeldt et al. (2009) could show that cod in the Bornholm basin undertook frequent short migrations into water layers of extremely low oxygen content, most likely for feeding or to reduce osmotic stress. This observation may explain why in our data few cod were always detected in extremely unfavorable oxygen conditions near the bottom, whereas the majority of the fish were detected in layers with higher oxygen content. Alternatively, Stepputtis et al. (2011) showed small scale horizontal variation in the depth of the oxygen minimum layer, which may have not been resolved by the hydrographic grid measurements and subsequent interpolation of hydrographic data between point measurements.

The distribution patterns presented in this study, characterized by the halocline as upper and oxygen concentration as lower habitat boundary, are consistent with these findings as generally only a small fraction of all cod detected was distributed outside the referring boundary layers. Given the fact that cod are considered euryhaline and do not experience severe osmotic disturbances in salinities as low as 7 (Dutil et al. 1992, Claireaux et al. 1995), it seems surprising that the permanent halocline mainly constituted the upper distribution boundary in this study. Especially, as cod outside their spawning activities are distributed over most parts of the Baltic, including areas with reduced salinities (e.g. Aro 1989). During spawning however, Baltic cod tolerate less variability in salinity and prefer salinities >11 psu below the permanent halocline (Tomkiewicz et al. 1998, Wieland et al. 2000, Schaber et al. 2009).

In June 2007 and -to a lesser extent in June 2008- a rather high proportion of cod have been detected in < 1 ml l⁻¹ O₂ concentrations. As hydroacoustic observations represent a real-time *in-situ* snap-shot of fish distribution, the cod observed in low oxygen layers could either have been on brief vertical foraging excursions as described by Neuenfeldt et al. (2009) or displaying courtship and mating behavior as indicated by extended vertical movements (Rose 1993, Lawson & Rose 2000). These behavioral patterns might possibly contribute to the 24 % of unexplained variance in the GLM. Whether cod

actively seek oxygen depleted layers for spawning or to seek relief from osmotic stress and thus eventually jeopardize the successful development of eggs and larvae however remains questionable.

Both during peak spawning (also see Schaber et al. 2009) and in preceding months, ambient temperature obviously had no pronounced effect on cod vertical distribution in the Bornholm Basin. This is in accordance with recent descriptions of a broad thermal niche of European cod stocks including the Baltic Sea. Even though the thermal niche is narrower during spawning, cod observed in this study were on average well within the known thermal limits both during growth and feeding as well as maturation and spawning (Righton et al. 2010).

A distinct fraction of cod is distributed in the pelagial, and so far this fraction is not taken into account in cod stock assessment. Baltic cod stock assessment is tuned with a survey index derived from bottom trawl surveys. Extreme environmental conditions in the deep basins with cod exclusively distributed pelagically in areas with oxygen depletion as observed e.g. in August 2007 and 2008 could lead to a distinct bias in the stock assessment tuning indices (ICES 2009). This is especially obvious as the present survey strategy regulates sampling in a way that trawl hauls are to be omitted if ambient oxygen concentration in the region of vertical net opening is below 1.5 ml l^{-1} , based on the assumption that due to oxygen deficiency no cod are distributed in this area and “zero catches” are to be expected (ICES 2008). Possible consequences of neglecting the pelagic fraction of cod in the central Baltic basins are underestimations of stock size in predictive runs for assessment.

Even though the survey manual restricts sampling to the first and fourth quarter of each year (March & November) and therefore rules out biases resulting from e.g. spawning aggregation behavior, and the sampling for this study was conducted outside the period of regular stock assessment surveys, we consider our findings expandable to other seasons. Avoiding oxygen depletion zones will persist, even if spawning aggregations disperse after the main spawning season (Aro 1989).

We consider our sampling on hydroacoustic transects not capable of resolving large-scale lateral migration behavior of cod as a reaction to deteriorating oxygen concentrations as the two transects sampled did not cover the whole Bornholm Basin including the basin rims. Lateral dispersion of cod above areas of oxygen depletion has been suggested by Hjelm et al. (2004) based on catch rates and also has been discussed in relation to biases in stock assessments. As their sampling however was based on (bottom) trawl surveys it can be concluded that a pelagic component of the population over oxygen depleted zones would not have been caught by their gear and thus remained undetected.

Decreasing salinity levels in the Baltic proper as predicted for future years together with low oxygen concentrations in deep layers (BACC Author Team 2008) could lead to further amelioration of the stock situation of eastern Baltic cod already challenged by adverse reproduction conditions and intense fishing pressure. As a result, the overall vertical range of favorable habitat available is likely to further diminish, which on the one hand can lead to a further reduction of successful spawning opportunities by vertical compression of the reproduction volume and on the other hand can increase susceptibility of the vertically more condensed cod aggregations to fishing pressure. This has also to be taken into account when incorporating the pelagic fraction into stock assessment indices, as a possible corresponding increase in catch per unit effort may lead to the false impression of an increase in stock size.

The present study has shown that hydroacoustic methods which so far are widely and mostly used for fish abundance estimation (see Simmonds & MacLennan 2005) can also be applied to assess the interaction of fishes and their environment. Limitations imposed by sampling gear (e.g. trawl nets, see Tomkiewicz et al. 1998, Hjelm et al. 2004) or a reduced number of samples (data storage tags, see Neuenfeldt et al. 2007) can be overcome by this non-invasive method due to a high spatial resolution that allows for scaling of results to a population level. Thus, corresponding studies can further contribute to our knowledge on the environmental ecology of different fish species, which is especially important in terms of the implementation of an ecosystem based fishery management.

ACKNOWLEDGEMENTS

We would like to thank all those involved in sampling operations during all cruises. Special thanks go to the crew of R/V "Alkor". Thanks also go to Prof. D. Schnack for valuable comments on an earlier version of this manuscript. This study was partly financed and conducted as part of the European Communities Specific Targeted Research Projects 022717 (UNCOVER) and Q5RT-2002-00813 (CODYSSEY). This paper does not necessarily reflect the views of the Commission.



III. Climate driven long-term trends in Baltic Sea oxygen concentrations, and the potential consequences for eastern Baltic cod (*Gadus morhua*)

Hans-Harald Hinrichsen¹, Bastian Huwer², Andrejs Makarchouk³, Christoph Petereit¹,
Matthias Schaber⁴ and Rudi Voss⁵

¹ *Leibniz Institute of Marine Sciences, Düsternbrooker Weg 20, 24105 Kiel, Germany*

² *Technical University of Denmark, National Institute of Aquatic Resources, Charlottenlund Castle, Jægersborg Allee 1, DK-2920 Charlottenlund, Denmark*

³ *Institute of Food Safety, Animal Health and Environment "BIOR", Fishery Resources Research Department, Daugavgrivas 8, Riga, LV-1048, Latvia*

⁴ *Johann Heinrich von Thünen-Institute, Federal Research Institute for Rural Areas, Forestry and Fisheries, Institute of Sea Fisheries, Palmallee 9, 22767 Hamburg, Germany*

⁵ *Sustainable Fishery, Department of Economy, University of Kiel, Wilhelm Seelig Platz 1, 24118 Kiel, Germany*

ABSTRACT

Variations in oxygen conditions in the Baltic are influenced by several mechanisms. Generally, the frequency and magnitude of major inflows have been identified as the most crucial process for the renewal of oxygen-depleted water masses in the Baltic Sea. Furthermore, enhanced degradation of suspended organic matter by bacteria over the past few decades has increased oxygen consumption. Finally, the effects of large-scale climate warming are causing long-term variations in oxygen content and saturation as an observed increase in temperature has led to a general decrease in oxygen solubility of water masses. Oxygen-dependent relationships based on field data and laboratory experiments were used to analyze the impact of the observed decrease of oxygen content on eastern Baltic cod (*Gadus morhua*) stock-specific processes (e.g. survival rates of eggs, settlement probability of juveniles, habitat utilization of spawning fish, age structure of successful spawners, food consumption rates of adult fish). The observed long-term decline of oxygen conditions in the Baltic Sea has had a seemingly generally negative impact on oxygen-related processes for the different life stages of eastern Baltic cod. Experimentally derived results of oxygen-driven processes were validated by field data.

Keywords: Baltic cod environment, climate change, condition factor, egg survival, gut evacuation, habitat utilization, juvenile settlement probability, oxygen deficiency, warming

INTRODUCTION

Apart from fishing pressure, several factors affecting the survival of eggs have been identified as major influences on recruitment processes and the subsequent stock abundance of eastern Baltic cod (*Gadus morhua*; hereafter referred to as Baltic cod) throughout the 20th century (Köster et al. 2005). These factors, including direct predation on cod eggs, eutrophication (impacting oxygen levels necessary for egg survival), and climate-driven change in salinity (impacting egg buoyancy), are considered to be crucial in shaping the resource dynamics in future (Brander 2010, Lindegren et al. 2010). Eastern Baltic cod utilize the deep basins (Fig. III-1; Bornholm Basin ICES Subdivision 25, Gdańsk Deep Subdivision 26, Gotland Basin Subdivision 28) as spawning habitats (Köster et al. 2001). However, the level of dissolved oxygen in these areas fluctuates widely and acute hypoxia is common. Successful cod spawning in the central Baltic Sea is restricted to areas with salinities varying between 11 and 20 psu. Cod eggs do not float in surface waters because of the low salinity in the upper waters of the highly stratified central Baltic, but concentrate in a narrow depth range within and below the permanent halocline (Wieland & Jarre-Teichmann 1997). Because of the commonly prevailing oxygen depletion at those depths, neutral egg buoyancy at depths above water layers with critical oxygen levels is hugely important for the survival of eggs and larvae (Vallin & Nissling 2000).

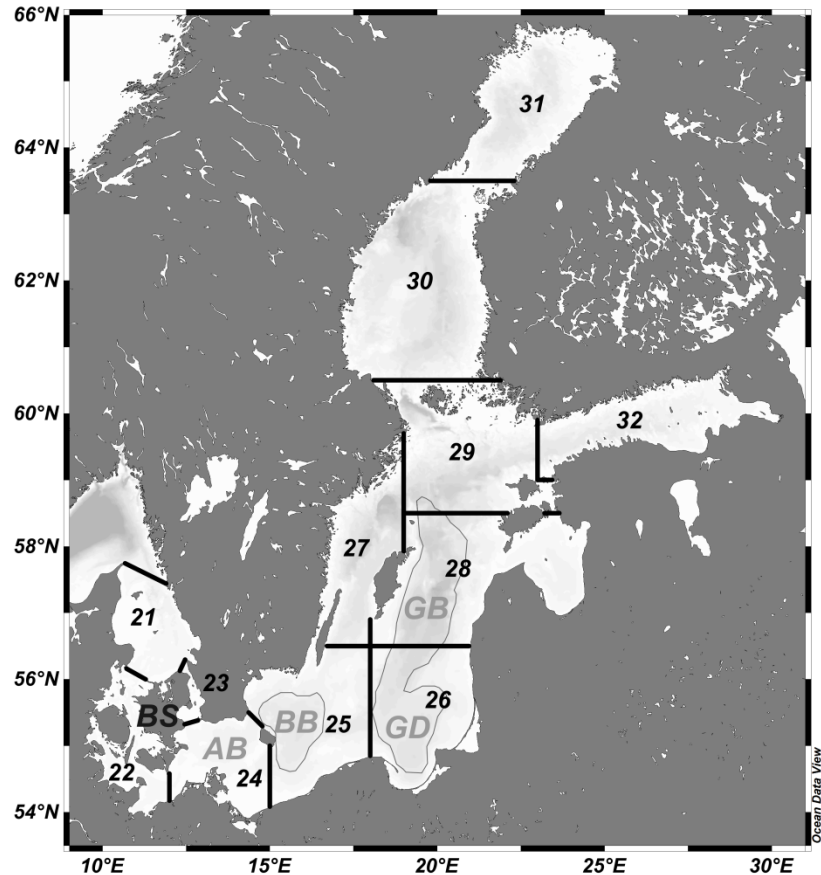
Other factors that are more indirectly related to oxygen levels could be additional sources of early life-stage mortality. For example, low oxygen at the seabed may force larger juveniles to stay in the pelagic zone, where they may not be able to cover their energy demands because they will only be able to feed on small zooplankton organisms. Without finding a suitable settling habitat in an appropriate timeframe, which would allow them to feed on larger benthic organisms, juvenile cod might face starvation and possibly death during winter (Hüssy et al. 1997). Sufficiently available benthic prey items are only found in regions with a relatively high concentration of oxygen at the seabed. Hence, the spatial and temporal variability of oxygen concentration in bottom layers might affect the benthic food supply for demersal juvenile cod.

From laboratory experiments, it has been concluded that cod settling habitat requires a minimum oxygen saturation of 40 % (Chabot & Dutil 1999). Data storage tag (DST) recordings obtained from adult cod revealed that, for feeding purposes, cod can only stay in less-oxygenated water masses for some 10 % of the time (Neuenfeldt et al. 2009).

Adverse oxygen conditions result in behavioural and physiological stress. Several studies have revealed the multiple effects of adverse oxygen conditions on cod: (i) overall hypoxia tolerance (Plante et al. 1998); (ii) physiological stress (Herbert & Steffensen 2005, Johansen et al. 2006); (iii) effects on metabolism (Schurmann & Steffensen 1997,

Claireaux et al. 2000, Chabot & Claireaux 2008, Petersen & Gamperl 2010); (iv) reduced growth (Chabot & Dutil 1999); and (v) reduced swimming performance (Herbert & Steffensen 2005, Johansen et al. 2006, Petersen & Gamperl 2010).

Figure III-1: ICES Subdivisions (numbers) in the Baltic Sea and Baltic cod spawning areas: BS – Belt Sea, AB – Arkona Basin, BB – Bornholm Basin, GD – Gdansk Deep, GB – Gotland Basin.



The principal mechanisms influencing the replenishment of oxygen in the deep basins of the Baltic Sea are inflows of highly saline, oxygen-rich water from the North Sea. These water masses enter the central Baltic through the Belt Sea (Fig. III-1). Inflow statistics based on long time-series of relevant parameters for the Baltic Sea (i.e. salinity, sea level, river run-off, precipitation, and air temperature), and for the North Atlantic and Europe (sea level pressure), compiled by Schinke & Matthäus (1998) identified the main driving forces of major Baltic inflow. Recorded major Baltic inflow events were relatively frequent until the mid-1970s, but less frequent thereafter (Fig. III-2). As shown by MacKenzie et al. (2000) and Hinrichsen et al. (2002), most inflow events comprise relatively small volumes of highly saline water that does not substantially influence the vertical salinity distribution. However, especially since the start of the 1980s, the oxygen conditions in the deep basins have varied considerably, independent of major Baltic inflows. A number of processes have been identified as influencing oxygen levels in the halocline and deep layers of the Baltic Sea: (i) lateral advection, which entails the inflow of water originating from the western Baltic and the Arkona Basin (Stigebrandt 1987), (ii)

river run-off, which has an effect on the volume and property exchange of the Baltic Sea (Lehmann & Hinrichsen 2000) as well as on the effectiveness of penetration of inflows into the Baltic (Matthäus & Schinke 1999), and (iii) variation in sea surface temperature in the western Baltic Sea, which results in differences in oxygen concentration at the sea surface and subsequent water-mass transport towards the east.

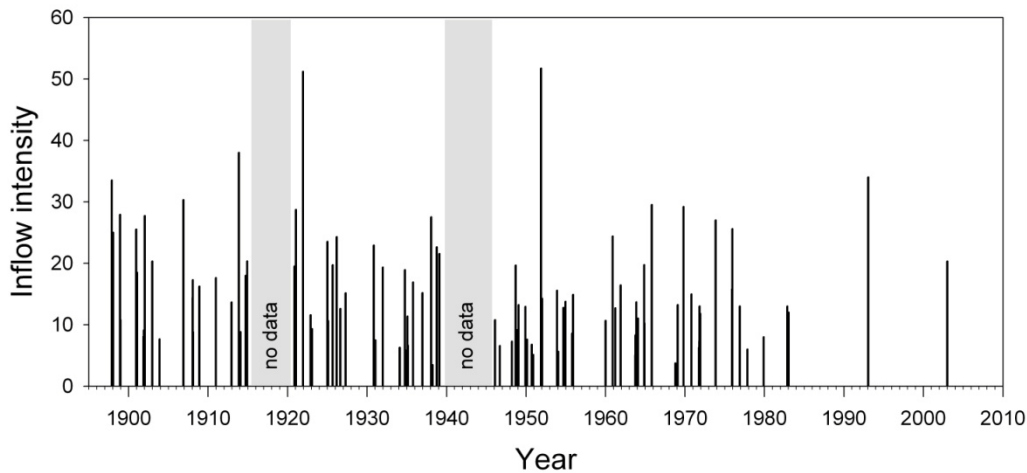
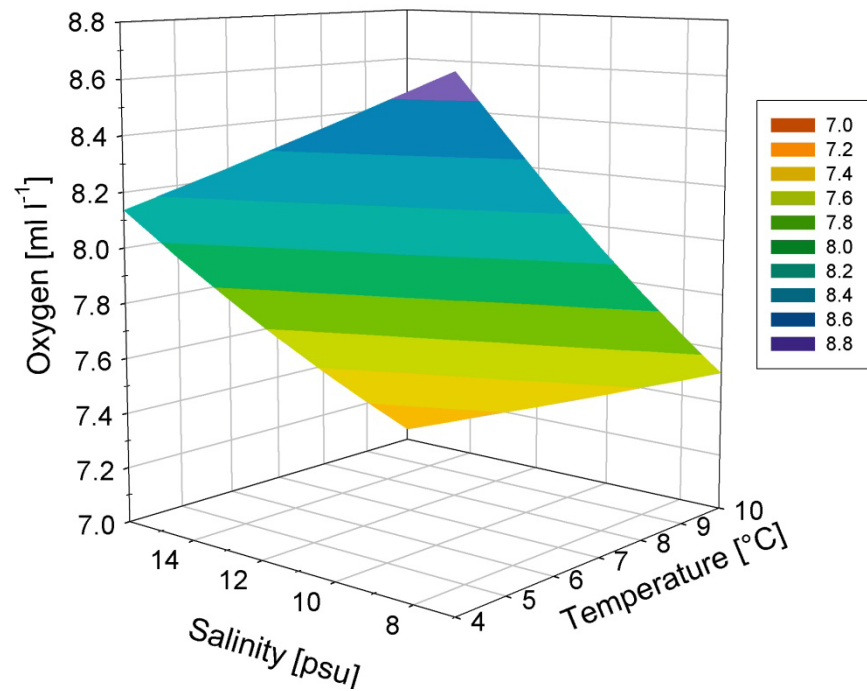


Figure III- 2: Time series of Major Baltic Inflows and their intensity (data from Matthäus 2006, Feistel et al. 2008).

Dissolved oxygen concentration at the sea surface is a function of temperature and salinity, with saturations typically reaching 100 % or more (Fig. III-3). However, such high levels of saturation below the halocline of the deep basins of the eastern Baltic can only be coupled to advective transport, because only advective transport can force vertical redistribution of temperature and oxygen within the deep basins of the Baltic Sea. Enhanced degradation of suspended organic matter by bacteria over recent decades has increased the oxygen consumption. Moreover, the effects of large-scale climate warming cause long-term variations in oxygen content and saturation as the observed increase in temperature leads to a general decrease in the oxygen solubility of water (Hinrichsen et al. 2002).

The main objective of this study was to assess whether the observed long-term trends of declining oxygen concentration and saturation in the Baltic Sea have implications for process variations acting during the entire life cycle of Baltic cod. Further, we examined field data in order to evaluate the validity of the relationships derived experimentally.

Figure III-3:
Temperature and salinity dependent oxygen solubility.



MATERIAL & METHODS

Oxygen data for the Bornholm Basin, Baltic Sea (Fig. III-1), were compiled from the ICES oceanographic database of depth-specific CTD (conductivity, temperature, depth) and bottle measurements. From the database, all available oxygen values were selected between 1951 and 2007. Data were subsequently aggregated to obtain monthly means per year and per 5 m depth stratum down to 100 m.

Spawning of Eastern Baltic cod

Compared with other stocks in the North Atlantic, the eastern Baltic cod stock has an extended spawning period (ICES 2005). During the first part of the time-series, the time of peak spawning identified on the basis of estimated egg abundance in the Bornholm Basin was between the end of April and mid-June, but from the early 1990s on, the time of greatest egg production changed gradually to later in summer (Wieland et al. 2000). Possible explanations for the shift in spawning time are high proportions of first-time spawners and decreasing water temperature (Wieland et al. 2000), as well as limits on the essential fatty acids in Baltic cod diet attributable to climate-driven changes in the Baltic Sea foodweb (Tomkiewicz et al. 2009). However, there have been indications of a slight reversal to earlier peak spawning during recent years (Schaber et al. 2011), so we decided to analyse oxygen-related processes acting only during the egg and larval phases in May and August.

Eggs

To obtain an index of potential egg survival, Plikshs et al. (1993) defined a “reproduction volume” (RV), the volume of water fulfilling the minimum requirements for successful egg development (see also MacKenzie et al. 2000). Salinities of 11 psu or more, a temperature >1.5°C, and an oxygen concentration of no less than 2 ml l⁻¹ are considered necessary for successful Baltic cod fertilization and egg development (Westin & Nissling 1991, Nissling et al. 1994, Wieland et al. 1994). However, because this index does not necessarily consider the actual oxygen conditions inside the reproduction volume, Rohlf (1999) developed a laboratory-based, oxygen-related egg survival index (OES) based on the fraction of the egg production expected to survive each year:

$$OES = (1 - e^{-(0.71 \cdot O_2)})^{11.63} \quad (1)$$

where O_2 (in ml l⁻¹) represents the ambient oxygen concentration.

Larvae

Newly hatched larvae and late-stage eggs of Baltic cod are buoyant at the same depths, so in accord with the vertical distribution of eggs, yolk-sac larvae in the central Baltic are restricted to depths >50 m (Wieland 1995). After depletion of yolk reserves, larvae have to migrate into the upper water layers to initiate feeding in a more-favorable habitat. The ability to perform those upward migrations depends mainly on the oxygen saturation level at the depths where the yolk-sac larvae reside. Based on laboratory experiments, Rohlf (1999) developed an index (larval vertical migration activity, LVMA) that represents the level of vertical migration activity at a given oxygen saturation:

$$LVMA = -28 + 2.3979 * O_{sat} - 0.0141 * O_{sat}^2 \quad (2)$$

where O_{sat} (%) represents the oxygen saturation.

Both OES and LVMA (\pm SD) were calculated at three different density levels (isopycnals) representing the mean vertical location of peak egg abundance (1010.40, 1011.33 and 1012.26 kg m⁻³; Nissling et al. 1994).

Juveniles

As there is no specific information on oxygen tolerance or the preference of juvenile eastern Baltic cod at settlement, it was assumed that the same threshold of oxygen saturation for adult cod described by Chabot & Dutil (1999) can be applied. Typically, adult cod have a minimum requirement of ~40 % oxygen saturation for survival, although short excursions into less-saturated water masses are possible (see below). To obtain a proxy for the settlement habitat size of juvenile cod in the Bornholm Basin (Fig. III-1), we selected all available depth values accounting for the minimum oxygen requirements of Baltic cod juveniles between 1951 and 2007 from the ICES

oceanographic database. These depth values were converted into potential juvenile habitat size by calculating the size of the area in the Bornholm Basin that had near-seabed oxygen saturations >40 %. Area sizes of suitable juvenile cod habitat were obtained from a hypsographic curve (Kossinna 1921), which shows the bottom depth distribution of the Baltic Sea below the sea surface. The calculation of this hypsographic curve was based on data provided by Seifert & Kayser (1995).

Adults

According to the laboratory data of Claireaux et al. (1995) and Plante et al. (1998), cod can enter hypoxic conditions for a limited period of time. From DST data (Neuenfeldt et al. 2007) and in situ hydroacoustic measurements (Schaber et al. 2009), cod in the vertically stratified Baltic Sea actively and frequently descend into hypoxic waters, even though the mean vertical distribution of pelagic cod decreases with progressing oxygen depletion in deeper layers (Schaber et al., 2009). The maximum residence time in hypoxic water increases with oxygen saturation to a constant level at oxygen conditions that are non-restrictive for cod activity (Neuenfeldt et al. 2009). Observations of sprat (*Sprattus sprattus*) concentrations at very low levels of oxygen levels, down to ca. 10 % saturation (Stepputtis 2006, Schaber et al. 2009), indicate that cod probably dive into hypoxic water to forage on sprat. To provide an estimate of the long-term trend of this vertical feeding migration of Baltic cod, we calculated the long-term evolution of the vertical extent of oxygen saturation levels between 15 and 40 %.

Gastric evacuation rates (GERs) of adult Baltic cod, here considered to be a representative measure of the growth potential of the species, were calculated based on a model initially developed by Temming & Andersen (1994). As hypoxia is frequent in the Baltic Sea, Teschner et al. (2010) modified that model to account for a slower rate of stomach evacuation under reduced oxygen saturation levels, as obtained from laboratory studies performed by Brach (1999):

$$GER \geq 65\% = 1 - 0.0017 * (100 - O_{sat}) \quad (3)$$

$$GER < 65\% = 1.4325 - 0.0141 * (100 - O_{sat})$$

where O_{sat} represents oxygen saturation.

The GER was calculated at three different levels, chosen approximately according to the mean \pm SD ambient salinity levels derived for hydroacoustically identified individual cod in the Bornholm Basin in the years 2006–2009. Overall, the mean \pm SD ambient

environmental salinity for a total of 13 745 cod was 14.5 ± 1.5 psu. For a detailed description of the methods employed to identify vertical distribution patterns of adult cod as well as for the allocation of ambient environmental parameters to each cod, the reader is referred to **Chapter II**.

Fulton's K condition factor was used as the main indicator of the overall condition of adult cod. In all, annual mean values of K (\pm SD) were calculated for 5267 male and female cod (maturity stage 5, initiation of spawning; Tomkiewicz et al. 2002) sampled during trawl surveys in the Bornholm Basin in July and August from 1994 to 2009. The minimum catch number for K to be considered representative for a year was set to $n \geq 10$. Hence,

$$K = 100 * (W * L^{-3}) \quad (4)$$

W representing weight (g) and L the total length (cm).

RESULTS

Hydrography

Assessment of the long-term development of Baltic Sea oxygen concentration and of oxygen saturation reveals significant negative trends (Fig. III-4). The results of the oxygen-related processes affecting the different life stages of Baltic cod are summarized in Tab. III-1. The minimum threshold value for OES ($O_2 > 2 \text{ ml l}^{-1}$) was observed increasingly shallower over recent decades (ca. $2.5 \text{ m decade}^{-1}$; Tab. III-1). The long-term trend in oxygen concentration ($O_2 > 2 \text{ ml l}^{-1}$) indicates oxygen-related successful egg development survival in depths $>90 \text{ m}$ at the beginning of the time-series (1951), but only to $\sim 80 \text{ m}$ in 2007 (Tab. III-1). The oxygen saturation level of 40 % changed from 80 m deep at the start of the time-series to around $\sim 65 \text{ m}$ deep at the end of the 2000s (Fig. III-4).

Eggs

Oxygen data collected in May and August illustrate the effect oxygen consumption could have on the seasonal development of RV and OES. The data indicate that RV and consequently OES below the halocline decreased quickly between May and August (Tab. III-1). On average, the vertical extension of RV is $\sim 5 \text{ m}$ larger in May than in August, but for both months there was an overall decreasing trend in RV and OES, with a decadal loss of $2\text{--}2.5 \text{ m}$ and $0.7\text{--}1.7 \%$, respectively (Tab. III-1, Fig. III-5a). Oxygen concentrations in the range where cod eggs are usually buoyant show a decreasing trend, indicating a

relatively high OES (64.3 %) in May 1951 for eggs with high buoyancy, but close to zero (i.e. 1.7 %) OES for eggs with low buoyancy in August 2007.

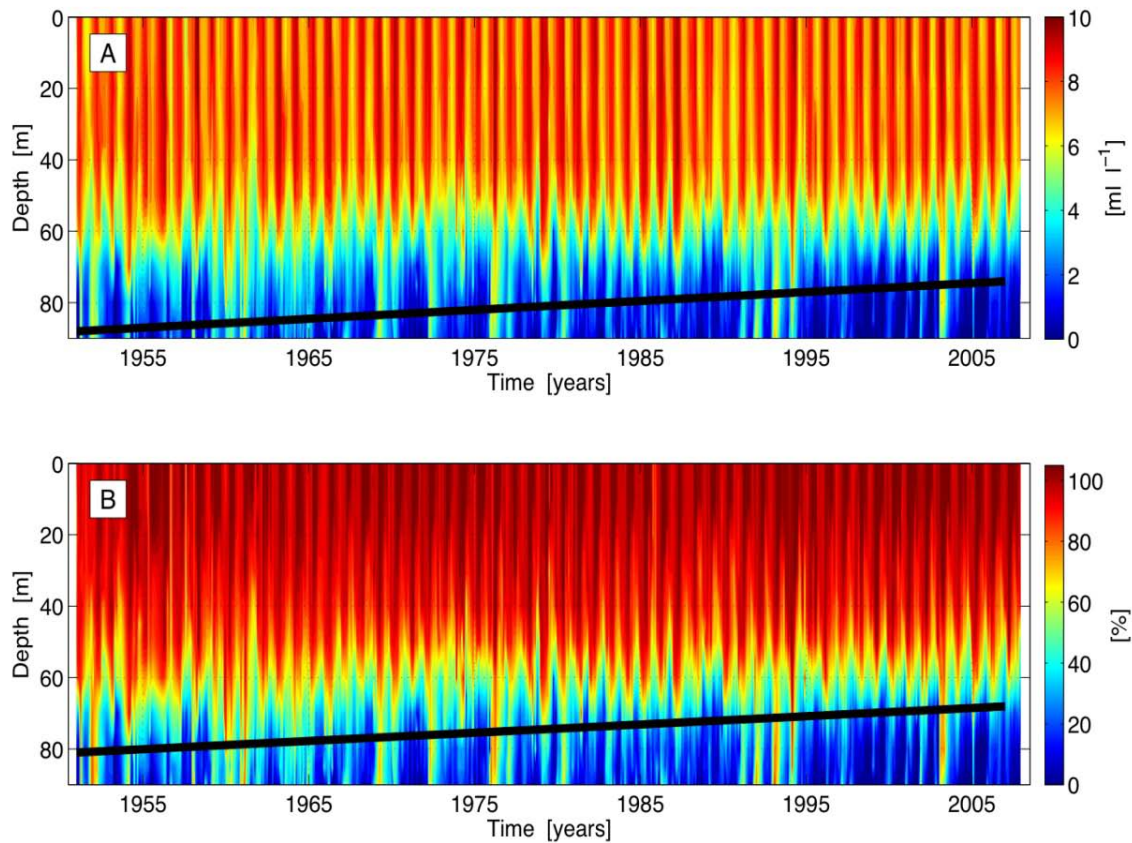


Figure III- 4: Long-term development of Baltic Sea oxygen concentration (a) and saturation (b) in the Bornholm Basin (from ICES oceanographic database). Heavy black lines represent temporal development of isolines for 2 ml l^{-1} oxygen content and 40 % oxygen saturation in a) and b) respectively, as derived from linear regressions for whole time series (1951-2007).

Yolk-sac and first feeding larvae

The LVMA shows a similar long-term trend as RV and OES (Fig. III-5b). The ability to perform ontogenetic vertical migration during the early larval phase was only slightly influenced by oxygen concentration at high levels of egg buoyancy in May, but the effect of decreasing oxygen was amplified for less-buoyant eggs throughout the time-series (Tab. III-1). Compared with the egg phase, the LVMA in August decreased at all buoyancy levels. At the end of the time-series, larvae that hatched from eggs of low buoyancy during the late spawning season showed a value of LVMA of 0 % (Tab. III-1), meaning that they could not complete the vertical migration to shallower layers of the water column needed to initiate first feeding. Hence, they probably failed to survive to more-advanced developmental stages.

Juveniles

The area providing favorable settling conditions for juvenile cod decreased by 900 km² per decade (Fig. III-5c). Compared with 1951, the area at the end of the time-series (2007) was reduced by >25 %. Moreover, the areas hosting juveniles up to the age of 2 years were the same as those inhabited by adult cod, on their overwintering or feeding grounds (Aro 1989, Hinrichsen et al. 2009).

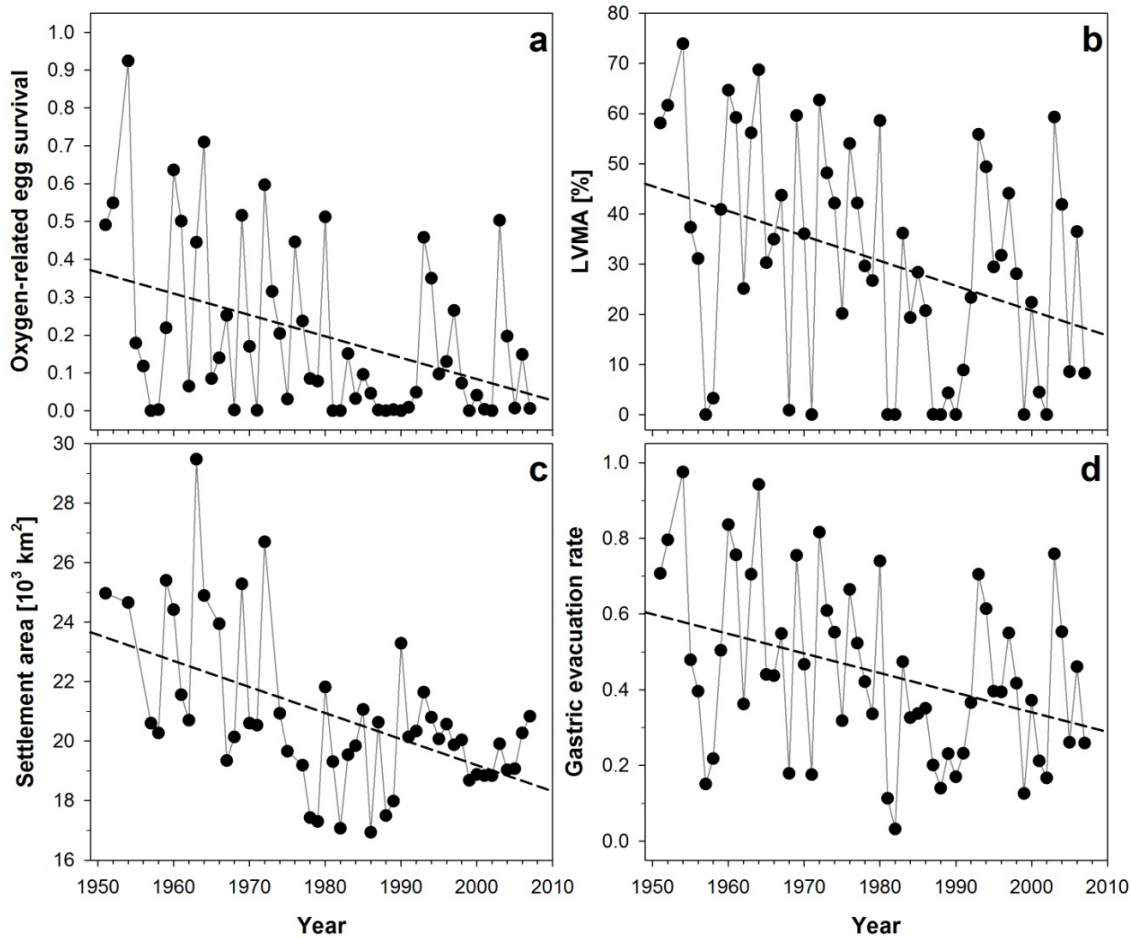


Figure III-5: Long-term development of (a) oxygen-related Baltic cod egg survival (OES); (b) oxygen-related vertical swimming activity of larval cod (LVMA); (c) size of juvenile cod settlement areas; and (d) oxygen-related gastric evacuation rates of adult Baltic cod (GER).

Adults

Predation of adult cod on clupeids might also be affected by the long-term development of oxygen conditions in the Bornholm Basin, because this parameter determines the lower distribution boundary and hence the extent of potential spatial overlap of predator (cod) and prey (clupeids). The observed depth range (15–40 % oxygen saturation) that adult cod occupy for feeding purposes during their spawning season

showed an increasing vertical extension in May (8.7–12.5 m), but a negative trend (16.5–11.6 m) for August, when vertical swimming activity decreased. The latter could potentially be due to greater frequencies of smaller so-called summer-inflows in recent years that led to an improvement in oxygen conditions in halocline waters during the late spawning season (Mohrholz et al. 2006).

The GERs of adult cod decreased gradually with time (Fig. III-5d). The vertical range preferred by adult cod (see Schaber et al. 2009) had relatively large differences in evacuation rates. Cod residing deeper, i.e. in higher ambient salinity, showed a constant and relatively high level of gastric evacuation over the whole time-series, whereas the GER was more strongly affected by temporal changes in oxygen development deeper in the water column. This effect was more pronounced for all vertical levels later in the spawning season.

Overall results

As a major validation step for the model results, field data obtained for various stages of Baltic cod during a long-term field programme in the Bornholm Basin, and evaluated by relating observations to simulated oxygen-related trends in a qualitative manner.

Measurements of egg size performed for Baltic cod in the Bornholm Basin since the early 1970s revealed an increasing tendency for survival of larger, more-buoyant eggs than for smaller, less-buoyant eggs (Fig. III-6). To obtain an index of selective survival, differences in mean diameter of the eggs in developmental stages III and I were determined. A higher index, i.e. a higher diameter in late eggs, corresponds to relatively greater survival of larger eggs. In the Bornholm Basin, there was an indication of better survival of larger eggs from the late 1980s, decreasing after the inflow in 1993, but increasing again from 1993 to 2003. A strong year class in 1976 can be related to high overall oxygen concentration in the deep Bornholm Basin despite an apparently low egg buoyancy (see Fig. III-4). This result is in accord with observations of cod egg development in incubation experiments. Wieland & Köster (1996) reported that the mean diameter of cod eggs had decreased from stage IA to stage IV by 6.9 %.

Reduced oxygen-related consumption rates as well as Fulton's K condition factor of adult male and female cod at maturity stage 5 show similar trends (Fig. III-7). The time-series (1994–2009) showed that an increase in adult Baltic cod nutritional condition could be expected after an improvement in habitat suitability based on oxygen concentration, e.g. after the major Baltic inflows in 1993 and 2003. Generally, however, the overall condition factor decreased continuously through the time-series (female $r^2 = 0.67$, male $r^2 = 0.70$).

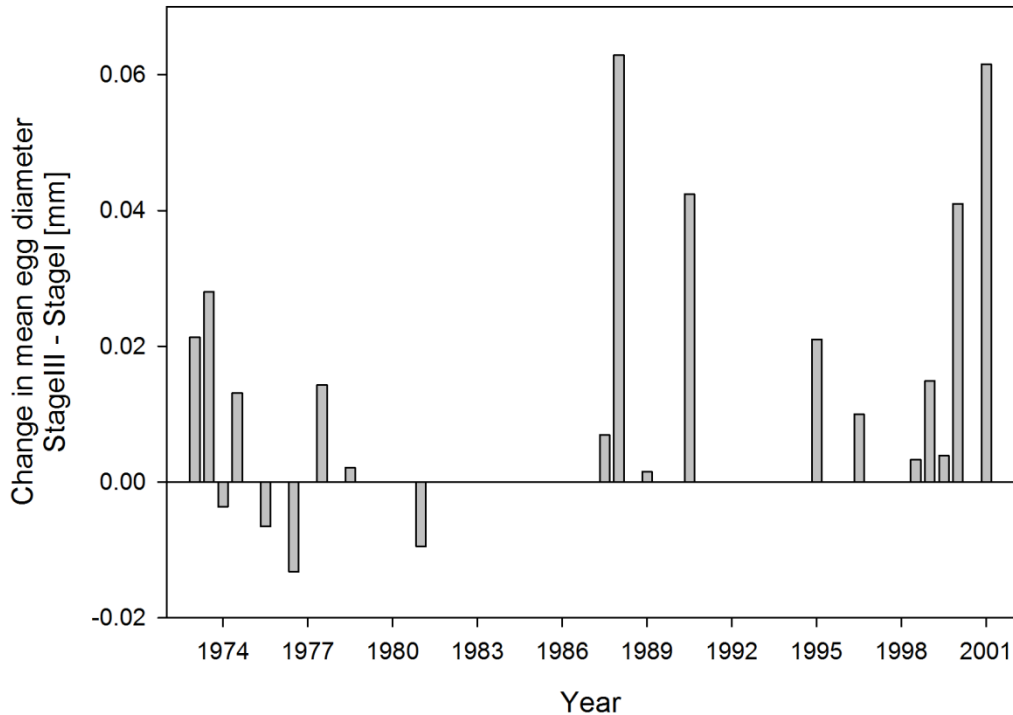


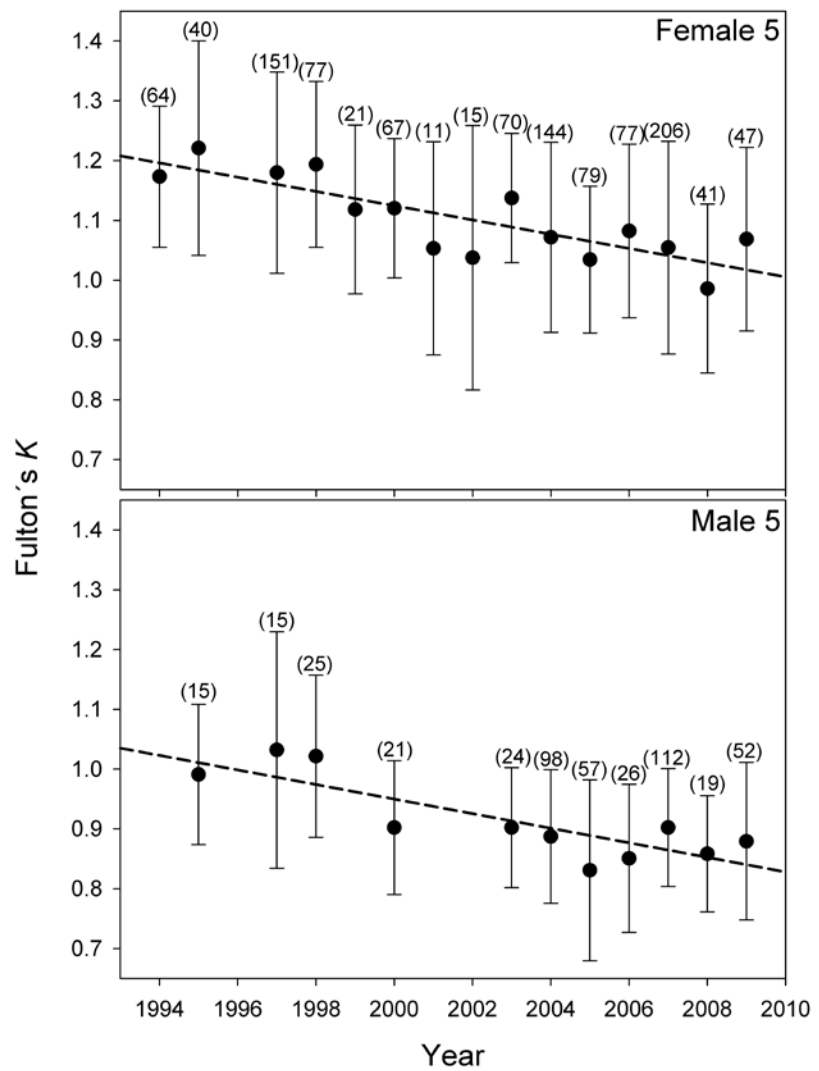
Figure III-6: Time series of the difference between Stage I and Stage III Baltic cod mean egg diameters in the Bornholm Basin.

DISCUSSION

The results of the analyses revealed that basin-wide, vertically resolved, monthly mean data can represent oxygen conditions for long periods, at least for the purpose of following their influence on processes acting during the different life stages of Baltic cod. Correlations among long-term data suggest that oxygen-related processes in cod life stages appear to be coupled to the temporal oxygen development in the inner deep basins of the Baltic Sea. Understanding of this linkage between physical processes and biological parameters of marine ecosystems has appeared as a consequence of the emergence of various methodologies, including laboratory experiments, field measurements, modeling, and data synthesis. In our case, oxygen as a measured physical ocean parameter was identified to permit short- to medium-term ecologically based process predictions. These predictions were possible because the process parameters were consistent over a long period.

Eggs of eastern Baltic cod need a minimum salinity of 11 psu for buoyancy (Wieland et al. 1994), and that level usually prevails in and below the halocline of the deep Baltic Sea basins. Because of the observed decrease in oxygen concentration at high density (salinity) levels in the past, and an anticipated continuing trend in future (BACC Author Team 2008), cod eggs were and potentially will continue to be frequently exposed to lethal concentrations of oxygen in the layer where they are neutrally buoyant.

Figure III-7: Mean annual condition factor K (Fulton) of adult male and female cod (ungutted weight, maturity stage V - initiation of spawning) from annual trawl samples collected between 1994 and 2009. Only yearly catches of $n \geq 10$ individuals of the corresponding sex / maturity stage were included.



The buoyancy of cod eggs varies with egg size and lipid content, both of which are related to the size and condition of females as well as to batch size (Kjesbu et al. 1992; Nissling & Vallin 1996), because eggs from large batches are generally smaller and have less lipid content than those from smaller batches. Larger females produce eggs with higher lipid content that are generally more buoyant than those produced by smaller cod (Nissling & Vallin 1996), so it is highly likely that larger females produce eggs and larvae with a greater probability of survival in the marginal oxygen conditions in the Baltic Sea. Large females might have a considerable impact on the production of eggs developing at lower density (salinity) and hence in more-clement oxygen concentrations. This also suggests an increase in the relative impact of female size with deteriorating spawning conditions, i.e. when the oxygen content in the RV decreases.

The OES relationship applied to oxygen concentration at various buoyancy levels revealed a notable decrease in oxygen-related egg survival during recent decades. Although environmentally driven rate processes cannot easily and directly be transferred from the laboratory to wild fish, the application of RV and OES to the model results on female size-specific egg production, egg size, and egg buoyancy would most

likely result in declining egg survival related to female size. Therefore, the number of cod that could contribute successfully to egg development and survival has probably declined as a consequence of the general increase in oxygen depletion at the egg buoyancy levels needed by Baltic cod. This trend appears to be diametrically opposed to the situation in which larger, older cod are more influenced by fishing pressure. Currently admissible mesh sizes for the Baltic cod fishery will only protect smaller females from capture, but these smaller females will likely not contribute significantly to egg production because of the ambient low oxygen concentrations at corresponding size-specific levels of egg buoyancy. Hence, there is a clear need to account for changing climate conditions in stock assessments and management advice. As an effective management tool, regulations on mesh sizes in trawl fisheries or a complete change from trawl to trap and/or gillnet fisheries could lead to more size-selective fishing, but the performance of these regulations still needs to be evaluated relative to the changing oxygen environment of Baltic cod.

Density-dependent processes operating after the onset of larval and juvenile settlement may be of substantially greater importance if the spatial extent of the habitat for Baltic cod juveniles decreases as a result of deteriorating oxygen concentrations. Such trends will probably continue, because general improvements in the environmental conditions necessary for successful cod spawning (increases in salinity and oxygen content) and a growing juvenile habitat area are not to be expected in the 21st century (BACC Author Team 2008). The output from climate-change scenarios predicts an overall increase in precipitation in the Baltic Sea catchment which could result in reduced inflow intensity of saline, well-oxygenated water masses into the Sea (Lehmann & Hinrichsen 2000).

During recent decades, hydrographic conditions in the central Baltic have been influenced by large-scale climate conditions that have resulted in above-average temperature throughout the water column, as well as declining salinity and oxygen concentrations below the halocline. These changes have negatively impacted the reproductive success of cod and, combined with high fishing pressure, resulted in a decline in the cod stock to the lowest level on record by the early 1990s (Köster et al. 2005).

An increase in precipitation in the Baltic Sea catchment along with a resulting increase in river run-off had, as a result of reduced frequency or less intense inflow (Lehmann & Hinrichsen 2000), an impact on the volume and property exchange of the Baltic Sea with the North Sea, and hence on the three-dimensional salinity and oxygen distribution in the Baltic. This trend accelerated the detrimental effects of decreasing oxygen concentration in the deep basins for the entire life cycle of cod, and this situation can be expected to continue in future. However, with a predicted decrease in salinity during the 21st century (BACC Author Team 2008), the Baltic Sea is likely to confront a reversed situation compared with past decades. As long as salinity in the deep basins of the Baltic

Sea remains high, the depth range below the halocline suffers from frequent anoxia. However, when salinity below the halocline is low and when the vertical position of the halocline is deep, oxygen concentrations in deep layers are more favorable and allow recolonization by macrofauna (Gerlach 1994). Unfortunately, this improvement of habitat for many macrofauna species has a detrimental effect on the survival of cod eggs. During periods of low salinity below the halocline, only eggs spawned by large, older females have a higher probability of survival, because only those eggs will be exposed to the optimal oxygen concentrations for their development.

Besides the negative impact of oxygen content on GER during recent decades, a decreasing oxygen content might also limit anabolism and hence the growth of Baltic cod, as indicated by the concomitant decreasing overall condition of adult cod. Gills, as the respiratory area of fish, cannot grow fast enough to compensate for increasing body weight and hence oxygen demand, so limiting overall growth performance (Pauly 1981). If the past trend of decreasing oxygen concentration and saturation in the deep basins of the Baltic Sea continues, it is highly likely that the effective population size of Baltic cod will drop in terms of spawning-stock biomass (SSB). This almost certainly would result in a negative impact on fisheries that generally select for the most valuable traits, i.e. in selecting larger fish.

An increase in cod SSB has been observed recently. This was predicted in short-term forecasts (ICES 2010b), and was mostly related to a reduction in fishing mortality combined with improved abiotic conditions after inflow events from the North Sea (Lindegren et al. 2010). Recently, there have been indications of a slight reversal of the spawning season to earlier in the year (Schaber et al. 2011), so considering that the results here have revealed that conditions for all the processes analyzed were generally better in May than in August, this may be an additional explanation for the improved recruitment and SSB recently (ICES 2010b). However, irrespective of any reduction in fishing pressure and potential changes in the spawning season, there remains a risk of long-term depression of the eastern Baltic cod stock with progressive climate change through both direct and indirect effects of changes in temperature, salinity, and oxygen concentration on early life stages. Additionally, progressive oxygen depletion will severely affect all life stages of Baltic cod.

Generally, the trends for the different oxygen-related processes acting on various different life stages are negative. However, it is impossible to rank their relative contributions to recruitment success. Currently, stock–recruitment relationships for Baltic cod do not consider life stages later than the egg, so future investigations need also evaluate the relative importance of later stages for recruitment success by combining the relationships used in this study with those already in existence. The metrics can be used as predictors in statistical stock–recruitment (Köster et al. 2001) or general additive models (Cardinale et al. 2009). Good recruitment of cod in the late

1970s is partly considered to have been attributable to the massive expansion of suitable spawning and feeding habitat in areas adjacent to the Bornholm Basin (Bagge et al. 1994), so it would be revealing to establish and analyze the oxygen-related relationships also for those areas in future.

ACKNOWLEDGEMENTS

This study was financed and conducted as part of the European Communities FP6 Specific Targeted Research Project 022717 (UNCOVER) as well as of the International Femern Belt Science Provision Contract. This paper does not necessarily reflect the views of the Commission.

Table III-1: Characteristic oxygen related hydrography, regression parameters and processes acting on Eastern Baltic cod (*Gadus morhua* L.) during its entire life cycle. For definition of reproduction volume (RV), calculations of oxygen related egg survival (OES), larval vertical migration activity (LVMA), juvenile settlement area and gut evacuation rate (*GER*) see text. Applied three density levels (σ_t) represent the mean vertical level of egg abundance \pm SD (Nissling *et al.* 1994). Salinity levels applied for *GER* calculations were derived from mean \pm SD vertical level of cod abundance.

Parameter	Decadal	May			August				Reference	
		Regression	Start	End	Decadal	regression	Start	End		
<u>Hydrography</u>										
Depth of O ₂ 2ml/l	-2.32 m	-0.3978	91.4 m	78.4 m	-2.69 m	-0.4542	87.8 m	72.7 m	Plikshs et al. (1993)	
Depth of 40 % O ₂ saturation	-2.58 m	-0.3954	86.3 m	71.9 m	-1.87 m	-0.4208	77.6 m	67.2 m	Chabot & Dutil (1999)	
Cod life cycle:										
<u>Egg phase</u>										
Vertical extension of RV (m)	-2 m	-0.2688	30.5 m	19.3 m	-2.64 m	-0.3646	28.2 m	13.4 m	Plikshs et al. (1993)	
OES (%) in RV	-0.7 %	-0.0676	50 %	45.8 %	-1.7 %	-0.2513	41.1 %	31.3 %	Rohlf (1999)	
O ₂ (ml/l)	on 10.4 σ_t	-0.17 ml/l	-0.1741	5.01 ml/l	4.05 ml/l	-0.28 ml/l	-0.3517	4.21 ml/l	2.64 ml/l	
	on 11.3 σ_t	-0.23 ml/l	-0.2085	4.09 ml/l	2.82 ml/l	-0.33 ml/l	-0.3979	3.43 ml/l	1.57 ml/l	
	on 12.26 σ_t	-0.24 ml/l	-0.2153	3.25 ml/l	1.89 ml/l	-0.31 ml/l	-0.3804	2.59 ml/l	0.87 ml/l	
OES (%)	on 10.4 σ_t	-2.9 %	-0.1599	64.3 %	48.1 %	-5.6 %	-0.3768	52.3 %	20.8 %	
	on 11.3 σ_t	-4.8 %	-0.256	50.7 %	23.8 %	-5.7 %	-0.4084	36.1 %	4.4 %	
	on 12.26 σ_t	-3.8 %	-0.20663	34.6 %	13.4 %	-3.5 %	-0.3086	21.1 %	1.7 %	
<u>Larval phase</u>										
LVMA (%)	on 10.4 σ_t	-0.62 %	-0.0562	58 %	54.5 %	-3.18 %	-0.2566	54.4 %	36.6 %	Rohlf (1999)
	on 11.3 σ_t	-2.23 %	-0.1462	48.7 %	36.2 %	-5.0 %	-0.3562	44.7 %	15.0 %	Rohlf (1999)
	on 12.26 σ_t	-4.53 %	-0.2486	40.1 %	14.7 %	-6.0 %	-0.3913	32.4 %	0.0 %	Rohlf (1999)
<u>Juvenile phase</u>										
Settlement area (km ²) in October	-900 km ²	-0.5282	23486km ²	18578km ²					Hinrichsen et al. (2009)	
<u>Adult phase</u>										
Distribution:										
Depth (m) at 15% saturation	-1.88 m	-0.3997	95 m	84.5 m	-2.76 m	-0.5002	94.1 m	78.7 m	Schaber et al. (2009)	
Adult range	0.7 m	0.1695	8.7 m	12.5 m	-0.89 m	-0.2095	16.5 m	11.6 m		
Physiology:										
GER	13.0 psu	-0.008	-0.063	0.79	0.75	-0.035	-0.2672	0.75	0.55	Brach (1999)
	14.5 psu	-0.027	-0.1719	0.66	0.51	-0.052	-0.3658	0.59	0.30	Brach (1999)
	16.0 psu	-0.042	-0.2279	0.54	0.31	-0.047	-0.341	0.42	0.16	Brach (1999)



GENERAL DISCUSSION

The aim of this thesis was to assess the influence of the (vertical) hydrographic structure in the Baltic Sea on small- to meso-scale distribution patterns of Baltic cod (*Gadus morhua*). This was achieved by combining hydroacoustic and hydrographic measurements in correspondingly high spatial resolution. In particular, the following scientific tasks were addressed:

- i) Investigate the applicability of hydroacoustic single target detection/single fish tracking for the *in-situ* identification of individual cod
- ii) Identify habitat limits and thresholds for environmental conditions by allocating *in-situ* environmental data to each individual cod
- iii) Assess trends in distribution patterns and habitat availability on a population level
- iv) Investigate possible effects of long-term trends in the abiotic environment based on distribution data

Hydroacoustics

Echorecordings and results from data storage tags revealed similar distribution patterns, and distributional boundaries were generally consistent from both datasets (**Chapter I**). Thus, the capacity of hydroacoustic data of scaling individual limitations to a population level is evident. A much larger fraction of the distribution area of the corresponding cod population can be covered when recording hydroacoustic data, and the number of individual cod identified is orders of magnitude higher than sample sizes from DSTs or trawl hauls.

However, hydroacoustic devices alone cannot discriminate between individuals of different fish species. A distinctive feature of the single target detection algorithm is the application of a minimum target strength (TS) threshold required for acceptance of the detected target. The TS of a fish is dependent on the size of the swimbladder as scattering organ, and therefore also a function of fish size (e. g. Rose & Porter 1996, McQuinn & Winger 2003). In this study, minimum thresholds of -50 db (**Chapter I**) and -37 db (**Chapter II & III**) have been applied to facilitate the identification of individual cod. The former threshold also allowed for detecting juvenile cod but led to a possible misidentification of echoes originating from clupeids (e.g. Didrikas & Hansson 2004, Fässler & Gorska 2009). However, manual post-processing of echograms and identification of clupeid schools greatly reduced the possibility of misidentification. The latter threshold largely ruled out a misidentification of echoes but did not resolve cod smaller than ca. 30 cm (Rose & Porter 1996) and thus did not allow conclusions for juvenile cod.

Previous studies on cod target strength have shown, that TS is not only a function of fish size but also varies with different orientation (tilt angle, Aglen 1994) (McQuinn & Winger 2003) and depth of the fish (Rose 2009), especially during vertical migration. However, this is considered uncritical for this study. Extended (diurnal) vertical migrations so far have not been identified in Baltic cod (e.g. Neuenfeldt et al. 2007, van der Kooij et al. 2007), and the corresponding changes in TS due to different orientation angles or depths of residency (McQuinn & Winger 2003, Rose 2009) would not significantly affect the results of the TS based single target identification.

The performance of hydroacoustic single fish tracking may be affected when fishes of different species but similar scattering characteristics and overlapping length ranges are present. Due to the low species diversity in the central Baltic pelagic ecosystem (ICES 2006), other species than cod, herring and sprat can virtually be ruled out as echo sources. However, comparative fishery hauls validating echorecordings and allowing for species allocation are especially important in areas with e. g. higher diversity of gadoid fishes that have similar scattering characteristics (Foote 1986). Additionally, the single target identification and fish tracking algorithms employed (Sonardata 2007) will due to the settings required perform weak in resolving individuals in a dense fish school. Thus, investigations that are based on individual fish are not applicable on e.g. clupeids. In that case, the “traditional” method of applying integration thresholds in combination with fisheries hauls to allocate fishes to echorecordings has to be applied (e.g. Stepputtis et al. 2011). Additionally, school detection algorithms based on known dimensional characteristics of fish schools can be applied (Nilsson et al. 2003 and **Chapter II**).

Habitat limits and environmental thresholds

Salinity and oxygen concentration have been identified as major driving forces affecting (vertical) cod distribution in the central Baltic Sea. Spawning cod were almost exclusively distributed below the permanent halocline and in that layers avoided salinities of less than 11 psu and oxygen concentrations of less than 1.5 ml l⁻¹ (during stagnation periods), which lead to a broad vertical distribution range in a situation with well oxygenized bottom layers (post inflow, 2003) and a distinct confinement in stagnation periods (2005) (**Chapter I**). This distribution pattern was also identified for quarters two and three of the years 2006 to 2009 (**Chapter II**) where only a small fraction of cod detected was distributed outside the referring boundary layers.

The upper limitation of preferred cod habitat, marked by the upper layers of the permanent halocline, seems surprising. Cod is an euryhaline fish species and was experimentally shown to not experience osmotic disturbances in salinities as low as 7 (Dutil et al. 1992, Claireaux et al. 1995). Additionally, non-spawning cod are distributed in large parts of the Baltic proper including shallow regions with salinities lower than the ambient salinities experienced below the permanent halocline in the Bornholm Basin (Aro 1989, 2000). However, during their spawning period EBC accumulate in the deep

Basins (e. g. Aro 1989), obviously tolerating less variability in salinity and preferring salinities higher than ca. 11 psu. This was also shown by Tomkiewicz et al. (1998) and Neuenfeldt & Beyer (2003) and could be related to a minimum requirement of ca. 11 psu for successful fertilization and egg development as shown by Westin & Nissling (1991).

In all studies of the present thesis, ambient temperature had no effect on distribution patterns of EBC in the Bornholm Basin. Despite temperature being the single most important factor determining metabolic rates and also playing a significant role in the development and viability of egg and larval stages (e. g. Wieland et al. 1994, Nissling 2004), the distribution of adult cod in the Bornholm Basin seems unaffected by temperature, or at least overridden by salinity and oxygen concentration. Multiple studies have shown that growth rates, metabolic scope, tolerance of hypoxic conditions (see below), recruitment and distribution, etc. of Atlantic cod are all related to ambient temperature (Drinkwater 2005 and references therein, Gröger & Fogarty 2011). In their natural habitat, cod experience temperature ranges from subzero to 18°C (Sundby 2000, Righton et al. 2010). However, the temperature range occupied by EBC in the studies contributing to this thesis was well within these limits and well within values reported as critically for this eurythermal species, despite a known reduction in thermal tolerance during spawning (e. g. Sartoris et al. 2003, Lannig et al. 2004, Sylvestre et al. 2007, Righton et al. 2010). Sylvestre et al. (2007) suggested that short-term thermal sensitivity of cod is of considerable relevance to metabolic performance in nature due to the exposure to distinct thermal fluctuations during seasonal migration and diel vertical movements as e.g. described by Godø & Michalsen (2005). An exposure effect on spawning cod in the central Baltic seems unlikely, as marked diurnal vertical movements were not detected nor did the depth layers inhabited by cod show temperature gradients considered critical.

The habitat limits derived in this study for (spawning) EBC are in general accordance with results from earlier investigations. Hjelm et al. (2004) found positive correlations for both salinity and oxygen concentration and cod abundance. Additionally, no cod were retrieved from trawl catches conducted in layers with an ambient oxygen concentration of less than 2 ml l⁻¹. Tomkiewicz et al. (1998) showed that spawning cod prefer salinities of 11-15 psu and are mostly absent from layers with an ambient oxygen concentration of less than 2.5 ml l⁻¹, which the authors compared to results from studies in the Gulf of St. Lawrence, where cod avoided oxygen concentrations of less than 2.4 ml l⁻¹ (D'Amours 1993).

In the present studies (**Chapter I** and **Chapter II**), the ambient oxygen concentrations acting as habitat limits were lower than those reported in previous studies, and a varying fraction of cod was distributed well outside the preferred habitat limits delineated above. Cod were identified in layers with ambient oxygen concentrations of sometimes

significantly less than 1.0 ml l^{-1} (corresponds to an ambient saturation of less than 17 %). This is in accordance with observations derived from data storage tag recordings as reported by Neuenfeldt et al. (2009). Dissolved oxygen generally is a major limiting factor for the metabolic performance of fishes (Chabot & Claireaux 2008 and references therein). It could be shown, that the metabolic scope (MS) of cod for swimming, feeding, etc. is proportional to the dissolved oxygen (DO) available and generally is too low to for long term survival when ambient DO is lower than ca. 20 % air saturation (Claireaux et al. 2000, Chabot & Claireaux 2008). Additionally, Plante et al. (1998) showed cod mortality rates of 50 % after 96h exposure to an average ambient oxygen saturation of ~21 %, whereas no fish survived long-time exposure to 10 % oxygen saturation. In the field, cod generally select DO values that generate a positive MS, but obviously do not completely avoid hypoxic zones where both growth and locomotor activities are limited – which possibly can be assigned to compromises cod have to take into account other than hypoxia (Chabot & Claireaux 2008). Additionally, Herbert & Steffensen (2005) proposed a highly variable, context-dependent avoidance reaction of cod towards hypoxic zones according to duration and rate of exposure.

There are several possible explanations for the distribution of cod in hypoxic layers as observed in **Chapter I & II**. Claireaux et al. (1995) showed in laboratory experiments that cod entered zones of very low oxygen (saturation <16 %) when food was offered. EBC main prey organisms sprat, and to a lesser extent herring, obviously are less affected by ambient oxygen concentration (Orlowski 1999) or tolerate oxygen concentrations of less than 1 ml l^{-1} (Orlowski 2005, Stepputtis 2006). Thus, the observations of cod in layers with low ambient oxygen concentrations could be related to short feeding excursions, as also suggested by Neuenfeldt et al. (2009). Predation on benthic organisms as, amongst others, suggested by Neuenfeldt et al. (2009) seems unlikely in the present studies, as especially in the summer months cod were only detected near the seafloor in regions with enhanced oxygen conditions but not in hypoxic regions. However, echoes that could be assigned to clupeid schools were detected in layers with low oxygen concentrations during the daytime recordings contributing to **Chapter I**. Cod were also found in oxygen depleted layers during nighttime (**Chapter II**) – a time when clupeids due to regular diurnal vertical migration (DVM) activity should mostly be distributed in shallower layers (e. g. Orlowski 2005). However, as Nilsson et al. (2003) have shown, a fraction of clupeid schools do not undertake DVM but disperse in deeper layers. Despite ambient DO levels that can be considered too low to allow for long time survival (Plante et al. 1998, Chabot & Claireaux 2008), that lead to reduced MS and swimming capacity (Herbert & Steffensen 2005, Petersen & Gamperl 2010) and also to lower GER (Teschner et al. 2010), short term movements into hypoxic layers are considered possible. Thus, feeding excursions of cod into these layers cannot be ruled out.

Another possibility for the extended vertical range that included zones of low oxygen could be swimming activity that is related to pre-spawning aggressive or courtship

behavior or to mating. Brawn (1961) described aggressive defending of individual territory by male cod in the weeks prior to spawning. Male to male competition in Atlantic cod was also observed by Hutchings et al. (1999). Increased vertical swimming activity due to this dominance behavior or due to evasive behavior of inferior males could contribute to the dispersion of cod into zones of low oxygen. Additionally, increased vertical movements of spawning cod that could be related to courtship and mating behavior were described by Rose (1999), Lawson & Rose (2000) and Fudge & Rose (2009) for cod spawning aggregations in Newfoundland.

As all possible causes for dispersion of individuals into almost anoxic layers most likely only take effect on a limited temporal scale due to a reduced long term MS (see above) and are only exerted by a fraction of the population at any given time, it is possible that distributional studies based on trawl catches (Tomkiewicz et al. 1998, Hjelm et al. 2004) overlooked this fraction of the population and thus identified different threshold oxygen levels, or at least different oxygen concentration levels above which cod started to aggregate. It has to be mentioned, that the field observations above contribute to studies on the MS of Atlantic cod (Chabot & Claireaux 2008), which in return do not account for the “hypoxic cod” observed by Neuenfeldt et al. (2009) and in this study.

Trends in distribution patterns and habitat availability; consequences and implications for stock assessment

Investigations on vertical distribution patterns of cod along longitudinal transects in the Bornholm Basin revealed a common seasonal trend for all years observed (**Chapter II**). A marked upward shift of mean cod depth occurred from April to August each year. This was caused by a decline in ambient oxygen concentrations in deep layers of the basin that was observed in all years investigated, and a general avoidance of these hypoxic layers by cod (also see **Chapter I**). Generally, this decline is related to biological processes and seems a common trait of the hydrodynamics of the Bornholm Basin (see Hinrichsen et al. 2007). Even in stagnation years, regular small to medium-sized inflows can occur. These take mostly place in the winter months (Hinrichsen et al. 2002a). It could be shown, that due to the significant effect of ambient oxygen concentration on the vertical distribution of cod, their distribution patterns mostly followed this decline and were characterized by deeper, near-bottom or demersal distribution in the second quarter of the year and a shallower, pelagic distribution in the third quarter.

Additionally, the upper distribution limit marked by the upper layers of the permanent halocline remained rather constant. This, in combination with a seasonal upward extension of poorly oxygenated layers, led to a decrease of available, favorable habitat for cod in the Bornholm Basin.

There are several possible consequences of this trend for both dynamics and assessment of EBC stock.

In recent years, after several strong year-classes, a significant increase in SSB and TSB of EBC was recorded which was mostly related to improved environmental conditions (ICES 2011a) or reduced fishing pressure (Cardinale & Svedäng 2011). Concurrently, a decline in the Baltic sprat stock has been observed (ICES 2011a). Apart from positive effects on the predation mortality of cod early life stages, this could also result in another feedback loop affecting survival of juvenile cod. Despite not significantly contributing to stock dynamics or recruitment success, cannibalism on juveniles by large adult cod still plays an important role in both WBC and EBC. Cannibalism is intense in years with high abundance of juveniles and large adult stock size and seems to be mainly controlled by the overlap between juvenile and adult distribution patterns (Uzars & Plikshs 2000, Neuenfeldt & Köster 2000). The reduced habitat availability for adults and larger juveniles (see **Chapter III**) could lead to a higher overlap, which in combination with higher densities of fishes in the corresponding habitats could significantly contribute to the predation mortality of juvenile cod by cannibalism. This effect is expected to be most pronounced in the basin rims, where the habitat overlap can be considered largest (e. g. Bagge et al. 1994, Hinrichsen et al. 2009).

EBC stock assessment is tuned with indices derived from annually conducted (bottom) trawl surveys covering ICES subdivisions 25-28 (ICES 2011b). Based on previous observations of cod absence from hypoxic layers, no trawl haul is operated when the ambient oxygen concentration in the region of vertical net opening is below 1.5 ml l^{-1} , as “zero catches” are expected in these layers (ICES 2008). Despite increasing awareness of a substantial biomass of cod distributed pelagically and beginning investigations on how to quantify the pelagic fraction of cod, no changes in the official survey strategy have been adopted as of yet (ICES 2011c). Neglecting this pelagic fraction of cod could lead to an underestimation of stock size in predictive runs for assessment. It has to be mentioned, that the manual for the bottom trawl survey restricts sampling to the first and fourth quarter of the year and therefore rules out biases from e. g. spawning aggregation behavior. Even though the sampling for the studies presented in this thesis was carried out in the second and third quarter, the results are considered expandable to other seasons. Despite a dispersal of spawning aggregations after the main spawning season (Aro 1989), a large fraction of cod remains in the Bornholm Basin (e. g. Bagge et al. 1974, 1994). Although salinity seems to be less limiting outside their spawning season (see above), an avoidance of oxygen depleted layers will persist.

Other possible consequences for stock assessment have also to be taken into account when adapting trawl surveys to the pelagic fraction of cod or using commercial catch data for tuning. When using catch rates (CPUE) as an index for an abundance trend, these could suggest higher abundances of cod than actually are present (e. g. Walters 2011). Due to the loss of favorable habitat and a vertical “compression” of cod distribution with decreasing oxygen concentration in deep layers, the remaining volume of preferred water may be in vertical dimensions largely covered by the trawl nets

employed – resulting in increased CPUE. Density dependent habitat preferences of cod in the Gulf of St. Lawrence were suggested by Swain & Kramer (1995) who showed that cod expand their habitat into regions with lower temperatures in times of high abundance. Additionally, a density dependent catachability was reported by Swain et al. (1994, 2000) (although this obviously did not result from density-dependent changes in distribution). It can be assumed that the avoidance of hypoxic layers by cod is not related to fish density, as physiological consequences resulting from reduced oxygen availability are considered more severe than changes in ambient temperature that still are within the thermal range of the fish (Plante et al. 1998, Sartoris et al. 2003, Lannig et al. 2004, Chabot & Claireaux 2008). Thus, cod density could be increased in layers over hypoxic zones, leading to an increased CPUE and a possible bias in abundance estimates. However, lateral dispersion of cod in these layers as suggested by Hjelm et al. (2004) also is a possibility to be taken into account.

Effects of abiotic long-term trends

Since 2005, several above average year-classes of EBC contributed to a significant increase of TSB and SSB (ICES 2011a). The environmental conditions on cod main spawning grounds however were not notably improved as compared to the stagnation years following the last major inflow in 2003 (e. g. Hinrichsen et al. 2007). Therefore, the increase in cod biomass was related to improved fisheries regulations and reduced fishing mortality by Cardinale & Svedäng (2011). The present trend could lead to the false impression of fisheries being the single most important factor affecting dynamics of EBC stock.

Distribution patterns of different life stages of cod were related to trends in ambient oxygen concentration. Apart from reduced habitat availability for adult cod with proceeding oxygen depletion (**Chapter II**), a negative effect of long-term oxygen reduction on all life stages could be shown (**Chapter III**). An observed general decline in oxygen concentrations at high density (salinity) levels and an expected persistence of this trend (BACC Author Team 2008) will most likely affect eggs, larvae, juveniles and adults in the future. This will comprise large proportions of eggs that float in layers with too low ambient oxygen concentrations to allow for successful development, larvae that are restricted in vertical migration activity, juveniles that face decreasing settling areas (and increasing density-dependent processes) and adults that lose favorable habitat and are physiologically affected by hypoxic conditions.

So far, the future environmentally driven development of different stocks of Atlantic cod has mainly been related to direct and indirect effects of increasing temperatures (Drinkwater 2005, Brander 2010). Anthropogenic warming is expected to lead to a northward extension of cod, a shift in distribution patterns and to the disappearance of different cod stocks already living at the upper end of their thermal range, like e. g. the Irish and Celtic Sea stocks (Drinkwater 2005). In the Baltic Sea, several influences have

been identified as critical for EBC development – with changing weights over the decades: Fishing pressure, predation by seals, eutrophication and climate variability. Nowadays, fishing pressure and climate variability are the most important factors (Eero et al. 2011). An increase in ambient temperature as predicted (BACC Author Team 2008) is per se considered uncritical for EBC. However, this predicted increase is accompanied by lower oxygen solubility and, due to also increased precipitation and river runoff, reduced ambient salinities. Multispecies model predictions taking into account the interactions between fishing pressure and climate change (here: temperature and salinity) and also incorporating internal and external sources of uncertainty (climate variability, food-web dynamics) even project the risk of extinction of Baltic cod during this century (Lindegren et al. 2009, 2010).

Adding to those factors included in the above mentioned modeling approaches, it was shown in **Chapter III** that decreasing ambient oxygen levels also evoke the risk of long-term diminution of EBC with progressing climate change, because corresponding trends negatively affect all life stages of cod. Adverse environmental conditions therefore can render fishing mortalities as too high, which were originally estimated as precautionary (Köster et al. 2010). Therefore it can be concluded that despite a sound fisheries management and regulations leading to significant increases in TSB and SSB, despite the assessment of EBC being characterized as appropriate and sustainably (ICES 2011a), there presently is the risk of anthropogenic long-term environmental changes that finally render the Baltic Sea unsuitable for cod.

Outlook

The hydroacoustic methods described in this thesis appear to be adequate for application on a larger spatial scale to further develop on some critical aspects related to the horizontal distribution of EBC: Lateral dispersion effects over hypoxic layers as e. g. suggested by Hjelm et al. (2004) could be evaluated in more detail. Highly resolving spatio-temporal distribution patterns could be used to assess the effectiveness of an MPA in the Bornholm Basin (Kraus et al. 2009) in reducing the overall fishing effort on cod. Finally, also biotic parameters potentially affecting cod distribution could be addressed. A highly resolved analysis of both cod and clupeid (sprat, herring) horizontal and vertical distribution patterns could aid in determining both predator-prey overlaps, driving mechanisms, aggregation effects of prey organisms on predators (e. g. Neuenfeldt & Beyer 2003, 2006), etc. Additionally, the assessment of corresponding overlap patterns during cod spawning time could also facilitate to evaluate the actual predation pressure on cod early life stages by planktivore sprat and herring in light of changing stock numbers.



REFERENCES

- Aglen A (1994) Sources of error in acoustic estimation of fish abundance. In: Marine Fish Behaviour in Capture and Abundance Estimation (Eds. Ferno A, Olsen S), Fishing News Books, Oxford, pp 107–129
- Anon (1934) Trials with an echosounder during the sprat fishery. Bulletin of the Canning Industry, July 1934, pp 222-223 (in Norwegian)
- Antonov JI, Seidov D, Boyer TP, Locarnini RA, Mishonov AV, Garcia HE, Baranova OK, Zweng MM, Johnson DR (2010) World Ocean Atlas 2009 Vol. 2: Salinity. NOAA Atlas NEDSIS 69, US Government Printing Office, Washington DC
- Apostolaki P, Milner-Gulland EJ, McAllister MK, Kirkwood GP (2002) Modelling the effects of establishing a marine reserve for mobile fish species. Canadian Journal of Fisheries and Aquatic Sciences 59: 405-415
- Arndt E-A (1996) Lebensgemeinschaften. In: Warnsignale aus der Ostsee (Eds. Lozán JL, Lampe R, Matthäus W, Rachor E, Rumohr H, von Westernhagen H). Parey, Berlin, pp 47-54 (in German)
- Aro E (1989) A review of fish migration patterns in the Baltic. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer 190: 72-96
- Aro E (2000) The spatial and temporal distribution patterns of cod (*Gadus morhua callarias*) in the Baltic Sea and their dependence on environmental variability – implications for fishery management. PhD thesis, University of Helsinki
- Alheit J, Möllman C, Dutz J, Kornilovs G, Loewe P, Mohrholz V, Wasmund N (2005) Synchronous ecological regime shifts in the central Baltic and the North Sea in the late 1980s. ICES Journal of Marine Science 62: 1205-1215
- Austin MP (2002b) Spatial prediction of species distribution: an interface between ecological theory and statistical modeling. Ecological Modelling 157: 101-118
- Austin, HM (2002a) Decadal Oscillations and Regime Shifts, a Characterization of the Chesapeake Bay Marine Climate. American Fisheries Society Symposium 32: 155-170
- Axenrot T, Ogonowski M, Sandström A, Didrikas T (2009) Multifrequency discrimination of fish and mysids. ICES Journal of Marine Science 66: 1106-1110
- BACC Author Team (2008) Assessment of Climate Change for the Baltic Sea Basin. Springer-Verlag Berlin, Heidelberg, 474 pp

- Bagge O (1981) Demersal fishes. In: The Baltic Sea (Ed. Voipio A). Elsevier Oceanographic Series No. 30. Elsevier Scientific Publishing Company, Amsterdam, Oxford, New York, pp 311-333
- Bagge O (1989) A review of investigations of the predation of cod in the Baltic. *Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer* 190: 51-56
- Bagge O, Tiews K, Lamp F, Otterlind G (1974) German, Swedish and Danish cod tagging experiments in the Baltic 1968-1969. *Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer* 166: 22-39
- Bagge O, Thurow F, Steffensen E, Bay J (1994) The Baltic cod. *Dana* 10: 1-28
- Bergstad OA, Jørgensen T, Dragesund O (1987) Life history and ecology of the gadoid resources of the Barents Sea. *Fisheries Research* 5: 119-161
- Bosman SH, Methven DA, Courtenay SC, Hanson JM (2011) Fish assemblages in a north Atlantic coastal ecosystem: Spatial patterns and environmental correlates. *Estuarine, Coastal and Shelf Science* 92: 232-245
- Brach H (1999) Experimente zur Nahrungsaufnahme und zum Wachstum von Dorschen bei unterschiedlichen Sauerstoffbedingungen. Diploma thesis, Institute of Marine Sciences, Kiel, 65 pp (in German)
- Brander KM (2010) Cod (*Gadus morhua*) and climate change: processes, productivity and prediction. *Journal of Fish Biology* 77: 1899-1911
- Brawn VM (1961) Reproductive behaviour of the Cod (*Gadus callarias* L.). *Behaviour* 18: 177-197
- Bretherton FP, Davis RE, Fandry CB (1976) A technique for objective analysis and design of oceanographic experiments applied to MODE-73. *Deep Sea Research I* 23(7): 559-582
- Cardinale M, Möllmann C, Bartolino V, Casini M, Kornilovs G, Raid T, Margonski P, Grzyb A, Raitaniemi J, Groehsler T, Flinkman J (2009) Effect of environmental variability and spawner characteristics on the recruitment of Baltic herring *Clupea harengus* populations. *Marine Ecology Progress Series* 388: 21-234
- Cardinale M, Svedäng H (2011) The beauty of simplicity in science: Baltic cod stock improves rapidly in a "cod hostile" ecosystem state. *Marine Ecology Progress Series* 425: 297-301

- Casini M, Cardinale M, Hjelm J (2006) Inter-annual variation in herring, *Clupea harengus*, and sprat, *Sprattus sprattus*, condition in the central Baltic Sea: what gives the tune? *Oikos* 112: 638-650
- Chabot D, Dutil JD (1999) Reduced growth of Atlantic cod in non-lethal hypoxic conditions. *Journal of Fish Biology* 55: 472-491
- Chabot D, Claireaux G (2008) Environmental hypoxia as a metabolic constraint on fish: The case of Atlantic cod, *Gadus morhua*. *Marine Pollution Bulletin* 57: 287-294
- Claireaux G, Dutil JD (1992) Physiological response of the Atlantic cod *Gadus morhua* to hypoxia at various environmental salinities. *Journal of Experimental Biology* 163: 97-118
- Claireaux G, Webber DM, Kerr SR, Boutilier RG (1995) Physiology and behavior of free-swimming Atlantic cod (*Gadus morhua*) facing fluctuating salinity and oxygen conditions. *Journal of Experimental Biology* 198: 61-69
- Claireaux G, Webber DM, Lagardère JP, Kerr SR (2000) Influence of water temperature and oxygenation on the aerobic metabolic scope of Atlantic cod (*Gadus morhua*). *Journal of Sea Research* 44: 257-265
- Clay A, Castonguay M (1996) In situ target strengths of Atlantic cod (*Gadus morhua*) and Atlantic mackerel (*Scomber scombrus*) in the Northwest Atlantic. *Canadian Journal of Fisheries and Aquatic Sciences* 53: 87-98
- D'Amours D (1993) The distribution of cod (*Gadus morhua*) in relation to temperature and oxygen level in the Gulf of St Lawrence. *Fisheries Oceanography* 2: 24-29
- Didrikas T, Hansson S (2004) In situ target strength of the Baltic Sea herring and sprat. *ICES Journal of Marine Science* 61: 378-382
- Dingsoer GE, Cianelli L, Chan KS, Ottersen G, Stenseth NC (2007) Density dependence and density independence during early life stages of four marine fish stocks. *Ecology* 88: 625-634
- Drinkwater KF (2005) The response of Atlantic cod (*Gadus morhua*) to future climate change. *ICES Journal of Marine Science* 62: 1327-1337
- Dutil JD, Munro J, Audet C, Besner M (1992) Seasonal variations in the physiological response of the Atlantic cod *Gadus morhua* to low salinity. *Canadian Journal of Fisheries and Aquatic Sciences* 49: 1149-1156
- Eero M, MacKenzie BR, Köster FW, Gislason H (2011) Multi-decadal responses of a cod (*Gadus morhua*) population to human-induced trophic changes, fishing, and climate. *Ecological Applications* 21: 214-226

-
- Ehrenberg JE, Torkelson TC (1996) Application of dual-beam and split-beam target tracking in fisheries acoustics. *ICES Journal of Marine Science* 53: 329-334
- Fässler SM, Gorska N (2009) On the target strength of Baltic clupeids. *ICES Journal of Marine Science* 66: 1184-1190
- Feistel R, Nausch G, Wasmund N (2008) State and Evolution of the Baltic Sea, 1952-2005: A Detailed 50-Year Survey of Meteorology and Climate, Physics, Chemistry, Biology, and Marine Environment, Wiley, Hoboken, NJ, 712 pp
- Fernandes PG (2009) Classification trees for species identification of fish-school echotraces. *ICES Journal of Marine Science* 66: 1073-1080
- Fonselius S, Valderrama J (2003) One hundred years of hydrographic measurements in the Baltic Sea. *Journal of Sea Research* 49: 229-241
- Foote KG (1987) Fish target strengths for use in echo integrator surveys. *Journal of the Acoustical Society of America* 82: 981-987
- Foote KG, Aglen A, Nakken O (1986) Measurement of fish target strength with a split-beam echosounder. *Journal of the Acoustical Society of America* 80: 612-621
- Frank KT, Petrie B, Choi JS, Leggett WC (2005) Trophic cascades in a formerly cod-dominated ecosystem. *Science* 308: 1621-1623
- Fréon P, Gerlotto F, Soria M (1996) Diel variability of school structure with special reference to transition periods. *ICES Journal of Marine Science* 53: 459-464
- Fudge SB, Rose GA (2009) Passive- and active-acoustic properties of a spawning Atlantic cod (*Gadus morhua*) aggregation. *ICES Journal of Marine Science* 66: 1259-1263
- Gerlach SA (1994) Oxygen conditions improve when the salinity in the Baltic Sea decreases. *Marine Pollution Bulletin* 28: 413-416
- Godø OR, Michalsen K (2000) Migratory behaviour of north-east Arctic cod, studied by use of data storage tags. *Fisheries Research* 48: 127-140
- Gröger JP, Fogarty MJ (2011) Brad-scale climate influences on Atlantic cod (*Gadus morhua*) recruitment on Georges Bank. *ICES Journal of Marine Science*, doi:10.1093/icesjms/fsq196
- Grønkjær P, Wieland K (1997) Ontogenetic and environmental effects on vertical distribution of cod larvae in the Bornholm basin, Baltic Sea. *Marine Ecology Progress Series* 154: 91-105
- Guisan A, Zimmermann E (2000) Predictive habitat distribution models in ecology. *Ecological Modelling* 135: 147-186
-

-
- Guisan A, Thuiller W (2005) Predicting species distribution: Offering more than simple habitat models. *Ecology Letters* 8: 993-1009
- Handegard NO, Michalsen K, Tjøstheim D (2003) Avoidance behaviour in cod (*Gadus morhua*) to a bottom-trawling vessel. *Aquatic Living Resources* 16: 265-270
- Handegard NO, Tjøstheim D (2005) When fish meet a trawling vessel: examining the behaviour of gadoids using a free-floating buoy and acoustic split-beam tracking. *Canadian Journal of Fisheries and Aquatic Sciences* 62: 2409-2422
- Harden Jones FR, Scholes P (1985) Gas secretion and resorption in the swimbladder of the cod *Gadus morhua*. *Journal of Comparative Physiology B* 155: 319-331
- HELCOM (2006) Changing Communities of Baltic Coastal Fish Executive summary: Assessment of coastal fish in the Baltic Sea. *Baltic Sea Environment Proceedings* 103 B, 13 pp
- Herbert NA, Steffensen JF (2005) The response of Atlantic cod, *Gadus morhua*, to progressive Hypoxia: fish swimming speed and physiological stress. *Marine Biology* 147: 1403-1412
- Hinrichsen H-H, Lehmann A, St. John M, Brüggel B (1997) Modeling the cod larvae drift in the Bornholm Basin in summer 1994. *Continental Shelf Research* 17: 187-201
- Hinrichsen H-H, St John M, Lehmann A, MacKenzie BR, Köster FW (2002a) Resolving the impact of short-term variations in physical processes impacting on the spawning environment of eastern Baltic cod: application of a 3-D hydrodynamic model. *Journal of Marine Systems* 32: 281-294
- Hinrichsen H-H, Möllmann C, Voss R, Köster FW, Kornilovs G (2002b) Biophysical modelling of larval Baltic cod (*Gadus morhua* L) growth and survival. *Canadian Journal of Fisheries and Aquatic Sciences* 59: 1858-1873
- Hinrichsen HH, Voss R, Wieland K, Köster F, Andersen KH, Margonski P (2007) Spatial and temporal heterogeneity of the cod spawning environment in the Bornholm Basin, Baltic Sea. *Marine Ecology Progress Series* 345: 245-254
- Hinrichsen H-H, Kraus G, Böttcher U, Köster FW (2009) Identifying eastern Baltic cod nursery grounds using hydrodynamic modelling: knowledge for the design of Marine Protected Areas. *ICES Journal of Marine Science* 66: 101-108
- Hjelm J, Simonsson J, Cardinale M (2004) Spatial distribution of cod in the Baltic Sea in relation to abiotic factors - a question of fish-age and area. *ICES CM L:16*: 35 pp
-

-
- Hüssy K, St.John MA, Böttcher U (1997) Food resource utilization by juvenile Baltic cod *Gadus morhua*: a mechanism potentially influencing recruitment success at the demersal stage? Marine Ecology Progress Series 155: 199-208
- Hutchings JA (2000) Collapse and recovery of marine fishes. Nature 406: 882-885
- Hutchings JA, Myers RA, Lilly GR (1993) Geographic variation in the spawning of Atlantic cod, *Gadus morhua*, in the Northwest Atlantic. Canadian Journal of Fisheries and Aquatic Sciences 50: 2457-2467
- Hutchings JA, Bishop TD, McGregor-Shaw CR (1999) Spawning behaviour of Atlantic cod, *Gadus morhua*: evidence of mate competition and mate choice in a broadcast spawner. Canadian Journal of Fisheries and Aquatic Sciences 56: 97-104
- Huwer B (2009) The recruitment process in Baltic cod. Spatio-temporal variation in starvation and predation during early life stages with special consideration of the invasive ctenophore *Mnemiopsis leidyi*. PhD thesis, DTU Aqua, National Institute of Aquatic Resources, Technical University of Denmark, 212 pp
- ICES (2001) Manual for the Baltic international acoustic surveys (BIAS). ICES CM 200 1/H: 02 (Annex 2), 25 pp
- ICES (2005) Spawning and life history information for North Atlantic cod stocks. ICES Cooperative Research Report No. 274, 152 pp (edited by K. Brander)
- ICES (2006) Report of the Study Group on Multispecies Assessment in the Baltic (SGMAB). ICES CM BCC: 07, 116 pp
- ICES (2007) Report of the Baltic International Fish Survey Working Group (WGBIFS). ICES CM 2007 / LRC: 06, 84 pp
- ICES (2008) Manual for the Baltic international trawl surveys (BITS). ICES CM 2008 / LRC: 08 (Addendum 1), 72 pp
- ICES (2009) Report of the Baltic International Fish Survey Working Group (WGBIFS). ICES CM 2009 / LRC: 05, 75 pp
- ICES (2010a) Report of the ICES Advisory Committee, 2010. ICES Advice, 2010. Book VIII, 119 pp
- ICES (2010b) Report of the Baltic Fisheries Assessment Working Group (WGBFAS), 15-22 April 2010, ICES Headquarter, Copenhagen. ICES CM 2010 / ACOM: 10, 633pp
- ICES (2011a) Report of the ICES Advisory Committee, 2011. ICES Advice, 2011. Book VIII, 127 pp
-

-
- ICES (2011b) Manual for the Baltic international trawl surveys (BITS). ICES CM 2011 / SSGESST: 05 (Addendum 1), 72 pp
- ICES (2011c) Report of the Baltic International Fish Survey Working Group (WGBIFS). ICES CM 2011 / SSGESST: 05, 102 pp
- Jakupsstovu SH, Reinert J (1994) Fluctuations in the Faroe Plateau cod stock. ICES Marine Science Symposia 198: 194-211
- Jennings S, Kaiser MJ (1998) The effects of fishing on marine ecosystems. *Advances in Marine Biology* 34: 201-352
- Johansen JL, Herbert NA, Steffensen JF (2006) The behavioural and physiological response of Atlantic cod *Gadus morhua* L. to short-term acute hypoxia. *Journal of Fish Biology* 68: 1918-1924
- Jónsson E (1982) A survey of spawning and reproduction of the Icelandic cod. *Rit Fiskideildar* 6: 1-45
- Kaartvedt S, Røstad A, Fiksen Ø, Melle W, Torgersen T, Tiseth Breien M, Klevjer TA (2005) Piscivorous fish patrol krill swarms. *Marine Ecology Progress Series* 299: 1–5
- Kändler R (1944) Untersuchungen über den Ostseedorsch während der Forschungsfahrten mit dem RFD „Poseidon“ in den Jahren 1925-1938. *Berichte der Deutschen Wissenschaftlichen Kommission für Meeresforschung* 11: 137-245
- Kändler R (1949) Die Häufigkeit pelagischer Fischeier in der Ostsee als Maßstab für die Zu- und Abnahme der Fischbestände. *Kieler Meeresforschungen* 6: 73-89
- Killworth PD, Stainforth D, Webb DJ, Paterson SM (1991) The development of a free-surface Bryan-Cox-Semtner ocean model. *Journal of Physical Oceanography* 21: 1333-1348
- Kimura K (1929) On the detection of fish-groups by an acoustic method. *Journal of the Imperial Fisheries Institute, Tokyo* 24: 41-45
- Kjesbu OS, Kryvi H, Sundby S, Solemdal P (1992) Buoyancy variation in eggs of Atlantic cod (*Gadus morhua* L.) in relation to chorion thickness and egg size: theory and observations. *Journal of Fish Biology* 41: 581-599
- Köster FW, Möllmann C (2000) Trophodynamic control by clupeid predators on recruitment success in Baltic cod? *ICES Journal of Marine Science* 57: 310-323
- Köster FW, Hinrichsen H-H, St.John MA, Schnack D, MacKenzie BR, Tomkiewicz J, Plikshs M (2001) Developing Baltic cod recruitment models. II - Incorporation of

- environmental variability and species interaction. *Canadian Journal of Fisheries and Aquatic Sciences* 58: 1534-1556
- Köster FW, Möllmann C, Hinrichsen H-H, Wieland K, Tomkiewicz J, Kraus G, Voss R, Makarchouk A, MacKenzie BR, St. John MA, Schnack D, Rohlf M, Linkowski T, Beyer JE (2005) Baltic cod recruitment – the impact of climate variability on key processes. *ICES Journal of Marine Science* 62: 1408-1425
- Köster FW, Vinther M, MacKenzie BR, Eero M (2010) Environmental Effects on Recruitment and Implications for Biological Reference Points of Eastern Baltic Cod (*Gadus morhua*). *Journal of Northwest Atlantic Fishery Science* 41: 205-220
- Korneliussen RJ, Ona E (2003) Synthetic echograms generated from the relative frequency response. *ICES Journal of Marine Science* 60: 636-640
- Korneliussen RJ, Heggelund Y, Eliassen IK, Johansen GO (2009) Acoustic species identification of schooling fish. *ICES Journal of Marine Science* 66: 1111-1118
- Kossinna E (1921) Die Tiefen des Weltmeeres. Veröffentlichungen des Instituts für Meereskunde, Heft 9 (Berlin).
- Koslow JA (2009) The role of acoustics in ecosystem-based fishery management. *ICES Journal of Marine Science* 66: 966-973
- Kraus G, Tomkiewicz J, Köster FW (2002) Egg production of Baltic cod in relation to variable sex ration, maturity and fecundity. *Canadian Journal of Fisheries and Aquatic Sciences* 59: 1908-1920
- Kraus G, Pelletier D, Dubreuil J, Möllmann C, Hinrichsen H-H, Bastardie F, Vermard Y, Mahévas S (2009) A model-based evaluation of Marine Protected Areas: The example of eastern Baltic cod (*Gadus morhua callarias* L.). *ICES Journal of Marine Science* 66: 109-121
- Lannig G, Bock C, Sartoris FJ, Pörtner HO (2004) Oxygen limitation of thermal tolerance in cod, *Gadus morhua* L., studied by magnetic resonance imaging and on-line venous oxygen monitoring. *American Journal of Physiology – Regulatory, Integrative and Comparative Physiology* 287: R902-R910
- Lawson GL, Rose GA (2000a) Seasonal movements of coastal cod (*Gadus morhua* L.) in Placentia Bay, Newfoundland. *Fisheries Research* 49: 61-75
- Lawson GL, Rose GA (2000b) Small-scale and temporal patterns in spawning of Atlantic cod (*Gadus morhua*) in coastal Newfoundland waters. *Canadian Journal of Fisheries and Aquatic Sciences* 57: 1011-1024

-
- Lebourges-Dhaussy A, Coetzee J, Hutchings L, Roudaut G, Nieuwenhuys C (2009) Zooplankton spatial distribution along the South African coast studied by multifrequency acoustics, and its relationships with environmental parameters and anchovy distribution. *ICES Journal of Marine Science* 66: 1055-1062
- Lehmann A (1995) A three-dimensional baroclinic eddy-resolving model of the Baltic Sea. *Tellus* 47: 1013-1031
- Lehmann A, Hinrichsen H-H (2000) On the thermohaline variability of the Baltic Sea. *Journal of Marine Systems* 25: 333-357
- Lilly GR, Wieland K, Rothschild BJ, Sundby S, Drinkwater K, Brander K, Ottersen G, Carscadden JE, Stenson GB, Chouinard GA, Swain DP, Daan N, Enberg K, Hammill MO, Rosing-Asvid A, Svedäng H, Vásquez A (2008) Decline and Recovery of Atlantic Cod (*Gadus morhua*) Stocks throughout the North Atlantic. In: Resiliency of gadid stocks to fishing and climate change (Eds. Kruse SGH, Drinkwater K, Ianelli JN, Link JS, Stram DL, Wespestad V, Woodby D). Fairbanks, AL: Alaska Sea Grant College Program, pp 39-66
- Lindegren M, Möllmann C, Nielsen A, Stenseth NC (2009) Preventing the collapse of the Baltic cod stock through an ecosystem-based management approach. *Proceedings of the National Academy of Sciences* 106: 14722-14727
- Lindegren M, Möllmann C, Nielsen A, Brander K, MacKenzie BR, Stenseth NC (2010) Ecological forecasting under climate change: the case of Baltic cod. *Proceedings of the Royal Society B* 277: 2121-2130
- Link JS, Bogstad B, Sparholt H, Lilly GR (2009) Trophic role of Atlantic cod in the ecosystem. *Fish and Fisheries* 10: 58-87
- MacKenzie BR, St. John MA, Plikshs M, Hinrichsen H-H, Wieland K (1996a) Oceanographic processes influencing seasonal and interannual variability in cod spawning habitat in the eastern Baltic Sea. *ICES CM 1996/C+J*: 4
- MacKenzie B, St. John M, Wieland K (1996b) Eastern Baltic cod: perspectives from existing data on processes affecting growth and survival of eggs and larvae. *Marine Ecology Progress Series* 134: 265-281
- MacKenzie BR, Hinrichsen H-H, Plikshs M, Wieland K, Zezera AS (2000) Quantifying environmental heterogeneity: habitat size necessary for successful development of cod *Gadus morhua* eggs in the Baltic Sea. *Marine Ecology Progress Series* 193: 143-156

-
- MacKenzie BR, Alheit J, Conley DJ, Holm P, Kinze CC (2002) Ecological hypotheses for a historical reconstruction of upper trophic level biomass in the Baltic Sea. *Canadian Journal of Fisheries and Aquatic Sciences* 59: 173-190
- MacKenzie BR, Gislason H, Möllmann C, Köster FW (2007) Impact of 21st century climate change on the Baltic Sea fish community and fisheries. *Global Change Biology* 13: 1348-1367
- MacLennan DN, Simmonds EJ (1992) *Fisheries Acoustics*. Chapman and Hall, London, 336 pp
- Mason DM, Brandt SB (1996) Effects of spatial scale and foraging efficiency on the predictions made by spatially-explicit models of fish growth rate potential. *Environmental Biology of Fishes* 45: 283-296
- Mason DM, Brandt SB (1999) Space, time, and scale: new perspectives in fish ecology and management. *Canadian Journal of Fisheries and Aquatic Sciences* 56: 1-3
- Massé J, Gerlotto F (2003) Foreword: Introducing nature in fisheries research: the use of underwater acoustics for an ecosystem approach of fish population. *Aquatic Living Resources* 16: 107-112
- Matthäus W (2006) The history of investigation of salt water inflows into the Baltic Sea – from the early beginning to recent results. *Meereswissenschaftliche Berichte Nr. 65*. Institut für Ostseeforschung, Warnemünde, Rostock, Germany, 74 pp
- Matthäus W, Franck H (1992) Characteristics of major Baltic inflows – a statistical analysis. *Continental Shelf Research* 12: 1375-1400
- Matthäus W, Schinke H (1994) Mean atmospheric circulation patterns associated with major Baltic inflows. *Deutsche Hydrographische Zeitschrift* 46: 321-339
- Matthäus W, Schinke H (1999) The influence of river runoff on deep water conditions of the Baltic Sea. *Hydrobiologia* 393: 1-10
- Maxwell DL, Stelzenmüller V, Eastwood PD, Rogers SI (2009) Modelling the spatial distribution of plaice (*Pleuronectes platessa*), sole (*Solea solea*) and thornback ray (*Raja clavata*) in UK waters for marine management and planning. *Journal of Sea Research* 61: 258-267
- McKinstry CA, Simmons MA, Simmons CS, Johnson RL (2005) Statistical assessment of fish behavior from split-beam hydro-acoustic sampling. *Fisheries Research* 72: 29-44
- McQuinn IH, Winger PD (2003) Tilt angle and target strength: target tracking of Atlantic cod (*Gadus morhua*) during trawling. *ICES Journal of Marine Science* 60: 575-583

-
- Mitson RB, Wood RJ (1962) An automatic method of counting fish echoes. *Journal du Conseil International pour l'Exploration de la Mer* 26: 281-291
- Møller JS, Hansen IS (1994) Hydrographic processes and changes in the Baltic Sea. *Dana* 10: 87-107
- Mohrholz V, Dutz J, Kraus G (2006) The impact of exceptionally warm summer inflow events on the environmental conditions in the Bornholm Basin. *Journal of Marine Systems* 60: 285–301
- Morris L, Ball D (2006) Habitat suitability modeling of economically important fish species with commercial fisheries data. *ICES Journal of Marine Science* 63: 1590-1603
- Myers RA, Worm B (2003) Rapid worldwide depletion of predatory fish communities. *Nature* 423: 280-283
- Nellen W, Thiel R (1995) Fische. In: *Meereskunde der Ostsee* (Ed. Rheinheimer G). Springer, Berlin, pp 190-196 (in German)
- Neuenfeldt S (2002) The influence of oxygen saturation on the distributional overlap of predator (cod, *Gadus morhua*) and prey (herring, *Clupea harengus*) in the Bornholm Basin of the Baltic Sea. *Fisheries Oceanography* 11: 11-17
- Neuenfeldt S, Köster FW (2000) Trophodynamic control of recruitment success in Baltic cod: the influence of cannibalism. *ICES Journal of Marine Science* 57: 300-309
- Neuenfeldt S, Beyer JE (2003) Oxygen and salinity characteristics of predator–prey distributional overlaps shown by predatory Baltic cod during spawning. *Journal of Fish Biology* 62: 168-183
- Neuenfeldt S, Beyer JE (2006) Environmentally driven predator-prey overlaps determine the aggregate diet of the cod *Gadus morhua* in the Baltic Sea. *Marine Ecology Progress Series* 310: 151-163
- Neuenfeldt S, Hinrichsen H-H, Nielsen A, Andersen KH (2007) Reconstructing migrations of individual cod (*Gadus morhua* L.) in the Baltic Sea by using electronic data storage tags. *Fisheries Oceanography* 16: 526-535
- Neuenfeldt S, Andersen KH, Hinrichsen H-H (2009) Some Atlantic cod *Gadus morhua* in the Baltic Sea visit hypoxic water briefly but often. *Journal of Fish Biology* 75: 290-294
- Netzel J (1963) Polish cod tagging experiments in the Gdansk Area 1957-62. *ICES CM* 1963/96
-

-
- Netzel J (1968) Polish cod tagging experiments in the Region of Slupsk Furrow in the years 1957/63. ICES CM 1968/F: 7
- Netzel J (1974) Polish cod tagging experiments in the Baltic in 1969 and 1970. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer 166: 40-46
- Nilsson LAF, Thygesen UH, Lundgren B, Nielsen BF, Nielsen JR, Beyer JE (2003) Vertical migration and dispersion of sprat (*Sprattus sprattus*) and herring (*Clupea harengus*) schools at dusk in the Baltic Sea. Aquatic Living Resources 16: 317-324
- Nissling A (2004) Effects of temperature on egg and larval survival of cod (*Gadus morhua*) and sprat (*Sprattus sprattus*) in the Baltic Sea – implications for stock development. Hydrobiologia 514: 115-123
- Nissling, A, Kryvi H, Vallin L (1994) Variation of egg buoyancy of Baltic cod *Gadus morhua* and its implication for egg survival in prevailing conditions in the Baltic Sea. Marine Ecology Progress Series 110: 67-74
- Nissling A, Vallin L (1996) The ability of Baltic cod eggs to maintain neutral buoyancy and the opportunity for survival in fluctuating conditions in the Baltic Sea. Journal of Fish Biology 48: 217-227
- Österblom H, Hansson S, Larsson U, Hjerne O, Wulff F, Elmgren R, Folke C (2007) Human-Induced Trophic Cascades and Ecological Regime Shifts in the Baltic Sea. Ecosystems 10: 877-889
- Orlowski A (1999) Acoustic studies of spatial gradients in the Baltic: Implications for fish distribution. ICES Journal of Marine Science 56: 561-570
- Orlowski A (2005) Experimental verification of the acoustic characteristics of the clupeoid diel cycle in the Baltic. ICES Journal of Marine Science 62: 1180-1190
- Parmanne R, Rechlin O, Sjöstrand B (1994) Status and future of herring and sprat stocks in the Baltic Sea. Dana 10: 29-59
- Pauly D (1981) The relationships between gill surface area and growth performance in fish: a generalization of von Bertalanffy's theory of growth. Verlag Paul Parey, Berichte der Deutschen Wissenschaftlichen Kommission für Meeresforschung / Reports on Marine Research 28: 251-282
- Peltonen H, Balk H (2005) The acoustic target strength of herring (*Clupea harengus* L.) in the northern Baltic Sea. ICES Journal of Marine Science 62: 803–808

- Petersen LH, Gamperl AK (2010) Effect of acute and chronic hypoxia on the swimming performance, metabolic capacity and cardiac function of Atlantic cod (*Gadus morhua*). *Journal of Experimental Biology* 213: 808-819
- Pikitch E, Santora C, Babcock EA, Bakun A, Bonfil R, Conover DO, Dayton P (2004) Ecosystem-based fishery management. *Science*, 305: 346-347
- Planque B, Loots C, Petitgas P, Lindstrøm U, Vaz S (2011) Understanding what controls the spatial distribution of fish populations using a multi-model approach. *Fisheries Oceanography* 20: 1-17
- Plante S, Chabot D, Dutil JD (1998) Hypoxia tolerance in Atlantic cod. *Journal of Fish Biology* 53: 1342-1356
- Plikshs M, Kalejs M, Grauman G (1993) The influence of environmental conditions and spawning stock size on the yearclass strength of the Eastern Baltic cod. *ICES CM* 1993/J: 22
- Porter SM, Ciannelli L, Hillgruber N, Bailey KM, Chan KS, Canino MF, Haldorson LJ (2005) Environmental factors influencing larval walleye pollock *Theragra chalcogramma* feeding in Alaskan waters. *Marine Ecology Progress Series* 302: 207-217
- Remane A (1934) Die Brackwasserfauna. *Verhandlungen der Deutschen Zoologischen Gesellschaft* 36: 34-74 (in German)
- Rechlin O (1999) Fischbestände der Ostsee, ihre Entwicklung in den Jahren seit 1970 und Schlußfolgerungen für ihre fischereiliche Nutzung – Teil 1: Dorsch. *Informationen für die Fischwirtschaft aus der Fischereiforschung* 46: 10-15 (in German)
- Righton D, Metcalfe J, Connolly P (2001) Different behaviour of North Sea and Irish Sea cod. *Nature* 441: 156
- Righton DA, Andersen KH, Neat F, Thorsteinsson V, Steingrund P, Svedäng H, Michalsen K, Hinrichsen H-H, Bendall V, Neuenfeldt S, Wright P, Jonsson P, Huse G, van der Kooij J, Mosegaard H, Hüsey K, Metcalfe J (2010) Thermal niche of Atlantic cod *Gadus morhua*: limits, tolerance and optima. *Marine Ecology Progress Series* 420: 1-13
- Robichaud D, Rose GA (2001) Multiyear homing of Atlantic cod to a spawning ground. *Canadian Journal of Fisheries and Aquatic Sciences* 58: 2325–2329
- Rohlf N (1999) Aktivität und Vertikalwanderung der Larven des Ostseedorsches (*Gadus morhua callarias*) während der Dottersackphase. PhD thesis, Institute of Marine Sciences, Kiel. *Berichte aus dem Institut für Meereskunde Kiel Nr. 312*, 60 pp (in German)

- Rose GA (1993) Cod spawning on a migration highway in the north-west Atlantic. *Nature* 366: 458-461
- Rose GA (2003) Monitoring coastal northern cod: towards an optimal survey of Smith Sound, Newfoundland. *ICES Journal of Marine Science* 60: 453-462
- Rose GA (2009) Variations in the target strength of Atlantic cod during vertical migration. *ICES Journal of Marine Science* 66: 1205-1211
- Rose GA, Leggett WC (1990) The importance of scale to predator-prey spatial correlations: an example of Atlantic fishes. *Ecology* 71: 1699-1713
- Rose GA, Porter DR (1996) Target-strength studies on Atlantic cod (*Gadus morhua*) in Newfoundland waters. *ICES Journal of Marine Science* 53: 259-265
- Rudstam LG, Aneer G, Hildén M (1994) Top-down control in the pelagic Baltic ecosystem. *Dana* 10: 105-129
- Sartoris FJ, Bock C, Serendero I, Lannig G, Pörtner HO (2003) Temperature-dependent changes in energy metabolism, intracellular pH and blood oxygen tension in the Atlantic cod. *Journal of Fish Biology* 62: 1239-1253
- Schaber M, Hinrichsen H-H, Neuenfeldt S, Voss R (2009) Hydroacoustic resolution of small-scale vertical distribution in Baltic cod *Gadus morhua* – habitat choice and limits during spawning. *Marine Ecology Progress Series* 377: 239-253
- Schaber M, Haslob H, Huwer B, Harjes A, Hinrichsen H-H, Storr-Paulsen M, Schmidt JO, Voss R, Neumann V, Köster FW (2011) Spatio-temporal overlap of the invasive predatory ctenophore *Mnemiopsis leidyi* and ichthyoplankton in the central Baltic Sea. *Biological Invasions*. doi:10.1007/s10530-011-9936-7
- Schinke H, Matthäus W (1998) On the causes of major Baltic inflows - an analysis of long time series. *Continental Shelf Research* 18: 67-97
- Simmonds J, MacLennan D (2005) *Fisheries Acoustics: Theory and Practice*. 2nd Edition. Fish and Aquatic Resource Series 10. Blackwell Publishing, Oxford, 437 pp
- Schlitzer R (2007) Ocean Data View (ODV). <http://odv.awi.de>
- Schurmann H, Steffensen JF (1997) Effects of temperature, hypoxia and activity on the metabolism of juvenile cod. *Journal of Fish Biology* 50: 1166-1180
- Seifert T, Kayser B (1995) A high resolution spherical grid topography of the Baltic Sea. *Meereswissenschaftliche Berichte/Marine scientific reports*, No. 9, Institut für Ostseeforschung –Warnemünde, Rostock, Germany, 17 pp
- Sonardata (2007) Echoview. <http://www.echoview.com>

- Sparholt H (1994) Fish species interactions in the Baltic Sea. *Dana* 10: 131-162
- Sparholt H, Aro E, Modin J (1991) The spatial distribution of cod (*Gadus morhua* L.) in the Baltic Sea. *Dana* 9: 45-56
- Stepputtis D (2006) Distribution patterns of Baltic sprat (*Sprattus sprattus* L.) - causes and consequences. PhD thesis, Christian-Albrechts-University of Kiel, 153 pp
- Stepputtis D, Hinrichsen H-H, Böttcher U, Götze E, Mohrholz V (2011) An example of meso-scale hydrographic features in the central Baltic Sea and their influence on the distribution and vertical migration of sprat, *Sprattus sprattus balticus* (Schn.). *Fisheries Oceanography* 20: 82-88
- Stigebrandt A (1987) A model for the seasonal pycnocline in rotating systems with application to the Baltic. *Journal of Physical Oceanography* 15: 1392-1404
- Strand E, Huse G (2007) Vertical migration in adult Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences* 64: 1747-1760
- Sund O (1935) Echo sounding in fishery research. *Nature* 135: 953
- Sundby S (2000) Recruitment of Atlantic cod stocks in relation to temperature and advection of copepod populations. *Sarsia* 85: 277-298
- Swain DP, Kramer DL (1995) Annual variation in temperature selection by Atlantic cod *Gadus morhua* in the southern Gulf of St. Lawrence, Canada, and its relation to population size. *Marine Ecology Progress Series* 116: 11-23
- Swain DP, Poirier GA, Sinclair FA (2000) Effect of water temperature on catchability of Atlantic cod (*Gadus morhua*) to the bottom-trawl survey in the southern Gulf of St. Lawrence. *ICES Journal of Marine Science* 57: 56-68
- Swain DP, Nielsen GA, Sinclair AF, Chouinard GA (1994) Changes in catchability of Atlantic cod (*Gadus morhua*) to an otter-trawl fishery and research survey in the southern Gulf of St. Lawrence. *ICES Journal of Marine Science* 51: 493-504
- Sylvestre EL, Lapointe D, Dutil JD, Guderley H (2007) Thermal sensitivity of metabolic rates and swimming performance in two latitudinally separated populations of cod, *Gadus morhua* L. *Journal of Comparative Physiology B* 177: 447-460
- Temming A, Andersen NG (1994) Modelling gastric evacuation without meal size as a variable. A model applicable for the estimation of daily ration of cod (*Gadus morhua* L.) in the field. *ICES Journal of Marine Science* 51: 429-438

- Teschner E, Kraus G, Neuenfeldt S, Voss R, Hinrichsen H-H, Köster FW (2010) Impact of hypoxia on consumption of Baltic cod in a Multispecies Stock Assessment context. *Journal of Applied Ichthyology* 26: 836-842
- Tomkiewicz J, Lehmann KM, St. John MA (1998) Oceanographic influences on the distribution of Baltic cod, *Gadus morhua*, during spawning in the Bornholm Basin of the Baltic Sea. *Fisheries Oceanography* 7: 48-62
- Tomkiewicz J, Tybjerg L, Holm N, Hansen A, Broberg C, Hansen E (2002) Manual to determine gonadal maturity of Baltic cod. DFU rapport 116-02, Charlottenlund: Danish Institute for Fisheries Research, 49 pp
- Tomkiewicz J, Støttrup JG, Jacobsen C, Røjbek MC, Köster FW (2009) Influence of lipids and fatty acid composition on Baltic cod (*Gadus morhua* L.) maturation and timing of spawning. *ICES CM 2009/C*: 10
- Towler RH, Jech JM, Horne JK (2003) Visualizing fish movement, behavior, and acoustic backscatter. *Aquatic Living Resources* 16: 277-282
- Uzars D, Plikshs M (2000) Cod (*Gadus morhua* L.) cannibalism in the central Baltic: interannual variability and influence of recruit abundance and distribution. *ICES Journal of Marine Science* 57: 324-329
- Vallin L, Nissling A (2000) Maternal effects on egg size and egg buoyancy of Baltic cod, *Gadus morhua*. Implications for stock structure effects on recruitment. *Fisheries Research* 49: 21-37
- van der Kooij J, Righton D, Strand E, Michalsen K, Thorsteinsson V, Svedäng H, Neat FC, Neuenfeldt S (2007) Life under pressure: insights from electronic data-storage tags into cod swimbladder function. *ICES Journal of Marine Science* 64: 1293-1301
- van der Lingen CD, Hutchings L, Merkle D, van der Westhuizen JJ, Nelson J (2001) Comparative spawning habitats of anchovy (*Engraulis capensis*) and sardine (*Sardinops sagax*) in the southern Benguela upwelling ecosystem. In: *Spatial Processes and Management of Marine Populations* (Eds. Kruse GH, Bez N, Booth T, Dorn M, Hills S, Lipcius RN, Pelletier D, Roy C, Smith SJ, Witherell D). University of Alaska Sea Grant, Fairbanks, p 185-209
- Walters C (2011) Folly and fantasy in the analysis of spatial catch rate data. *Canadian Journal of Fisheries and Aquatic Sciences* 60: 1433-1436
- Westin L, Nissling A (1991) Effects 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 (1995) Einfluss der Hydrographie auf die Vertikalverteilung und Sterblichkeit der Eier des Ostseedorsches (*Gadus morhua callarias*) im Bornholm Becken, südliche zentrale Ostsee. PhD thesis, Institute of Marine Sciences, Kiel. Berichte aus dem Institut für Meereskunde Kiel Nr. 266, 114 pp
- Wieland K, Waller U, Schnack D (1994) Development of Baltic cod eggs at different levels of temperature and oxygen content. Dana 10: 163-177
- Wieland K, Köster FW (1996) Size and visibility of Baltic cod eggs with reference to size-selected and stage-dependent predation mortality. Journal of Applied Ichthyology 12: 83-89
- Wieland K, Jarre-Teichmann A (1997) Prediction of vertical distribution and ambient development temperature of Baltic cod, *Gadus morhua* L., eggs. Fisheries Oceanography 6: 172-187
- Wieland K, Jarre-Teichmann A, Horbowa K (2000) Changes in timing of spawning of Baltic cod: possible causes and implications for recruitment. ICES Journal of Marine Science 57: 452-464
- Wood SJR (2000) Modelling and smoothing parameter estimation with multiple quadratic penalties. Journal of the Royal Statistical Society - Series B 62: 413-428



ANNEX I: LIST OF FIGURES

Figure 1: The Baltic Sea.....	11
Figure 2: Mean summer sea surface salinity (psu) in the Baltic Sea.....	12
Figure 3: Hydrography profiles from the Bornholm Basin and adjacent areas in summer 2009	13
Figure 4: Development of Eastern Baltic cod (ICES SD 25-32) SSB and recruitment from 1966 to 2010.....	16
Figure 5: Inverse development of Eastern Baltic cod and sprat SSB.....	17
Figure 6: The main types of control of spatial fish distribution	20
Figure 7: Identification of individual cod from hydroacoustic data	27
Figure 8: General data sources and methods applied.....	29
Figure I-1: Station grid for measuring hydrographic and biological parameters in August 2003 and July 2005.	34
Figure I-2: Depth distribution of single fish echoes in August 2003 and July/August 2005 in relation to mean hydrographic environment.....	40
Figure I-3: Relative depth distribution of echo tracks in comparison with depth distribution data obtained from data-storage-tags in 2003 and 2005.....	41
Figure I-4: Distribution of cod echoes below the halocline in August 2003 and July/August 2005 in relation to ambient temperature, relative availability and selection of habitat by cod.....	43
Figure I-5: Distribution of cod echoes below the halocline in August 2003 and July/August 2005 in relation to ambient salinity, relative availability and selection of habitat by cod	44
Figure I-6: Distribution of cod echoes below the halocline in August 2003 and July/August 2005 in relation to ambient oxygen concentration, availability and selection of habitat by cod.....	45
Figure I-7: Distribution of cod echoes within depth layers with a salinity >11 in August 2003 and July/August 2005 in relation to ambient Oxygen Related Egg-survival, availability and selection of habitat with correspondent OES by cod.....	46

Figure II-1: Sampling area in the Bornholm Basin	54
Figure II-2: Mean annual depth distribution of adult cod	57
Figure II-3: Horizontal and vertical distribution patterns of adult cod in 2007	59
Figure II-4: Horizontal and vertical distribution patterns of adult cod in 2008	60
Figure II-5: Correlation matrix between endogenous and exogenous variables	62
Figure II-6: Effect-modeling of cod vertical distribution in the Bornholm Basin	63
Figure III-1: ICES subdivisions in the Baltic Sea and Baltic cod spawning areas.....	71
Figure III- 2: Time series of Major Baltic Inflows and their intensity	72
Figure III-3: Temperature and salinity dependent oxygen solubility	73
Figure III- 4: Long-term development of Baltic Sea oxygen concentration and saturation in the Bornholm Basin.....	77
Figure III-5: Long-term development of oxygen-related Baltic cod egg survival, oxygen-related vertical swimming activity of larval cod, size of juvenile cod settlement areas; and oxygen-related gastric evacuation rates of adult Baltic cod	78
Figure III-6: Time series of the difference between Stage I and Stage III Baltic cod mean egg diameters in the Bornholm Basin.....	80
Figure III-7: Mean annual condition factor K (Fulton) of adult male and female cod from annual trawl samples collected between 1994 and 2009	81

ANNEX II: LIST OF TABLES

Table 1: Hypotheses, null hypotheses and methodical approaches followed in the contributing chapters.....	30
Table I-1: Transducer settings	34
Table II-1: Parameter estimates and p values from ANCOVA (GLM).....	64
Table III-1: Characteristic oxygen related hydrography, regression parameters and processes acting on Eastern Baltic cod during its entire life cycle.	84

ANNEX III: LIST OF ABBREVIATIONS

AB	Arkona Basin
BB	Bornholm Basin
BH	Bornholm Island
BS	Belt Sea
CA	Cod Abundance
CTD	Conductivity, Temperature, Depth
CPUE	Catch Per Unit Effort
DO	Dissolved Oxygen
DST	Data Storage Tag
DVM	Diurnal Vertical Migration
EBC	Eastern Baltic Cod
EBFM	Ecosystem Based Fishery Management
FT	Fish Track
GAM	Generalized Additive Model
GB	Gotland Basin
GCV	Generalized Cross Validation
GD	Gdansk Deep
GER	Gastric Evacuation Rate
GLM	Generalized Linear Model
ICES	International Council for the Exploration of the Sea
K	Condition Factor (Fulton)
LVMA	Larval Vertical Migration Activity
MPA	Marine Protected Area
MS	Metabolic Scope
NAO	North Atlantic Oscillation
NASC	Nautical Area Scattering Coefficient
OES	Oxygen-related Egg Survival
PL	Poland
PSU	Practical Salinity Units
R/V	Research Vessel
RV	Reproduction Volume
S	Sweden
SD	ICES Subdivision
SF	Slupsk Furrow
SSB	Spawning Stock Biomass
TS	Target Strength
TSB	Total Stock Biomass
WBC	Western Baltic Cod



CONTRIBUTIONS OF AUTHORS

The chapters of this thesis are already published (Chapter I) or accepted for publication (Chapters II and III). The following list clarifies my personal contribution to each manuscript.

I. Hydroacoustic resolution of small-scale vertical distribution in Baltic cod *Gadus morhua* – habitat choice and limits during spawning

(Published 2009 in MARINE ECOLOGY PROGRESS SERIES 377: 239-253)

Collection (partly) and analysis of all hydroacoustic data, text writing and graphical presentation were done by Matthias Schaber. Hans-Harald Hinrichsen provided modeled hydrographical data. Stefan Neuenfeldt provided comparative data from archival data-storage-tags. Rüdiger Voss assisted in the statistical, GAM-based validation of results.

II. Seasonal changes in vertical distribution patterns of cod (*Gadus morhua*) in the Bornholm Basin, central Baltic Sea

(Accepted for publication in FISHERIES OCEANOGRAPHY)

Data collection (hydroacoustic and oceanographic), analysis of hydroacoustic data, text writing and graphical presentation were done by Matthias Schaber. Hans-Harald Hinrichsen provided modeled hydrographic data. Joachim Gröger provided support in testing the hypothesis and results by biological effect modeling.

III. Climate driven long-term trends in Baltic Sea oxygen concentrations, and the potential consequences for eastern Baltic cod (*Gadus morhua* L.)

(Accepted for publication in ICES JOURNAL OF MARINE SCIENCE)

The majority of analyses were performed by Hans-Harald Hinrichsen in close cooperation with the individual contributors of different datasets. Bastian Huwer, Andrejs Makarchouk, Christoph Petereit and Rüdiger Voss provided field- and experimental data on distribution and characteristics of cod eggs and larvae. Matthias Schaber provided a time series of in-situ distribution data of individual cod as derived from hydroacoustic measurements as well as a dataset of biological parameters (length, weight, sex, maturity stage, etc.) of individual cod collected during multi-annual trawl surveys. Analysis of distribution data and parameters derived from single-fish data was done by Matthias Schaber. Text writing and graphical presentation were accomplished in close cooperation of Hans-Harald Hinrichsen, Matthias Schaber and Bastian Huwer.

ACKNOWLEDGEMENTS

I thankfully acknowledge Prof. Dr. Dietrich Schnack for supervising the present thesis, for valuable comments and critical reviews of each contributing manuscript - and for his patience in waiting for this thesis to finally be finished.

I also would like to thank Prof. Dr. Joachim Gröger for proof reading, reviews and comments on some chapters.

Thanks go to Dr. Gerd Kraus for hiring me in the former “Fisheries Biology” department of the IFM-GEOMAR, Kiel and later in the Institute of Sea Fisheries of the Johann Heinrich von Thünen-Institute, Hamburg and also for valuable comments on parts of the manuscripts.

I additionally would like to thank the crews of all research vessels I spent time on collecting data for this thesis or writing parts of this thesis, namely R/V “Alkor”, R/V “Solea”, R/V “Walther Herwig III” and R/V “Itaf Deme”.

Dr. Daniel Stepputtis is acknowledged for initially convincing me that hydroacoustics indeed is pretty cool.

Further thanks go to all “FiBio” friends and colleagues: Dr. Holger Haslob, Hans-Harald Hinrichsen, Dr. Christoph Petereit, Lasse Marohn, Enno Prigge, Dr. Jörn O. Schmidt, Dr. Rüdiger Voss, Dr. Bastian Huwer, Dr. Jan Schröder, Dr. Norbert Rohlf, Rudi Lüthje, Svend Mees.

Special thanks go to my parents for never losing faith in me and for incessantly encouraging and supporting me in pursuing my vocation.

Viola, thank you so much for keeping me grounded with all your love, laughs and patience.



CURRICULUM VITAE

PERSONAL INFORMATION

Name: Matthias Schaber
Date of birth: 12.11.1974
Place of birth: Nördlingen (Germany)
Nationality: German

EDUCATION

2005 – 2011 **Elaboration of PhD-thesis at the Leibniz-Institute of Marine Sciences (IFM-GEOMAR), Kiel, Germany.**

Title: Small to meso-scale distribution of Baltic cod (*Gadus morhua* L.) as resolved by hydroacoustics: Habitat preferences, environmental limits, and resulting implications for stock development.

2001 **Diploma thesis at the Institute for Marine Science at the Christian-Albrechts University (IFM), Kiel, Germany.**

Title: Spatial variability in the food composition of selected fish species in the Bornholm Basin.

1995-2001 **Study in Biology at the Christian-Albrechts-University, Kiel, Germany**

Major subject: Fishery Biology

Subsidiary subjects: Zoology

 Oceanography

1994 Abitur at the Ostalbgymnasium Bopfingen, Germany

WORK EXPERIENCE

05/2010-today Scientist at the Johann Heinrich von Thünen-Institute, Federal Research Institute for Rural Areas, Forestry and Fisheries, Institute of Sea Fisheries, Hamburg, Germany.

Project:

Team leader hydroacoustics. Evaluation, assessment and distribution of pelagic fish stocks in North Atlantic, North Sea and Baltic Sea.

01/2007-06/2011 Consultant / Demersal resources expert for GOPA Consultants GmbH, Bad Homburg, Germany / Ministry of Fisheries and Marine Resources, Freetown, Sierra Leone

Project:

Institutional Support for Fisheries Management in Sierra Leone, the European Union's 9th EDF programme for Sierra Leone.

01/2004-12/2009 Scientist at the Leibniz Institute of Marine Sciences (IFM-GEOMAR), Kiel, Germany.

Projects:

BECAUSE (Critical Interactions between Species and their Implications for a Precautionary Fisheries Management in a variable Environment – a Modelling approach), EU 6th Framework Programme, Specific Targeted Research Project, Contract No.: 502482 / IFM-GEOMAR, Kiel.

CODYSEY (Cod Spatial Dynamics and Vertical Movements in European Waters and Implications for Fishery Management), EU, Project No: QoL-2001-3 / IFM-GEOMAR, Kiel.

PROTECT (Marine Protected Areas as a Tool for Ecosystem Conservation and Fisheries Management), EU 6th Framework Programme, Specific Targeted Research Project, Project No: SSP8-CT-2004-513670 / IFM-GEOMAR, Kiel.

UNCOVER (Understanding the Mechanisms of Stock ReCOVERy), EU 6th Framework Programme, Specific Targeted Research Project, Contract No.: 502482 / IFM-GEOMAR, Kiel.

Wege zu einer natur- und ökosystemverträglichen Fischerei am Beispiel ausgewählter Gebiete der Ostsee. F+E-Vorhaben, Bundesamt für Naturschutz (BfN), Bonn. FKZ 802 25 010 / IFM-GEOMAR, Kiel.

11/2001-12/2003 Scientist at MariLim Gewässeruntersuchung und Forschung, Kiel, Germany.

Projects:

Wege zu einer natur- und ökosystemverträglichen Fischerei am Beispiel ausgewählter Gebiete der Ostsee. F+E-Vorhaben, Bundesamt für Naturschutz (BfN), Bonn. FKZ 802 25 010 / MariLim Gewässeruntersuchung und Forschung, Kiel.

Investigations on possible effects of 4 planned offshore-windparks in North Sea and Baltic Sea.

Monitoring of Baltic Sea Protected Areas (BSPA) and littoral zones of the German Baltic Sea coast.

1999 – 2001 Research assistant at the Federal Research Institute for Fisheries (Bundesforschungsanstalt für Fischerei), Hamburg, Germany.

Project:

Sampling of commercial fisheries catches and collecting bycatch and discard data.

MEMBERSHIP IN SCIENTIFIC ORGANIZATIONS

- ICES WGIPS: Working Group for International Pelagic Surveys (since 2010).
- ICES WGNAPES: Working Group on Northeast Atlantic Pelagic Ecosystem Surveys (since 2010).
- ICES WGFAST: Working Group on Fisheries Acoustics Science and Technology (since 2007).
- ICES WGBIFS: Baltic International Fish Survey Working Group (since 2006)

PUBLICATIONS

- Hinrichsen H-H, Huwer B, Makarchouk A, Petereit C, **Schaber M**, Voss R. Climate-driven long term trends in Baltic Sea oxygen concentrations, and the potential consequences for eastern Baltic cod (*Gadus morhua*). ICES Journal of Marine Science (accepted for publication)
- Schaber M**, Hinrichsen H-H, Gröger J. Seasonal changes in vertical distribution patterns of cod (*Gadus morhua* L.) in the Bornholm Basin, central Baltic Sea. Fisheries Oceanography (accepted for publication)
- Schaber M**, Marohn L, Petereit C, Schroeder JP, Zumholz K, Hanel R (2011) Newcomers in the Baltic Sea: an attempt to trace the origins and whereabouts of thicklip grey mullet *Chelon labrosus*. Fisheries Science, doi: 10.1007/s12562-011-0384-1
- Schaber M**, Haslob H, Huwer B, Harjes A, Hinrichsen H-H, Storr-Paulsen M, Schmidt JO, Voss R, Neumann V, Köster FW (2011) Spatio-temporal overlap of the alien invasive ctenophore *Mnemiopsis leidyi* and ichthyoplankton in the Bornholm Basin (Baltic Sea). Biological Invasions, doi: 10.1007/s10530-011-9936-7
- Schaber M**, Haslob H, Huwer B, Harjes A, Hinrichsen H-H, Köster FW, Storr-Paulsen M, Schmidt JO, Voss R (2011) The invasive ctenophore *Mnemiopsis leidyi* in the central Baltic Sea: seasonal phenology and hydrographic influence on spatio-temporal distribution patterns. Journal of Plankton Research 33: 1053-1065
- Schaber M**, Petereit C, Paulsen M (2010) Diet composition and feeding of European anchovy *Engraulis encrasicolus* L. in Kiel Bight, western Baltic Sea. Journal of Fish Biology 76: 1856-1862
- Schaber M**, Hinrichsen, H-H, Neuenfeldt S, Voss R (2009) Hydroacoustic tracking of individuals in environmental gradients - Baltic cod (*Gadus morhua* L.) vertical distribution during spawning. Marine Ecology Progress Series 377: 239-253
- Haslob H, Clemmesen C, **Schaber M**, Hinrichsen H-H, Schmidt JO, Voss R, Kraus G, Köster FW (2007) Invading *Mnemiopsis leidyi* as a potential threat to Baltic fish. Marine Ecology Progress Series 349: 303-306
- Fleischer D, **Schaber M**, Piepenburg D (2007) Atlantic snake pipefish (*Entelurus aequoreus*) extends its northward distribution range to Svalbard (Arctic Ocean). Polar Biology 30: 1359-136



ERKLÄRUNG

Hiermit erkläre ich, dass die vorliegende Dissertation selbständig von mir unter Einhaltung der Regeln guter wissenschaftlicher Praxis der DFG angefertigt wurde. Die Dissertation ist nach Form und Inhalt meine eigene Arbeit und es wurden keine anderen als die angegebenen Hilfsmittel verwendet. Diese Arbeit wurde weder ganz noch zum Teil einer anderen Stelle im Rahmen eines Prüfungsverfahrens vorgelegt. Teile der Arbeit wurden bei Fachzeitschriften zur Veröffentlichung eingereicht und akzeptiert bzw. bereits veröffentlicht wie in „Contributions of Authors“ dargelegt. Dies ist mein einziges und bisher erstes Promotionsverfahren. Die Promotion soll im Fach Fischereibiologie erfolgen.

Kiel, den

Matthias Schaber

