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Huwer, Bastian

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Ph.D. Thesis

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Oceans

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Front cover illustrations:
Cod (*Gadus morhua*) egg and larva, courtesy of Christoph Petereit
Mnemiopsis leidyi, courtesy of Thomas Warnar

Back cover illustrations:
Research vessel “DANA” at Langelinie, Copenhagen
Deployment of Bongonet and Multinet from Research Vessel “ALKOR”

Preface

This Ph.D. study was carried out at the National Institute of Aquatic Resources, Technical University of Denmark (DTU Aqua) in collaboration with the Department of Biological Sciences, Marine Ecology at Aarhus University. The research was supported by PhD grant number WP6-SYSBS-1048 from the European Network of Excellence for Ocean Ecosystem Analysis (EUR-OCEANS, FP 6 NoE 511106-2), by the SLIP research school under the Danish Network for Fisheries and Aquaculture Research (www.fishnet.dk) financed by the Danish Ministry for Food, Agriculture and Fisheries and the Danish Council for Independent Research, Technology and Production Sciences, and by the Commission of the European Communities, specifically SSP8-2004-513670, PROTECT.

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I am indebted to my former colleagues from the Fisheries Ecology section at the Leibniz-Institute of Marine Sciences in Kiel, Germany, for the lasting cooperation and for giving me the opportunity to continue to take part in their research cruises. In particular, I would like to thank Holger Haslob, Matthias Schaber and Catriona Clemmesen for the good collaboration, as well as Rudi Lüthje for his competent help with various sampling gears. Special thanks go also to Rudi Voss and Jörn Schmidt, who in the meantime found new challenges in the Sustainable Fisheries section at Kiel University.

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I highly appreciate the always fast and friendly help from Carina Anderberg and her colleagues at the institute library, as well as Anders Nielsens advice on statistical questions. A big thank you also to the officers and crews of the research vessels DANA and ALKOR for their invaluable assistance during the field work. Furthermore, I am very happy that the following people were willing to join the aforementioned night-shifts on DANA: Thomas “Bongobrother” Warnar, Cornelia Jaspers, Christine Røllike Ditlefsen, Caroline-Marie Vandt Madsen and Line Bøttiger. Thanks for the nice cruises, for keeping each other awake and for the great help during field sampling. 1000 tak also to Stina B.S. Hansen for always finding a little extra space for my samples in her already packed storage facilities.

Last but not least, I would like to thank my family. My parents have encouraged my interest for the sea and its inhabitants since I was a child. In fact, the first fish I showed interest for was a plaice on my mothers plate – I was 8 months old and ate half of it! Heide and Norbert, I am grateful for your lasting faith and support throughout my studies, even though I kept moving further and further away, first to Kiel and now even further northwards to Denmark.
My “parents-in-law”, Ruth Ilkjær and Hans Christian Gulløv, I would like to thank for their warm welcome to a new country and culture, for many “hyggelige” hours in their company and for their great help with “børnepasning” and managing my new Danish life in general.

Finally, I would not have succeeded with this PhD without the incessant faith and love of the two dearest persons in my life, my girlfriend Grith Gulløv Ilkjær and my precious little son Viggo. You have suffered a lot under this entire process, yet never gave up supporting me.
For al jeres støtte, tålmodighed og kærlighed fortjener I den største tak af alle.

Copenhagen, October 2009

Bastian Huwer

Contents

Paper 1: Characteristics of surviving juvenile Baltic cod I: field evidence for the critical period hypothesis?

Paper 2: Characteristics of surviving juvenile Baltic cod II: field evidence for the growth-mortality hypothesis?

Paper 3: Vertical distribution and growth of Baltic Cod larvae - field evidence for a spatial match-mismatch hypothesis?

Paper 4: Abundance, horizontal and vertical distribution of the invasive ctenophore *Mnemiopsis leidyi* in the central Baltic Sea, November 2007

Paper 5: Changes in distribution and lengths of *Mnemiopsis leidyi* in the central Baltic Sea between fall and spring

Paper 6: Seasonal distribution patterns of the invasive ctenophore *Mnemiopsis leidyi* in the central Baltic Sea in relation to ichthyoplankton

Summary

The recruitment success of most marine fish stocks shows strong interannual fluctuations. There is general consensus that this variability is caused by differential survival during early life, and that starvation and predation are the main mortality agents during the highly vulnerable early life stages. Both processes are likely influenced by spatio-temporal dynamics, i.e. a spatial and temporal match or mismatch of larval fish and their prey and variable degrees of overlap between ichthyoplankton and organisms preying upon it. Low oxygen concentration and predation by clupeid fish are known mortality sources of Baltic cod eggs. However, processes during the larval stage and other sources of predation mortality on eggs and larvae, e.g. by invertebrate predators, are less well understood. Especially the recent introduction of the invasive, carnivorous ctenophore *Mnemiopsis leidyi* to the Baltic Sea has caused concerns about its potential predatory impact on zoo- and ichthyoplankton.

The main aim of this PhD study was to investigate larval stage processes potentially influencing recruitment in Baltic cod. The specific focus was twofold: 1) to substantiate the importance of starvation-induced mortality during the larval stage, that was suggested in previous modelling studies, with empirical data from a field setting and (2) to assess seasonal dynamics in abundance and distribution of a new invertebrate ichthyoplankton predator in the Baltic Sea ecosystem, the recently introduced ctenophore *M. leidyi*, and its potential predation impact on fish early life stages. Larval condition, growth, starvation and survival were studied with biochemical (RNA-DNA) and otolith-based methods, as well as by a coupling of otolith analyses and hydrodynamic modeling, following a characteristics of survivors approach. The potential predatory impact of *M. leidyi* on eggs and larvae of cod and sprat was investigated with field surveys aimed to resolve seasonal dynamics in occurrence and overlap of predator and prey.

Estimates of growth performance from RNA-DNA based growth estimates and the analysis of survivor origins by otolith analyses and hydrodynamic modelling were found to be valuable tools for studying larval stage recruitment processes, and may aid in the evaluation and design of Marine Protected Areas. Results show spatio-temporal differences in larval growth, starvation and survival, which are probably related to the seasonal and spatial dynamics of the Baltic zooplankton community. The majority of Baltic cod surviving to the pelagic juvenile stage were found to originate from the edges of the Bornholm Basin, the presently most important spawning ground, whereas only relatively few individuals originated from the Basin centre. Besides, results indicate a temporal, but less clear, pattern of lower larval survival in the middle of the spawning season. Pelagic juveniles were found to have larger otolith hatch-checks and increment widths than larvae, indicating faster growth during early life. While the exact mechanisms behind this observation remain elusive, maternal effects, selection for faster growth or better environmental conditions for individual sub-cohorts are discussed as possible explanations. The need for Baltic cod larvae to conduct an ontogenetic vertical migration to depths of peak nauplii abundances in upper water layers was corroborated. However, the size-dependent vertical distribution suggests that larger larvae are again migrating to deeper layers, possibly to follow increasingly larger prey items and to save energy in cooler waters at larger depths. Significant growth differences between larvae in relation to their size and their vertical and horizontal catch locations were found, showing poorer growth of larvae in deep layers and in the centre of the Bornholm Basin.

The spatio-temporal patterns in larval growth and survival, inter-annual variability in the number of larvae surviving to the well-established feeding stage, and the generally poor nutritional condition and growth in comparison with cod larvae from other areas show that starvation mortality, especially during the early larval stage, has a high potential to influence recruitment variability in Baltic cod.

In contrast, predation by *M. leidyi* does not have a significant impact on recruitment regulation at present. This is due to a limited temporal co-occurrence with ichthyoplankton peaks and generally low predator abundances in the relevant egg and larval habitats. However, relatively high vertical overlaps with fish eggs, local abundance peaks and experiences from areas previously invaded by this ctenophore give persisting reason to concern. Thus, a future impact of *M. leidyi* on cod recruitment, and the Baltic Sea ecosystem in general, can not be ruled out.

Resumé (Danish Summary)

Rekrutteringssuccesen af de fleste marine fiskebestande er underlagt store fluktuationer årene imellem. Det bliver generelt antaget, at det skyldes variabel overlevelse af de tidlige livsstadier, og at dødeligheden især skyldes fødemangel og predation. Begge processer bliver sandsynligvis påvirket af rumlig og tidsmæssig dynamik i f. eks. match eller mis-match mellem rumlig og tidsmæssig forekomst af fiskelarver og deres bytte og variabel overlap mellem ichthyoplankton og de organismer der bruger det som fødekilde. Det er kendt at lav iltkoncentration og sildefisk som rovdyr forårsager høj dødelighed af Østersøtorskens æg. Men de processer der påvirker larvestadiet og andre kilder til predation på æg og larver, f.eks. ved invertebrater, er kun dårlig belyste. Specielt den nylig opdagede indførelse af den invasive, kødædende gople *Mnemiopsis leidyi* i Østersøen har medført bekymringer om dens indflydelse på zoo- og ichthyoplankton.

Det overordnede formål med denne Ph.D. afhandling var at undersøge de processer der potentielt har den største indflydelse på overlevelsen i larvestadiet, og der påvirker rekrutteringen af Østersøtork. Afhandlingen bygger på to komponenter: (1) At understrege effekten af fødemangel-relateret dødelighed i larvestadiet, som tidligere modelleringsstudier antydede, med empiriske data fra feltindsamlinger; og (2) At evaluere sæsonmønstre i forekomst og fordeling af en ny invertebrat predator på ichthyoplankton i Østersøen, den nylig indførte gople *M. leidyi*, og dens potentielle indflydelse på fisks tidligste livsstadier. Larvernes kondition, vækst, fødemangel og overlevelse blev undersøgt med biokemiske (RNA-DNA ratio) og ørestens-baserede metoder, samt en kobling af ørestens analyser med hydrodynamisk modellering ved at bruge den såkaldte ”characteristics of survivors” metode. Den potentielle rolle af *M. leidyi* som rovdyr på æg og larver af torsk og brisling blev undersøgt gennem en serie feltindsamlinger målrettet til klarlægning af sæsonale mønstre i forekomst og overlap mellem rovdyr og byttedyr.

Estimater af vækstpotentiale fra RNA-DNA-baserede vækst rater og analysen af de overlevende fisks herkomst fra ørestensanalysen og den hydrodynamiske modellering viste sig at være værdifulde redskaber for at studere rekrutteringsprocesser i larvestadiet. De redskaber er dermed meget anvendelige til evalueringen og udformningen af fredede havområder. Resultaterne viser rumlig-tidsmæssige forskelle i larvernes vækst, fødemangel og overlevelse, hvilke sandsynligvis er knyttede til sæson- og rumlige mønstre i Østersøens zooplankton samfund. Hovedparten af Østersøtorsk der overlevede til det pelagiske juvenilstadie stammede fra gydeaktivitet langs kanterne af Bornholmer dybet, det for tiden vigtigste gydeområde. Kun få individer stammede fra det centrale bassin. Desuden viste der sig et tidsmæssigt mønster med

lavere overlevelse midt i gydeperioden, selvom det mønster var mindre tydelig. Ørestenene af pelagiske juvenile havde større klækningsmærker og bredere dagringe end ørestenene af larver, hvilket tyder på, at de voksede hurtigere lige efter klækning. De helt præcise processer der forårsager de forskelle ikke er kendte, men faktorer relateret til moderen, selektion for hurtig vækst eller forskellige miljøforhold for de individuelle kohorter kan alle have haft indflydelse. Resultaterne understreger nødvendigheden af at larverne foretager vertikale migrationer til dybder med de højeste koncentrationer af nauplier i de øvre vandlag. Men den størrelsesspecifikke vertikalfordeling antyder, at større larver søger mod dybere vand, formodentlig for at følge byttedyr af stigende størrelse og for at udnytte de kolde vandtemperaturer for at spare på metaboliske udgifter. Signifikante forskelle blev fundet i vækst mellem larver afhængig af deres størrelse og deres vertikale og horisontale fangst områder, hvor væksten er dårligst i dybe vandlag og i det centrale Bornholmerdybet.

De rumlig-tidsmæssige mønstre i larvernes vækst og overlevelse, årlig variation i antal larver, der overlever til det stadie, hvor fiskene er veletablerede i relation til eksogen fødeindtag, og den generelt meget lavere ernæringsmæssige kondition og vækst sammenlignet med torskelarver fra andre områder viser at føderelateret mortalitet, især i den tidlige larvefase, har et højt potentiale at påvirke variabiliteten i Østersøtorskens rekruttering.

I modsætning dertil, ser predation af *M. leidyi* på nuværende tidspunkt ikke ud til at have en signifikant indflydelse på rekrutteringen. Det skyldes især begrænset sammenfald i forekomst med ichthyoplankton og generel lav forekomst af *M. leidyi* i de relevante habitater af æg og larver. Ikke des mindre giver relativ stor overlap i vertikalfordeling med fiskeæggene, lokale områder med høj forekomst af gopler og ikke mindst erfaringer fra andre områder der tidligere er blevet invaderet af denne art grund til vedvarende bekymring. Det kan derfor ikke udelukkes, at *M. leidyi* i fremtiden vil få indflydelse på rekrutteringen af torsk, og økosystemet i Østersøen generelt.

List of original papers

This dissertation is based on the following papers, which will be referred to in the text by their number:

1 Huwer, B., Hinrichsen, H.-H., Böttcher, U., Voss, R., Köster, F. Characteristics of surviving juvenile Baltic cod I: field evidence for the critical period hypothesis? (manuscript).

2 Huwer, B., Hinrichsen, H.-H., Böttcher, U., Voss, R., Köster, F. Characteristics of surviving juvenile Baltic cod II: field evidence for the growth-mortality hypothesis? (manuscript).

3 Huwer, B., Clemmesen, C., Grønkjær, P. Vertical distribution and growth of Baltic Cod larvae - field evidence for a spatial match-mismatch hypothesis? (manuscript).

4 Huwer, B., Storr-Paulsen, M., Riisgård, H.-U., Haslob, H. (2008). Abundance, horizontal and vertical distribution of the invasive ctenophore *Mnemiopsis leidyi* in the central Baltic Sea, November 2007. Aquatic Invasions 3, 2: 113-124.

5 Storr-Paulsen, M., Huwer, B. (2008) Changes in distribution and lengths of *Mnemiopsis leidyi* in the central Baltic Sea between fall and spring. Aquatic Invasions 3, 4: 429-434.

6 Schaber, M., Haslob, H., Huwer, B., Harjes, A., Hinrichsen, H.-H., Köster, F., Storr-Paulsen, M., Schmidt, J., Voss, R. Seasonal distribution patterns of the invasive ctenophore *Mnemiopsis leidyi* in the central Baltic Sea in relation to ichthyoplankton (submitted).

1 Introduction

1.1 The recruitment process in marine fish

The primary objectives of fishery science and management are to ensure long term sustainability of fish stocks, to prevent biological and economic overfishing, and to minimize disruption of ecosystems (Rutherford 2002). In the assessment of many marine fish stocks, medium to long term predictions commonly rely on stock - recruitment relationships, but they often fail to adequately forecast year-class strength. A number of mathematical models have been applied to describe this essential relationship, including dome-shaped (Ricker 1954) and asymptotic (Beverton & Holt 1957) curves or more flexible functions (Shepherd 1982). However, in most cases, a large residual variance within stock - recruitment relationships remains.

There is common consensus that the tremendous fluctuations in recruitment level or year-class strength in marine fishes is caused by processes during early life (Fig. 1, Rothschild 1986, Houde 1987, Houde 1997). Thus, while in early days of fishery science the studies mainly focused on the dynamics of adult populations, many fishery scientists now concentrate their efforts on the investigation of the early life stages as the first days, weeks and months in a fish's life are assumed to be very critical in terms of recruitment to the adult stock.

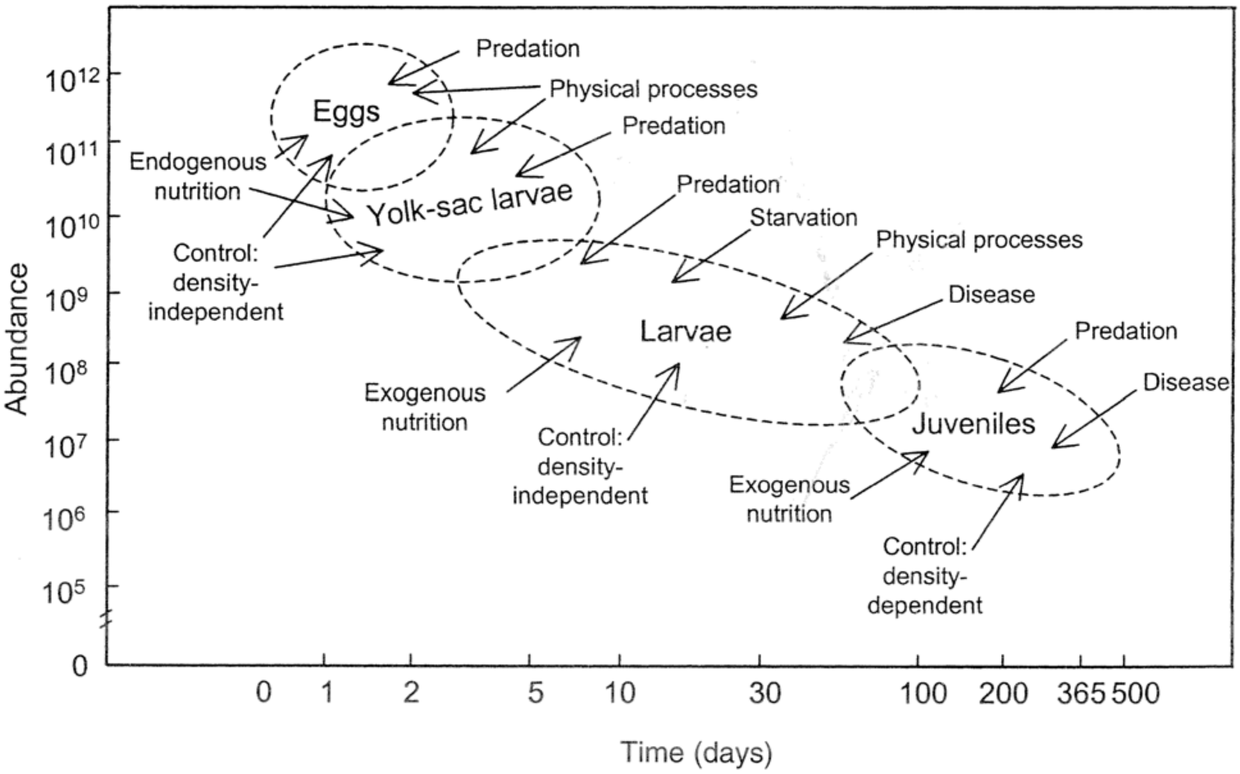


Fig. 1: Conceptualization of the recruitment process in fishes, including factors affecting mortality and growth of individual early life history stages (from Houde 1987).

A major challenge of fisheries science is finding solutions for the question of how reproductive success is depending on the adult stock, the stock-recruitment problem. Prediction of stock development is problematic, as the developmental success of early life stages is largely depending on fluctuating and largely unpredictable environmental conditions. The increasing reductions of fish stocks observed in recent years are certainly partly caused by heavy fishing. However, large natural stock fluctuations due to changes in climate and independent of fishery impact were shown, e.g., for an unfished population of Pacific sardine, *Sardinops sagax*, by analysing scales from sediment cores off California (Soutar & Isaacs 1974, Baumgartner et al. 1996). Thus, fishery biologists aim to find explanations for the factors causing the observed natural stock variabilities. Obviously, the distribution, abundance and survival of fish early life stages and the subsequent recruitment are controlled by numerous biotic and abiotic influences (Fig. 1), and the understanding of the recruitment processes is a complex issue that can not solely be explained by simple correlation analyses of physical environment and early life stage abundance (Cowan & Shaw 2002).

By the end of the 19th century, major stock depletions of commercial species fueled the search for a better understanding of the dynamics of marine populations and led to the establishment of the International Council for the Exploration of the Sea (ICES), heralding the modern era of fishery science. The first ICES investigations focused on two central hypotheses to explain the declining catches. One hypothesis stated that declining harvests were due to shifting migration routes of adults caused by changing oceanographic conditions. The other hypothesis, proposed by the Norwegian fishery scientist Johan Hjort (1914), attributed fluctuations in stocks and catches to variable survival rates in the egg and larval stages. In a time series of harvest data from 1902 to 1914 for the Atlanto-Scandian herring (*Clupea harengus*), the very strong year-class in 1904 was eminent. This suggested that annual fluctuations in catches were due to variations in year-class strength. Hjort proposed two possible reasons for the observed year-class success or failure. The first one were variations in food availability at the critical stage when the transition from endogenous (yolk) to exogenous (plankton) feeding occurs. The second one was the transport of eggs and larvae away from appropriate nursery areas due to inter-annual variability in ocean circulation. He came to these conclusions by observing extremely high *in situ* mortality rates of eggs and larvae. Although he had no direct measurements to support his ideas that became known as the “Critical Period Hypothesis”, they had a strong influence on fishery science.

After a hiatus of 60 years, Hjort’s classic ideas came to the scientist’s interest again in the 70’s, resulting in many efforts to collect evidence from field studies and laboratory experiments to test their basic principles. A lot of effort has been put into determining on which organisms fish larvae are feeding, how much they eat, how much energy they gain from different food and if prey densities in the sea are sufficient for larval survival (Schnack 1972, De Silva & Baldontin 1974, Ciechomski & Weiss 1974, Houde 1976, Scura & Jerde 1977, Lasker & Zweifel 1978, Uotani et al. 1978). By comparing food consumption rates and plankton densities, some of these studies have shown that a feeding paradox seems to exist. Fish larvae are obviously able to feed at satiation levels, even if food densities should in theory be too low to support for it. Many of the recruitment hypotheses that followed Hjort's contribution attempt to find solutions for this feeding paradox. Cushing's "Match-Mismatch Hypothesis" (Cushing 1975, Cushing 1990) extended Hjort's ideas about the role of early life stages in recruitment variability. He actually merged Hjort's initial two hypotheses into one, suggesting that fish spawn in relation to the timing of spring and plankton blooms in the geographic area of inferred larval drift from spawning grounds to nursery areas. In his hypothesis, variable times of spawning and plankton blooms cause differential larval survival and, thus, variable recruitment. If there is a "match", i.e. a large overlap of larval and food occurrence, good recruitment results, and vice versa. Like in the "Critical Period Hypothesis", the reason for larval mortality is starvation. However, in contrast to Hjort's notion, the influence of food limitation is not restricted to a critical period in the larva's development, but is thought to affect any stage of the larval period.

Another extension of Hjort's hypotheses was developed by Lasker (1981), based on his observations on Northern anchovy (*Engraulis mordax*), both in the laboratory and the field off the Californian coast. He agreed with the theory that food for first feeding larvae might be limited, but suggested the existence of times and areas in the ocean where food organisms aggregate, thus enhancing the possibility of larval survival. He investigated the effect of the distribution of prey in the water column on the foraging and ultimately the survival of larval fish (Lasker 1975, Lasker et al. 1978) and found high food aggregations to be associated with chlorophyll maxima in a stratified water column caused by calm and stable ocean conditions. This led to the term "Stable Ocean Hypothesis", implying that calm or stormy conditions would have different influences on larval mortality, larval food aggregations and subsequent year-class success.

Thus, the critical period and match-mismatch hypotheses obviously have to be extended with a spatial factor, acknowledging differences in the horizontal and vertical overlap of larval fish and their suitable prey items (Letcher & Rice 1997).

Rothschild and Osborn (1988) tried to explain the aforementioned feeding paradox by their "Plankton Contact Hypothesis". They suggested that approaches based only on the relative density of predator and prey will probably underestimate predator-prey contact rates as contact depends on both the relative density and the relative velocity of predator and prey. Their hypothesis states that small scale, wind-driven turbulences lead to an increase in encounter rates between larvae and prey items, thus enabling larvae to survive at prey densities that are theoretically too little to support sufficient feeding. However, it needs to be kept in mind that if wind-induced turbulence becomes too high, the exact opposite effect might result, as the larvae's ability to catch their prey is suppressed.

Special considerations have to be taken in terms of larval transport and retention and the resulting implications for recruitment. In many cases, spawning and nursery grounds of fish are not located in the same areas. Therefore, eggs and larvae must be transported by appropriate currents and, in the case of larvae, must find sufficient food on the way in order to reach the nursery areas in proper time, size and condition. The effects of such transports of early life stages of fish were already considered by Hjort in the second of his two hypotheses. Sinclair and Iles (1985) have further elaborated upon this idea and proposed the "Larval Retention" or "Member/Vagrant Hypothesis". It states that fish have a tendency to spawn at distinct times and places in relation to certain hydrographical features. The hydrographical situation provides favorable conditions for larval development and survival and reduces dispersal of the more or less passively drifting eggs and larvae. If larvae are retained in the area, remain "members" of a group and thereby have the opportunity to form schools, they are more likely to complete their life cycle than larvae that are lost from the retention area and become "vagrants". The hypothesis emphasizes the importance of getting to and remaining in a suitable habitat. If the spawning stock increases and the spawning grounds are extended, the degree of vagrancy increases as well. This density-dependent process may result in a limitation of population size that is independent of any previously defined, density-dependent food chain mechanisms.

The hypotheses that have been described so far all intended to further elaborate upon one or the other of Hjort's initial two ideas. However, in recent years fishery science has recognized the tremendous influence of predation on survival chances of eggs and larvae and thereby on recruitment success. Many scientists now believe that predation is one of the most important factors influencing the survival of fish early life stages (Bakun et al. 1982, Houde 1986, Bailey & Houde 1989). In the 1970's, Cushing (1974, 1975) already recognized the potential influence of predation as a recruitment regulator in his "Single Process Concept". He stated that egg or larval mortality rates will increase the longer these early life stages stay vulnerable to predator attacks, i.e. larvae that experience favorable feeding conditions will grow faster, have a higher ability to escape from predator attacks and are more likely to reach the next developmental stages. Thus, the chances of survival to metamorphosis and adulthood increase with increasing growth rate.

Houde (1986, 1987) revived these ideas in the "Stage Duration Hypothesis". He analysed the dynamics of egg, yolk-sac larva, larva, and juvenile stages for different fish species. He argued that recruitment success or failure are not necessarily caused by ideal or catastrophic environmental conditions but can simply result from relatively subtle variations in mortality rates, growth rates or stage duration during these delicate and vulnerable early life stages. In contrast to the hypotheses that were mentioned above, the Stage Duration Hypothesis approaches the recruitment problem from a different point of view. However, this does not mean that it makes prediction of recruitment more facile. Actually, the contrary is true, as there is a multitude of environmental factors that could account for very small changes in growth and mortality rates. Houde (1986) states that an additional complication is given by the fact that it is extremely difficult to determine mortality rates in the field, especially down to a level of accuracy that allows to derive any implications for recruitment. Thus, he concludes that the analysis of growth rate variability in early life can provide important insight into the problem of fluctuating recruitment levels since this proxy for survival chances can be accurately determined by otolith readings and, therefore, may be more reliable than survey estimations of mortality rates.

Whereas some recruitment hypotheses emphasized the importance of either predation or food abundance, feeding success and starvation, the “growth-mortality hypothesis” addresses feeding success and predation in an integrated framework: growth increases with increasing feeding success, while mortality due to starvation or predation decreases (Anderson 1988), e.g. because larger larvae have better prey capture and predator avoidance abilities than smaller larvae (Hunter 1981, Miller et al. 1988).
While it is less likely that large size or other single attributes of an individual will afford it a clear advantage for survival over others, it seems to be clear that survivors are most likely members of faster growing cohorts of larvae as their duration of stay in stages vulnerable to starvation and predation is limited (Cowan & Shaw 2002). As a matter of fact, a recent study by Folkvord (2005) suggests that surviving cod larvae in the sea typically grow at rates close to their size- and temperature-dependent capacity. Whether growth is regarded on an individual or on cohort level, growth rate, and variability in it, are now recognized as important contributors to recruitment variability (Campana 1996, Meekan & Fortier 1996, Houde 1997).

A probably less well-known recruitment hypothesis is the “Gelatinous predator hypothesis”, which suggests that larval fish survival may be influenced through predation by gelatinous zooplankton showing inter-annual variability in occurrence and abundance (Fraser 1970, Anderson 1988). However, rising numbers of reports about mass occurrences of in particular jellyfish and ctenophores (Mills 2001, Xian et al. 2005, Purcell et al. 2007, Boero et al. 2008) are increasing the awareness of the potentially high influence of gelatinous predators in marine ecosystems, although their impact is still little quantified and acknowledged (Mills 1995, Purcell 1997, Moeller & Riisgard 2007, Boero et al. 2008).

1.2 The Baltic Sea

The Baltic Sea is a semi-enclosed estuary with a surface area of approximately 393000 km^2 and is considered to be one of the largest brackish water areas in the world (Leppäranta & Myrberg 2009). Its average depth is only 54 m, and the bottom topography is characterized by a series of deep basins separated by shallow sills. The only connections to the main Atlantic Ocean are the narrow and shallow waters of the Danish Straits (Fig. 2). The water balance in the Baltic Sea is governed by inflows of North Sea water through these straits, freshwater inflows from rivers and precipitation and evaporation. A surface freshwater surplus, originating from rivers and precipitation, causes a constant outflow of Baltic sea water in upper layers, which is counterbalanced by inflowing North Sea water in deeper layers. This is in turn leading to a marked surface salinity gradient, ranging from ca. 10 psu in the southwest to only about 2 psu in the Bothnian Bay and the eastern Gulf of Finland (Fig. 2).

Besides a surface thermocline developing in spring and summer due to solar radiation, the most characteristic hydrographic feature is a permanent halocline separating the upper freshwater layer from a dense, saline bottom water layer. This strong permanent vertical stratification largely prevents transport of oxygen from the surface to deeper layers, and biological processes in the deep basins are causing oxygen depletion in bottom waters. Dispersion concurrently leads to a slow decrease in the salinity.

Oxygen and salinity conditions in the bottom layers of the deep basins can only be improved by infrequent lateral intrusions of water originating from the Kattegat and the North Sea, entering the Baltic Sea through the Danish Straits (Store Belt, Lille Belt and Øresund) and flowing over the sills in the deeper basins. These intrusions of oxygen-rich, highly saline water masses are termed ‘‘Baltic inflows’’ (Matthaeus & Franck 1992). Usually, minor inflows will only enter the Bornholm Basin, with little or no eastern transport. The deep basins further to the east, the Gdansk Deep and the Gotland Basin, are only reached by the inflows if (i) the transported volume of water has a substantial magnitude, a ‘‘major inflow’’ (for definition see Matthaeus & Nausch 2003), (ii) the advected water is replaced by an even denser water mass in a subsequent inflow (ICES 2004), or (iii) a subsequent inflow of less dense water glides over water from an earlier inflow (Matthaeus & Nausch 2003).

Hydrographic conditions in the central Baltic are affected by large-scale climatic conditions, and inflows are mainly forced by strong wind events and are coupled to the North Atlantic Oscillation (NAO) (Matthaeus & Schinke 1994, Schinke & Matthaeus 1998). Major inflow events occurred more or less randomly at intervals of one to several years during the last century.

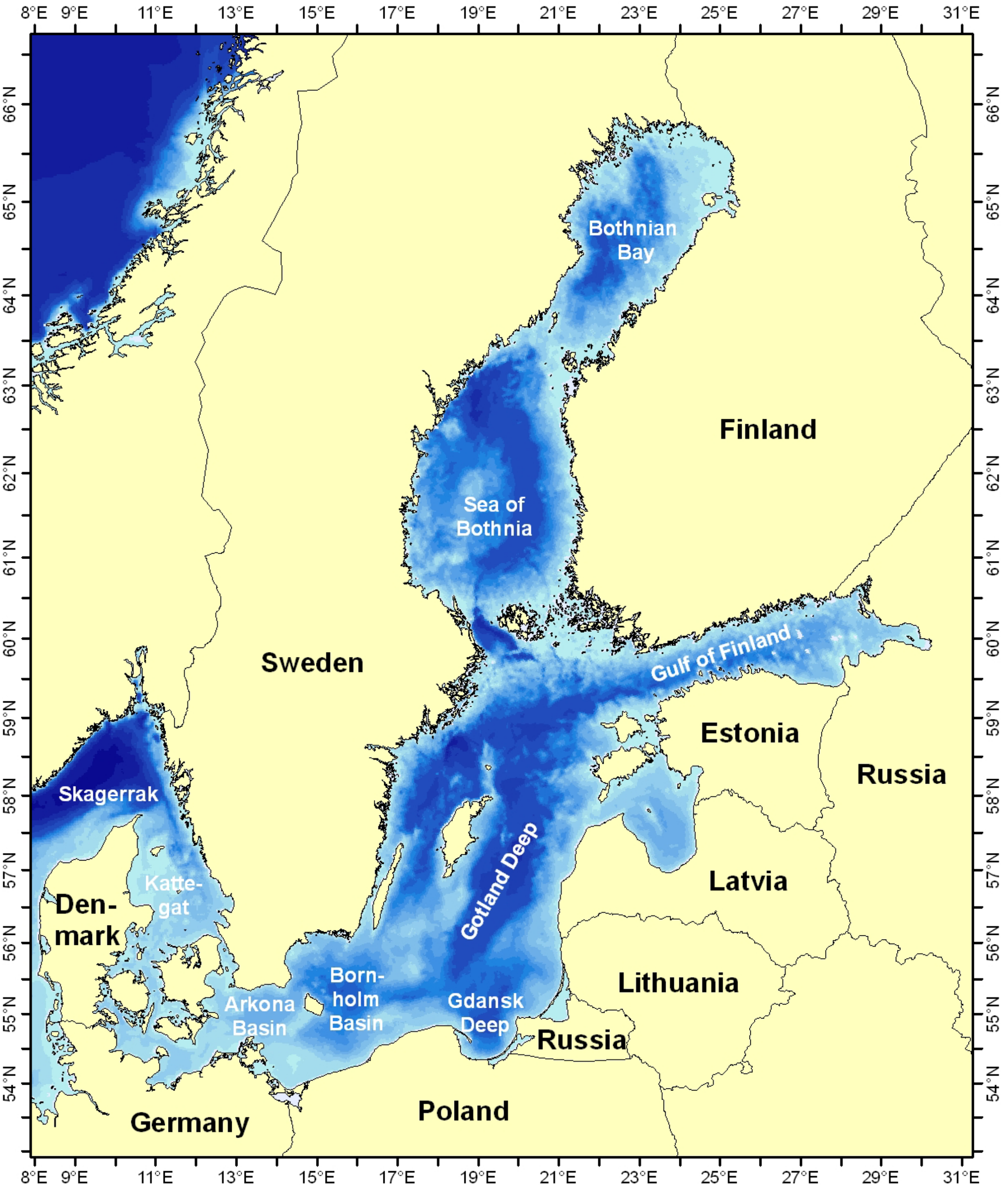


Fig. 2. The Baltic Sea. Neighbouring countries, bottom topography and important deepwater areas. The focus of the present PhD is on the Bornholm Basin. The only connection of the Baltic Sea to the North Sea and the Atlantic Ocean are the Danish Straits between the Arkona Basin and the Kattegat.

However, since the late-1980s, prevailing weather conditions with strong westerly winds resulted in mild winters, above normal rainfall, increased river run-off, and reduced frequency of major inflows (Matthaeus & Schinke 1994). Since 1980, significant inflows were only recorded in 1983, 1993 and 2003 (Fig. 3).

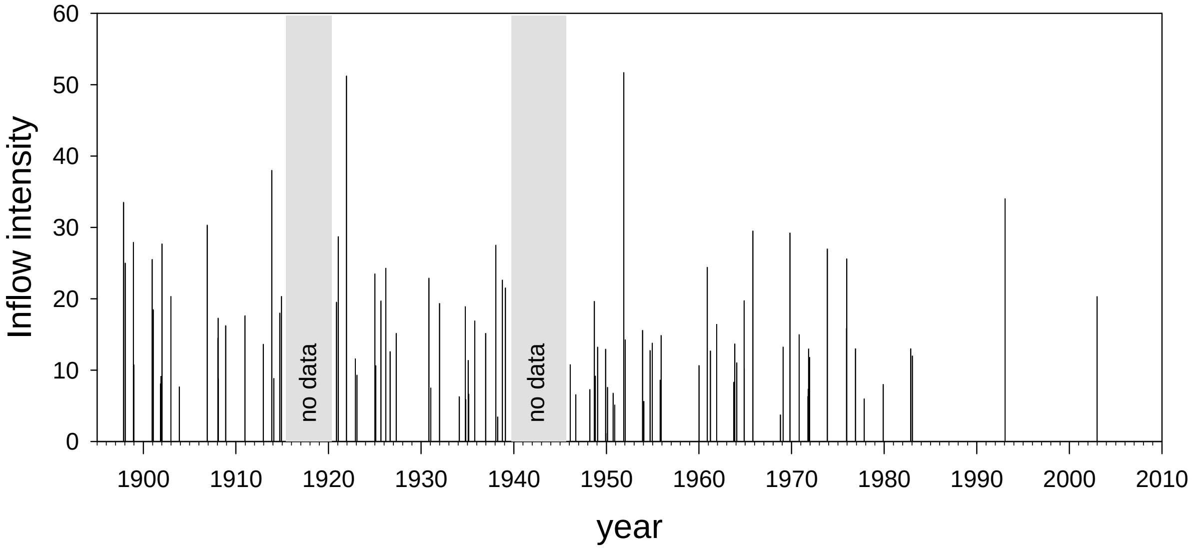


Fig. 3: Time series of major Baltic Inflows and their intensity (data from Matthaeus 2006, Feistel et al. 2008).

The lack of salt water inflows caused above average temperatures in intermediate and bottom waters and long lasting stagnation periods, characterized by a cease of Baltic deep water ventilation, with decreasing oxygen and increasing hydrogen sulphide concentrations in the deep Baltic basins (Matthaeus & Nausch 2003, Meier et al. 2006). Figure 4 shows a typical profile of the presently prevailing stagnation situation in the central Bornholm Basin from August 2000, with a summer thermocline in the upper layer, an intermediate cold water layer, the permanent halocline at about 50-60 m and the low-oxygen deep layer below the halocline.

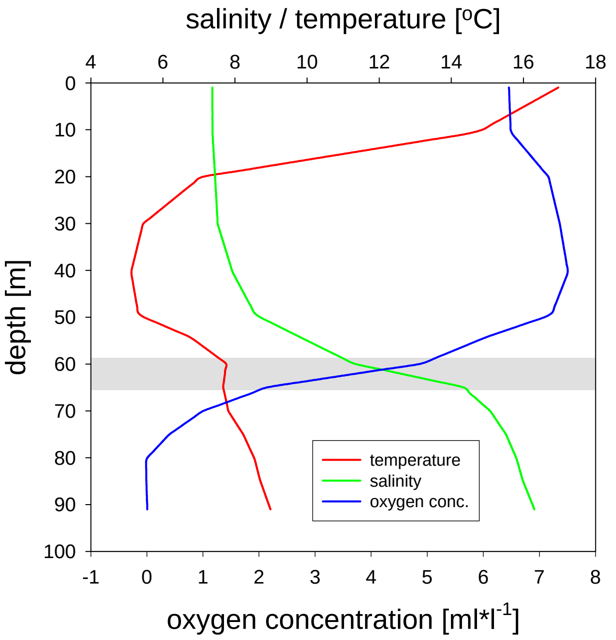


Fig. 4: Vertical profiles of temperature, salinity and oxygen concentration at a station in the central Bornholm Basin in august 2000, showing the summer thermocline, the permanent halocline and the oxygen stagnation situation typical for recent years without inflows of oxygen-rich, highly saline water from the North Sea. The grey area marks the extent of the reproductive volume suitable for Baltic cod egg survival, which is characterized by salinities > 11 and oxygen concentrations > 2 ml*l^{-1}.

Although the hydrography itself is not a central topic of this thesis, we will see in the following that the special hydrographic situation in the Baltic has major implications for the distribution, vital rates and interactions of the organisms dwelling in this unique ecosystem.

1.3 The Eastern Baltic cod stock and its role in the ecosystem

From a fisheries management point of view, two distinct cod stocks are distinguished in the Baltic Sea, the western stock or “Belt Sea cod” (*Gadus morhua morhua* L.) west of the island of Bornholm in ICES subdivisions 22-24 and the eastern stock or “true” Baltic cod (*Gadus morhua callarias* L.) east of Bornholm in subdivisions 25-32 (Fig. 5). The distinction of two separate stocks is supported by meristic (Poulsen 1931, Kaendler R. 1944) and genetic studies (Nielsen et al. 2003, Nielsen et al. 2005, Thaulow 2009) as well as tagging experiments (Aro 1989). However, recent evidence from analyses of seasonal maturity development (Bleil et al. 2009) and genetics (Thaulow 2009) suggests that the eastern stock is utilizing the Arkona Basin in subdivision 24 as spawning ground. Besides, exchange of spawning products between the two stocks is possible through advection (Hinrichsen et al. 2001a).

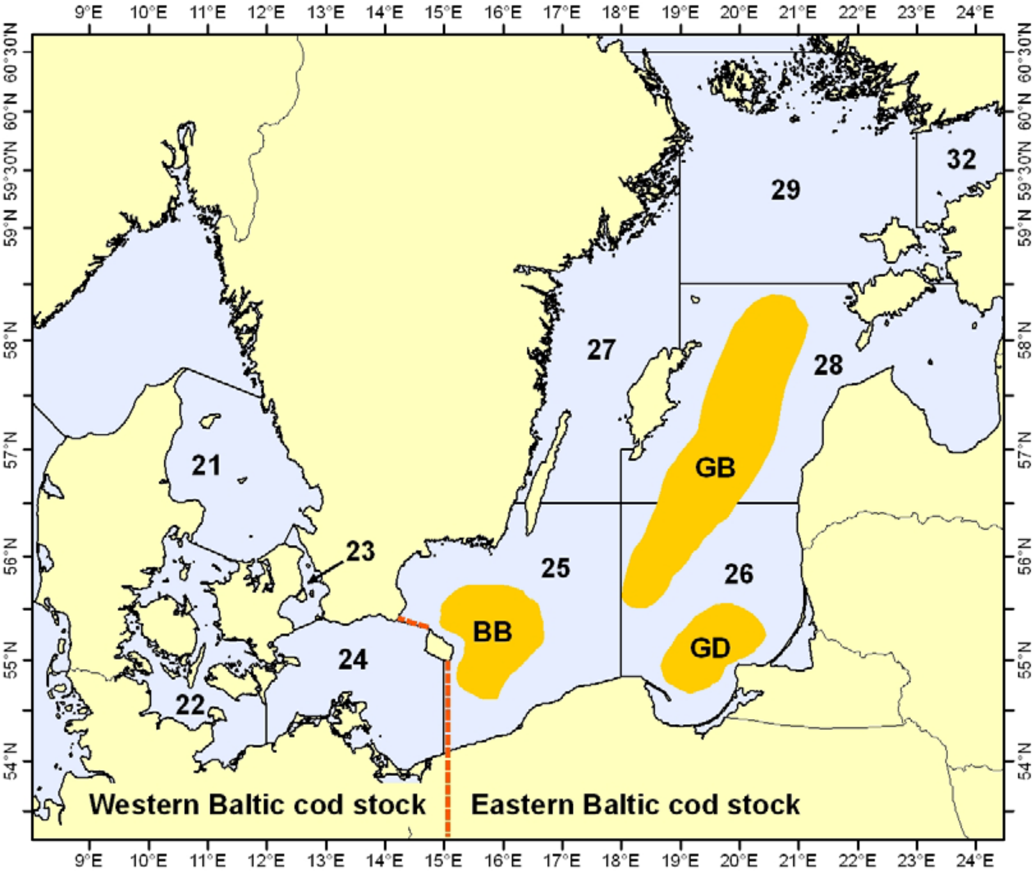


Fig. 5: Map of the Baltic sea showing the stock boundaries of the western and the eastern stock (red line) and the historical main spawning grounds of the eastern stock (yellow: BB = Bornholm Basin, GD = Gdansk Deep, GB = Gotland Basin). Black lines and numbers indicate ICES subdivisions.

The main spawning areas of the western stock are found in regions deeper than 20 m in the Kiel Bight, the Fehmern Belt and the Mecklenburg Bight, with a spawning ground of minor importance in the Arkona Basin, and spawning activity begins as early as January, peaks in

March and April and is usually terminated by May (Bagge et al. 1994, Bleil & Oeberst 2002). In the past decade, average spawning stock biomass (SSB) has been about 25.000 tonnes (ICES 2009).

This thesis is exclusively focusing on the eastern Baltic cod stock. On the long-term average, the size of the eastern stock is about eight times larger than the western stock, but only ca. 4 times larger over the past 10 years. For the sake of convenience, the eastern Baltic cod will from now on be referred to as “Baltic cod”. The time of peak spawning of this stock occurred from the end of April to mid June in the 1970´s and 1980´s gradually shifting to late July in the 1990´s (Wieland et al. 2000). Decreasing water temperatures during the period of gonadal maturation and the declining stock sizes, concurrent with an increase in the proportion of young individuals in the stock, were suggested as key factors for the progressive delay of spawning in this stock (Wieland et al. 2000). In recent years, peak spawning time seems to shift back again to earlier months (paper 6, pers. obs.). The traditional spawning grounds of Baltic cod are located in the Bornholm Basin, the Gdansk Deep and the Gotland Basin (Fig. 5), with a minor spawning area in the Slupsk Furrow (Bagge et al. 1994). However, due to the lack of inflows and the associated deterioration of oxygen conditions in the eastern spawning areas during recent years, the Bornholm Basin is presently the only spawning ground of major importance, as successful egg development is only possible at certain salinities and oxygen saturation levels. The processes influencing egg survival in relation to the hydrography will be described in detail in section 1.6.

Traditionally, the Baltic cod stock is regarded as one of the largest in the North Atlantic (ICES 2005), with long-term averages of total stock size (TSB) and spawning stock biomass (SSB) being 421.000 tonnes and 266.000 tonnes, respectively (estimates from the last standard assessment including the years 1966-2008; ICES 2009). However, recent investigations by Eero et al. (2007, 2008) show that from a historical point of view, this is an overestimation, as average stock sizes were lower before the beginning of the assessment time-series in 1966. Furthermore, these studies and the most recent assessment (ICES 2009) show that the stock was on historically high levels during the late 1970’s and early 1980’s, with SSB and TSB reaching close to 700.000 and more than 1.000.000 tonnes, respectively (Fig. 6a). After this extraordinary peak, the stock rapidly declined to 93.000 tonnes SSB and 134.000 tonnes TSB in 1992. Thereafter, stock size generally remained on low levels, reaching a time-series low of 66.000 tonnes SSB and 123.000 tonnes TSB in 2005. In most recent years, the stock is showing a slow recovery, and the latest estimates for 2008 are 139.000 tonnes SSB and 241.000 tonnes TSB.

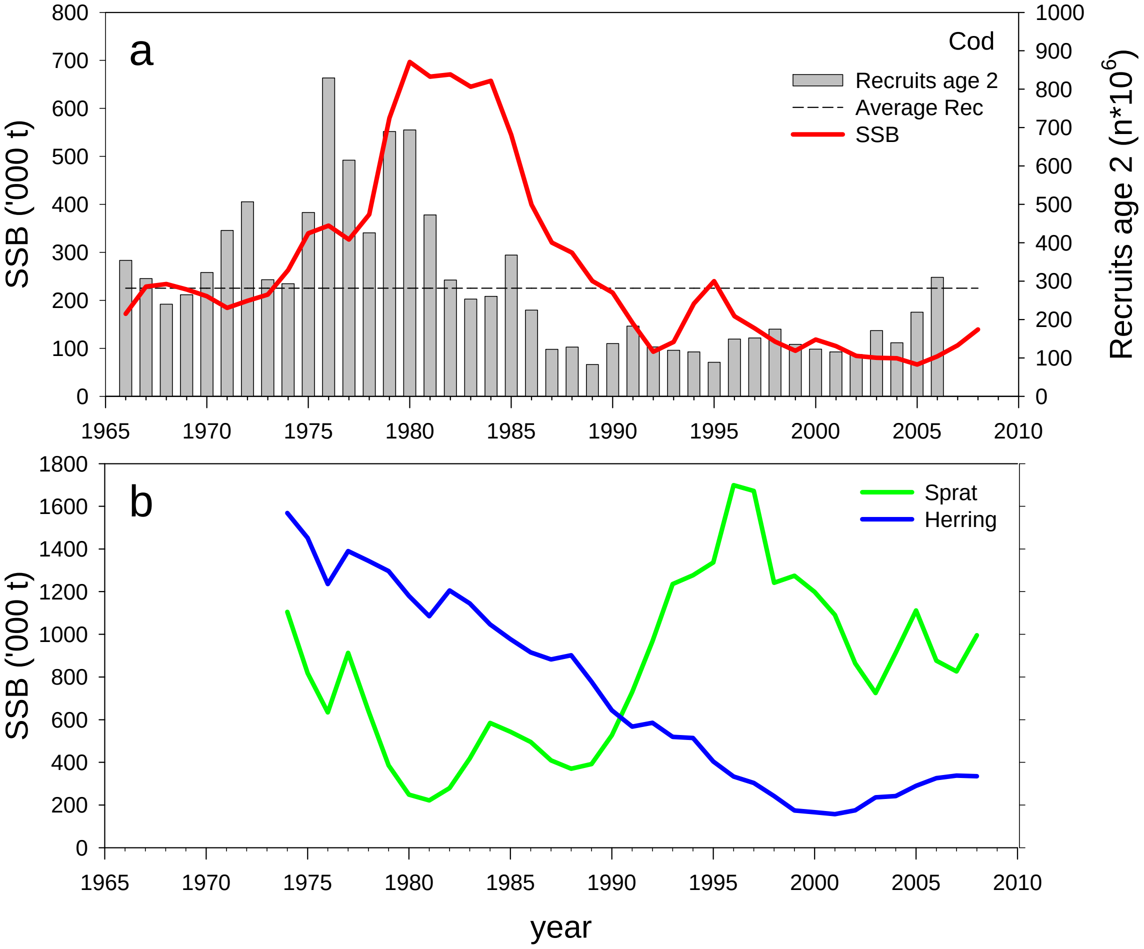


Fig. 6: Time series of (a) Baltic cod spawning stock biomass (SSB) and recruitment (age 2, backshifted to the recruitment year) and of (b) SSB of the two other dominant fish species in the Baltic, sprat and herring (ICES 2009). The stippled line in (a) shows the long-time recruitment average.

Due to the strong horizontal salinity gradients, species diversity is continuously decreasing from the Kattegat to the Bothnian Bay, and the Baltic Sea is therefore considered a relatively simple ecosystem in terms of species diversity and trophic interactions (Link et al. 2009). The upper trophic levels are dominated by a very simple fish community, which comprises only three major species. Cod (*Gadus morhua*) is the dominant top predator and sprat (*Sprattus sprattus*) and herring (*Clupea harengus*) are the two most abundant planktivorous fish species (Sparholt 1994). Marine mammals may have been important top predators in former times, but at the presently low abundances their importance is regarded negligible (Eero 2008). Likewise, seabirds might be locally important predators in coastal areas, but play only a subordinate role in the Bornholm Basin. The major zooplankton species in the ecosystem are the copepods *Pseudocalanus acuspes*, *Temora longicornis*, *Acartia bifilosa* and *Acartia longiremis* (Moellmann et al. 2000, Schmidt 2006). The phytoplankton consists of a series of abundant species partly forming large algal blooms in spring and summer.

However, while biologically relatively simple, the Baltic Sea is hydrographically a rather complex system, and the distribution and interactions of the different biotic ecosystem compartments are strongly influenced by the vertical structure of the water column. Baltic cod conduct a spawning migration into the deep basins, which takes place from May to July (Aro 1989, Aro 2000). Here, they stay in the deeper water layers below the halocline but avoid the deepest layers as they are usually characterized by oxygen deficiencies (Schaber et al. 2009). Cod are preying on the clupeids herring and sprat, which are dwelling in the same depth layers during daytime (Sparholt 1994, Link et al. 2009). Both sprat and herring perform daily vertical migrations to near-surface layers at night (Nilsson et al. 2003, Stepputtis 2006). As they are visual predators not feeding at night, they are mainly preying on the plankton community around the halocline during day time. Their main prey items are copepods, cladocerans and other zooplankton, and they can consume significant numbers of cod eggs (Koester & Schnack 1994, Koester & Moellmann 2000).

Strong interactions between cod, sprat and to a lesser extent herring have lead to a marked change in the central Baltic Sea fish community. The system has changed from being cod-dominated during the 1980’s to the present situation characterized by domination of sprat (Fig. 6, Alheit et al. 2005, ICES 2008b). The cod stock collapsed, probably due to climate-induced recruitment failure and continuous high fishing pressure (Koester et al. 2005), while the sprat stock increased to record levels during the 1990s. This was probably a result of climate-induced recruitment success and lower predation pressure by cod (Koester et al. 2003b, MacKenzie & Koster 2004). Besides, an additional negative feed-back loop was caused by high cod egg predation of the increasing sprat stock. Herring biomass decreased (Fig. 6b), mainly due to reduced growth (Moellmann et al. 2005) and lower recruitment. A more detailed summary of the interactions between cod, sprat and herring with respect to impacts on cod recruitment is provided in section 1.6.

1.4 Biology of early life stages of Baltic cod

In comparison with other cod stocks, the Baltic cod attains first maturity at a low age of about 2 to 4 years, with females maturing later than males (Lambert et al. 2003, Storr-Paulsen et al., in prep.). Cod is considered a determinate batch spawner (Kjesbu et al. 1990), and depending on female size and condition, egg production of individual Baltic cod can range from 100.000 to more than 10 million eggs (Kraus et al. 2000). Cod eggs usually have a diameter of ca. 1.5 mm (Muus & Nielsen 1999). However, Vallin and Nissling (2000) report larger egg sizes for eastern Baltic cod, ranging from 1.49 to 1.80 mm depending on female size (average 1.62 mm). This is thought to be an adaptation to the low salinities in the Baltic, as larger eggs are more buoyant and, thus, are floating at lower salinities.

Wieland et al. (1994) found Baltic cod egg development times to range from 28-30 days at 2 celsius over 13 d at 7°C to 10 d at 10°C. Petereit (2004) studied the temperature influence on developmental rates of Baltic cod eggs and early larvae. He determined the time until hatch, mouth opening and depletion of yolk-sac reserves, as well as hatching lengths and length after different intervals of early larval life, at temperatures ranging from 2-13.8°C. In comparison with the study by Wieland et al., he observed slightly faster developmental times. At this point, it seems noteworthy that the Baltic cod already hatches at egg developmental stage 4, while other Atlantic cod stocks do not hatch until stage 5 (Thompson & Riley 1981). Mean lengths at hatch ranged from 3.47 to 3.78 mm, with minimal and maximal lengths of 3.25 and 4.05 mm, respectively. A dome-shaped relationship between temperature and length at hatch was observed, with maximal mean values at 4.7°C. From larval lengths at age 3 days, Petereit also calculated mean daily growth rates for early larvae, which ranged between 0.042 and 0.210 mm/d. In the investigated temperature range from 2°C to 10°C, cod larvae needed between 3 and 9 days until the development of a functional mouth, which occurred at a mean length of 4.22 mm (average over all temperatures), and a period of 9 days until complete yolk-absorption was observed. Larvae < 4.5 mm correspond roughly to larvae before first-feeding, larvae from 4.5-5.5 mm to first feeding larvae and larvae > 5.5 mm to established feeders (Grønkjær & Wieland 1997). At the end of the larval phase, the small fish metamorphose into pelagic juveniles. Metamorphosis is defined as the stage when larvae develop anatomical and morphological characteristics similar to those of adults (Balon 1984). In cod, metamorphosis is initiated with the replacement of the larval fin fold with dorsal and anal fins. This procedure begins at lengths of about 12 mm and is completed at about 25-30 mm (Pedersen & Falk-Pedersen 1992). After metamorphosis, the juvenile cod stay in a pelagic habitat, before they settle to the ground to begin the demersal juvenile stage. This settling process usually occurs at lengths of 40-50 mm (Hüssy et al. 2003).

1.5 The invasive alien ctenophore *Mnemiopsis leidyi* in the Baltic Sea

The American comb jelly *Mnemiopsis leidyi* (Figs. 7-9) belongs to the phylum Ctenophora, or ctenophores. The name ctenophore (“comb bearer”) refers to the characteristic eight rows of cilia along the body, which are arranged to form stacks of combs, also called comb plates or ctenes and are used for locomotion. Ctenophores are gelatinous, planktonic, carnivorous, transparent animals, whose bodies are largely composed of water. In these respects, they share a number of similarities with the Medusozoa or medusae, commonly known as “jellyfish”.

However, medusae and comb jellies are only distantly related. In contrast to the medusae, which belong to the phylum cnidaria (Scyphozoa, Hydrozoa, Cubozoa and Anthozoa), ctenophores are lacking stinging cells. Instead, in order to capture prey, ctenophores possess sticky cells called colloblasts. Some species, including *M. leidyi*, are known to be voracious predators on zooplankton, fish eggs (Fig. 8) and larvae.

Fig. 7: *Mnemiopsis leidyi* (photograph by Thomas Warnar)

Fig. 8: *Mnemiopsis leidyi* with fish egg in the stomach (from Haslob et al. 2008)

Gelatinous zooplankton (medusae, ctenophores and siphonophores) often occurs in irregular pulses and can grow rapidly, in both individual as well as population size, especially during periods of favourable environmental conditions (Boero et al. 2008). Blooms of gelatinous plankters can rapidly exploit available prey sources and were found to be capable of controlling zooplankton communities (Riisgård et al. 2007). In contrast, not many marine organisms seem to prey on gelatinous plankton, which is therefore traditionally seen as an energy sink in the marine food-web (Schneider G. 1999). However, the importance of gelatinous animals in marine food-webs and ecosystems is largely underestimated (Mills 1995, Purcell 1997, Moeller & Riisgard 2007, Boero et al. 2008).

Human activities, especially overfishing, can force marine food webs towards increases of jellyfish abundance (Mills 2001, Xian et al. 2005, Purcell et al. 2007). Overfishing and climate change could potentially lead to a top-down control of marine food webs by gelatinous predators (Mills 2001) and may be causing a suppression of high-energy food chains with a possible subsequent de-evolution of the pelagic marine ecosystem back to a Medusozoan dominance (Boero et al. 2008). In such a scenario, the understanding of ecological dynamics of gelatinous zooplankton becomes an impelling priority both in marine biology and conservation.

Interactions of gelatinous zooplankton with fish are of interest as they potentially affect commercially important fisheries, and have been reviewed by several authors (Moeller 1984, Arai 1988, Bailey & Houde 1989, Purcell & Arai 2001). Especially early life stages of fish, that share the pelagic habitat with gelatinous plankton, are affected by such interactions. There are two main principle ways in which jellyfish can influence ichthyoplankton, (1) by direct predation on eggs and larvae and (2) by competition for zooplankton prey organisms (Purcell & Arai 2001).

Scyphomedusae and ctenophores in particular are known to prey extensively on ichthyoplankton (Moeller 1984, Cowan & Houde 1992, Cowan & Houde 1993, Purcell & Arai 2001). This has lead to the “Gelatinous predator recruitment hypothesis”, stating that annual variations in the abundance of gelatinous zooplankton may significantly affect larval fish survival by direct predation (Fraser 1970, Anderson 1988). In Kiel Fjord, e.g., Moeller (1980, 1984) found high predation rates of *Aurelia aurita* on herring larvae and significant negative correlations between abundances of predator and prey. He estimated that *A. aurita* removes at least 2-5 % of yolk-sac larvae per day. Furthermore, Lynam et al. (2005) provided field evidence for the influence of jellyfish on North Sea herring recruitment.

Two common scyphomedusae, the moon jellyfish *Aurelia aurita* and the lion’s mane jellyfish *Cyanea capillata*, are regularly found in the Baltic. Furthermore, four native ctenophore species occur in the system: *Beroe cucumis*, *Beroe gracialis*, *Bolinopsis infundibulum* and *Pleurobrachia pileus* (Røllike Ditlefsen 2009). Due to salinity limitations for the other species, only *P. pileus* is regularly observed in the central and eastern Baltic, but in relatively low numbers. Due to a limited spatial overlap between *A. aurita* and fish eggs and larvae in the Baltic Sea, the predation impact of this species is low (CORE 1998, Lischka M. 1999, Barz & Hirche 2005). *C. capillata* is found in and below the halocline (Lischka M. 1999, Barz & Hirche 2005), i.e. in the same depth range as the eggs of cod and sprat (paper 6, Wieland & Zuzarte 1991). However, this jellyfish underlies strong seasonal differences in occurrence and distribution and generally only appears sporadically and in low densities (Barz & Hirche 2005).

Thus, while predation on fish eggs by pelagic fish (sprat and herring) can reach considerable levels in the central Baltic (cf. section 1.6, Koester & Schnack 1994, Koester & Moellmann 2000), the predatory impact of gelatinous organisms on ichthyoplankton is regarded as low. However, with the advent of the invasive alien ctenophore *Mnemiopsis leidyi* to the Baltic ecosystem, this situation may have abruptly changed.

The Baltic Sea has a long history of species introductions, and about 100 nonindigenous species are found in the system (Leppaekoski et al. 2002), spanning a wide range of taxonomic groups from aquatic plants to fish. However, an introduced species does not necessarily become an invasive species. While an introduced organism is merely an organism that is not native to a certain area, an invasive organism is one that significantly alters the functioning of an ecosystem. Invasive alien species are plants, animals, pathogens and other organisms that are non-native to an ecosystem, and which may cause economic or environmental harm or adversely affect human health (Levine 2008, The Global Invasive Species Programme: http://www.gisp.org/). In particular, they may disrupt local ecosystems and ecosystem functions and have adverse impacts on biodiversity, e.g. by causing decline or elimination of native species - through competition, predation, or transmission of pathogens. Invasive species are causing great socio-economic, health and ecological cost around the world. They exacerbate poverty and threaten development through their impact on agriculture, forestry, fisheries and natural systems. This damage is aggravated by climate change, pollution, habitat loss and human-induced disturbance.

Despite the large number of introduced alien species in the Baltic, relatively few quantified ecological or economic problems with introduced species have been documented (Leppaekoski et al. 2002). Exceptions are e.g. the cladoceran *Cercopagis pengoi*, which significantly influenced abundances of *Bosmina sp.* and the diet composition of Baltic herring, and the hydrozoan *Cordylophora caspia*, the barnacle *Balanus improvisus*, and the bivalves *Dreissena polymorpha* and *Teredo navalis*, which cause economical damage to fisheries, shipping, boating, fish farming and industry. These examples show that invasive species are able to modify abiotic and biotic conditions for other species, alter composition of both pelagic and benthic communities, and affect organic matter and energy transfer pathways of food webs (Olenin & Leppakoski 1999).

The American comb jelly *Mnemiopsis leidyi* must clearly be regarded as an invasive species, as it has seriously affected previously invaded areas (Vinogradov et al. 1989, Shiganova et al. 2001, Purcell et al. 2001b, Kideys 2002, Kideys et al. 2005, Oguz et al. 2008), and the Invasive Species Specialist Group considers it to be one of the worst invasive alien species world-wide (http://www.issg.org/). The high invasive potential of the species is related to the usual scarcity of enemies in invaded systems, its high tolerance towards environmental variability and its extraordinary reproductive capabilities.

M. leidyi is known to tolerate a wide range of salinities (2-38 psu) and temperatures (2-32 °C) (Purcell et al. 2001b), although reproduction may be limited by low temperatures and salinities (Purcell & Decker 2005). Besides, the species sustains low levels of oxygen (papers 4 & 6, Purcell et al. 2001a). At food deprivation, the animals do not die immediately but instead first begin to shrink, allowing them to sustain longer periods without food. Besides, they are capable of regenerating lost tissue and body structures (Martindale 1986).

Like most other ctenophores, *M. leidyi* is a functional hermaphrodite with the ability of self-fertilization (Martindale 1987). Large numbers of gametes can be produced for extended periods of time. Eggs and spermatophores are spawned freely and embryonic development is fast (often within 24 h), resulting in a feeding cydippid "'larva". *M. leidyi* is exhibiting dissogony (Martindale 1987), which means that the larval stage is already capable to reproduce by producing viable gametes (Fig. 9b). After this first reproduction, the larvae develop to lobate-stage adults which become reproductive again. These reproductive peculiarities, especially the strategy of "short-cutting" the life cycle by dissogony, allow populations to rapidly increase at favourable environmental conditions.

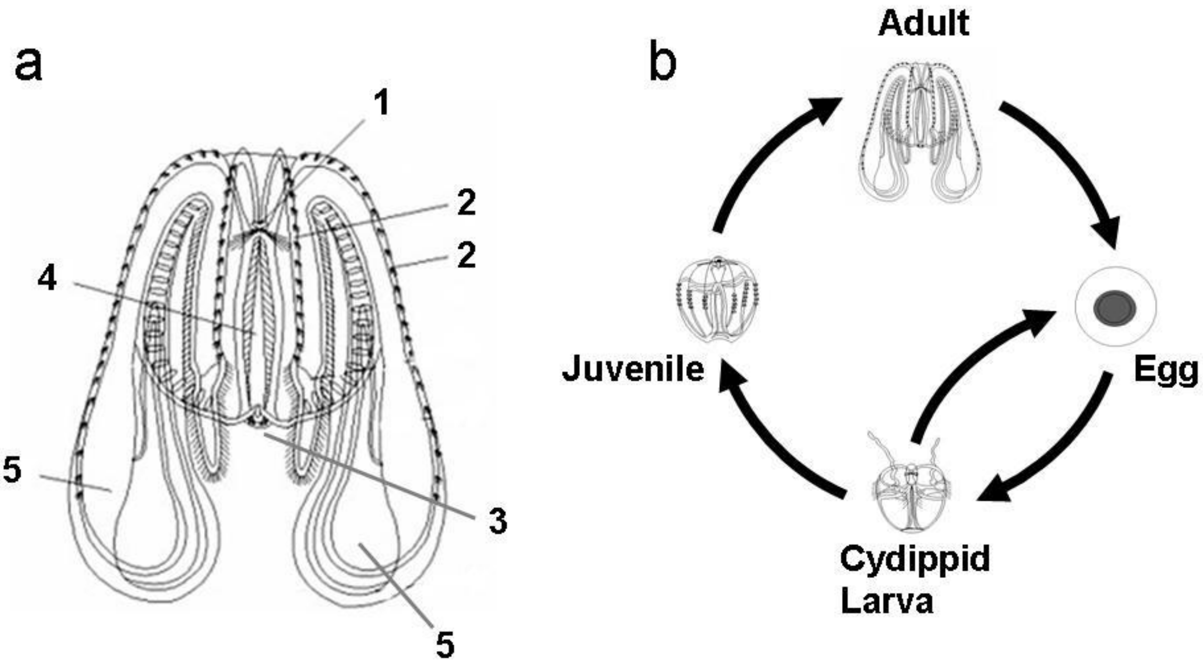


Fig. 9: *Mnemiopsis leidyi*. (a) Morphology: (1) aboral sense organ, (2) comb rows, (3) mouth, (4) stomach, (5) lobes (after Shiganova, 2000). (b) Life cycle. Note that the species is exhibiting dissogony, i.e. that the larval stage is already capable of reproduction (after Shiganova, 2000).

Mnemiopsis leidyi is native on the east coasts of North and South America (Purcell et al. 2001b). In the early 1980s, the species was accidentally introduced into the Black Sea, most likely via ballast-water, which is the dominant introduction vector in most alien species invasions in the marine environment. Here, it showed a massive population explosion until the late 1980s, reaching concentrations of up to 1.5 kg m^{-2} (Vinogradov et al. 1989). A following massive decline in the landings of the important anchovy (*Engraulis encrasicolus*) fishery could partly be related to *M. leidyi* as predator on eggs and larvae of *E. encrasicolus* (Purcell et al. 2001b, Kideys 2002, Kideys et al. 2005, Oguz et al. 2008), thus influencing the stock already affected by heavy fishing pressure (Bilio & Niermann 2004, Oguz et al. 2008). Additionally, prey competition with zooplanktivorous fish has been observed, intensifying potential negative effects on these fish stocks (Vinogradov et al. 1989, Daskalov & Mamedov 2007). Subsequently, *M. leidyi* spread into adjacent waters of the Mediterranean and to the Caspian Sea (Kideys & Niermann 1993, Ivanov V. et al. 2000, Shiganova et al. 2001), where it had similar negative impacts on the invaded ecosystems.

During recent years, *M. leidyi* has invaded northern European waters – most probably also via ballast-water. Almost simultaneous observations of this ctenophore were reported from several locations in the North and Baltic Seas during autumn 2006 (Faasse M.A. & Bayha K.M. 2006, Boersma et al. 2007, Oliveira 2007, Tendal O. et al. 2007) including initial evidence from the southwestern Baltic (Javidpour et al. 2006). However, the species may have been introduced considerably earlier to the North Sea, which possibly remained unnoticed due to a misidentification as the native ctenophore *Bolinopsis infundibulum* (Faasse M.A. & Bayha K.M. 2006). Later, a further proliferation into the central Baltic Sea between autumn 2006 and fall 2007 was reported (paper 4, Haslob et al. 2007, Kube et al. 2007). Mass occurrences of small ctenophores in the Bothnian Sea and the Gulf of Finland (Lehtiniemi et al. 2007), initially thought to be *M. leidyi*, were later identified as another ctenophore species, *Mertensia ovum*, previously unknown to the Baltic (Lehtiniemi 2009a, Lehtiniemi 2009b). Thus, the eastern borderline of the current spreading of the *M. leidyi* invasion into the Baltic is relatively unclear. However, the specimens observed in the Bornholm Basin, which are the focus of this PhD, were identified to be *M. leidyi* by genetic analyses (TBH Reusch, pers. comm.).

1.6 Cod recruitment in the unique environmental situation in the Baltic Sea

The different hypotheses on processes affecting fish stock recruitment summarized in section 1.1 above are not to be seen as individual trials to explain recruitment variability on their own. Rather, these hypotheses should be regarded as attempts to explain processes that act simultaneously or sequentially upon the fate of a year-class. Accordingly, processes acting upon the survival during the egg and larval stages of Baltic cod can be seen in the light of several of the aforementioned hypotheses.

Linear regression analysis of a stock-recruitment plot for Baltic cod reveals a significant relationship between spawning stock biomass and recruitment at age 2 (Fig. 10a, ICES 2009). However, the explained variance in age 2 recruitment is low, with a significant intercept and high outlying values, showing strong inter-annual differences in recruitment success. Furthermore, there is a clear time trend in the residuals (Fig. 10b). A number of very strong year-classes emerged from only intermediate SSB in the 1970’s, leading to record high stock sizes in the early 1980’s (Fig. 6a, Koester et al. 2005). Recruitment success began to sharply decline after 1980 despite high SSB, leading to a subsequent stock decline with a time-lag of about 5 years, and with the exception of 1985, recruitment remained below average. However, in recent years stronger year-classes were observed despite low SSB. Recruitment in 2006 was above average for the first time since 1985 and showed a positive residual value for the first time since 1980.

This becomes especially apparent from the stock-recruitment plot (Fig. 10a), which shows that the recruitment in 2005 and 2006 was exceptionally high in relation to the low SSB, reaching levels encountered in the early 1980's.

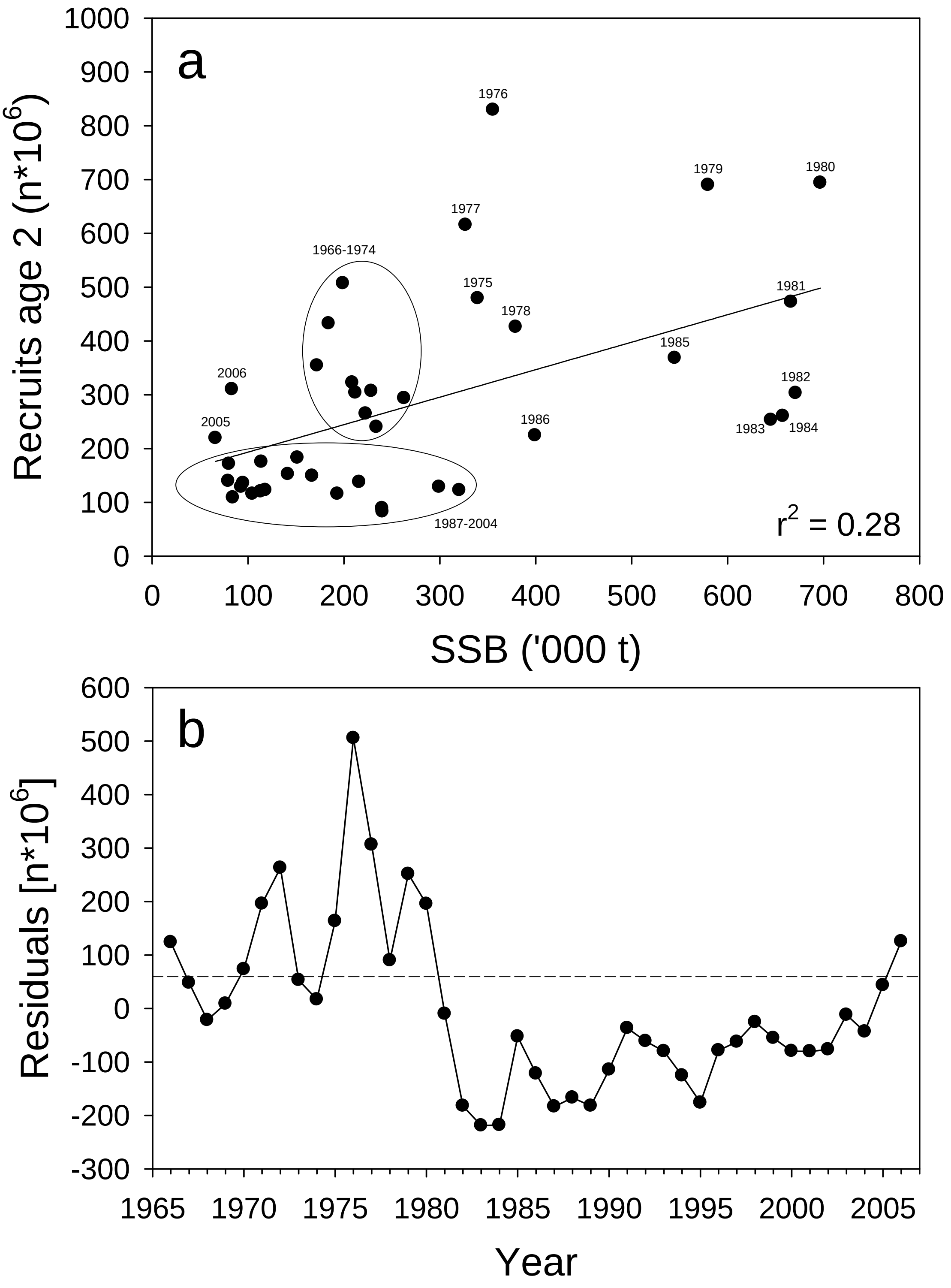


Fig. 10: Stock-recruitment relationship of Baltic cod (a) and corresponding residuals (b). Data source: standard stock assessment (ICES 2009).

Previous study programs (CORE 1998, STORE 2003) have addressed the recruitment process of eastern Baltic cod and identified oxygen- and predation-related egg mortality as major influences on recruitment success (Koester et al. 2001b, Koester et al. 2005). The reproductive success of the Baltic cod stock is closely linked to the unique hydrographic conditions. In most other spawning areas of Atlantic cod, the ambient salinity is usually sufficient to keep cod eggs floating in the surface layers. In contrast, salinity in the surface layers of the Central Baltic Sea is too low for cod eggs to achieve neutral buoyancy. Experimental studies revealed that the eggs of Baltic cod are neutrally buoyant at ~14 psu (Nissling et al. 1994, Nissling & Vallin 1996). As salinities around 14 psu in the Central Baltic are restricted to deep water layers, cod eggs occur exclusively within and below the permanent halocline (e.g. paper 6, Mueller 1988, Wieland & Jarre-Teichmann 1997) located at approximately 50 to 60 m depth in the Bornholm Basin (Leppäranta & Myrberg 2009). This is the reason that the main spawning grounds of Baltic cod are restricted to deepwater areas, i.e. the Bornholm Basin, the Gdansk Deep and the Gotland Basin, with a minor spawning area in the Slupsk Furrow (Fig. 5). However, oxygen concentration in the basins is decreasing with depth, and within these deep spawning layers cod eggs are exposed to variable and low oxygen concentrations.

According to laboratory experiments, oxygen saturation levels of at least 2 ml/l are needed for successful egg development (Nissling 1994, Wieland et al. 1994), and a minimum salinity of 11 is required for the activation of spermatozoa and successful fertilization (Westin & Nissling 1991). The combined influence of these two limiting factors, the oxygen and the salinity threshold, formed the basis for the definition of a so-called ‘‘reproductive volume’’ (RV), which describes the volume of water allowing for successful cod egg development (Plikshs et al. 1993, MacKenzie et al. 1999, MacKenzie et al. 2000). The oxygen situation in the deep basins can only be improved by inflows of highly saline, oxygen-rich water from the North Sea. Thus, the extent of the RV depends on the frequency and the magnitude of these inflows, as well as on the temperature of the inflowing water which influences oxygen solubility (Hinrichsen et al. 2002b), and on oxygen consumption rates by biological processes (MacKenzie et al. 1996). While major Baltic inflows occurred relatively frequently before the mid 1980s, only two major inflow events were observed thereafter, in 1993 and 2003 (Fig. 3, Matthaeus 2006, Leppäranta & Myrberg 2009).

Due to this lack of inflows and the resulting extended stagnation periods, successful reproduction of the Eastern Baltic cod stock is since the mid 1980’s mainly restricted to the westernmost Bornholm Basin, while the deep basins further east, the Gdansk Deep and the Gotland Basin, provide only very weak spawning environments (Plikshs et al. 1993, MacKenzie et al. 1999, MacKenzie et al. 2000). Consequently, the stock development was heavily dependent on recruitment success in the Bornholm Basin (Koester et al. 2009), and the present study is therefore focusing on this spawning ground.

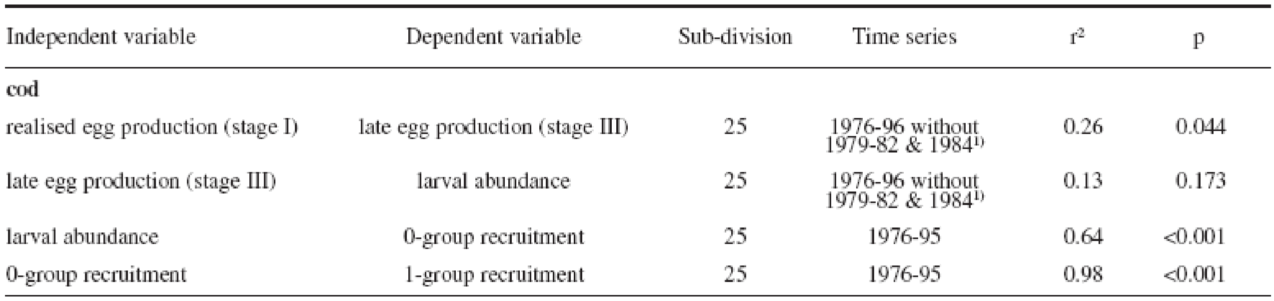
Despite being conceptually appealing, the RV explains only a limited amount of variance in cod recruitment (Sparholt 1996). One possible explanation for this is that the RV may not be the best proxy for egg survival, because egg mortality caused by low oxygen concentration above the threshold is not considered (Wieland et al. 1994). While 2 ml/l oxygen is only the minimum saturation needed for any egg survival, the survival rate increases remarkably with increasing oxygen content (Rohlf 1999). Koester et al. (2005) used this oxygen-egg survival relationship for the construction of a time-series of oxygen-related egg survival (OES). By multiplying estimates of potential egg production (PEP) with OES, they achieved an increase in the explained variance of a regression of observed egg production from ichthyoplankton surveys on PEP from $r^2 = 0.61$ to 0.73. Thus, estimations of oxygen-related egg survival seem to be a valuable tool in examining recruitment success of Baltic cod.
Besides OES, eggs may float in water layers outside the RV not sustaining their development, i.e. in water layers having a density allowing the eggs to float, but with insufficient oxygen conditions for their development (Koester et al. 2001). Further reasons for variable rates of egg survival are the quality of eggs produced, that have been observed to vary significantly in relation to stock structure (Vallin et al. 1999, Vallin & Nissling 2000).

Another major mortality agent is the predation on cod eggs by clupeids (Koester & Schnack 1994, Koester & Moellmann 2000, Koester et al. 2005). Both Baltic sprat and herring concentrate feeding on zooplankton in the vicinity of the halocline, and are known to include significant amounts of cod eggs in their diet. Predation intensity depends on the degree of vertical overlap between predator and prey, which is governed by the ambient hydrographic conditions. Stagnation periods with low oxygen concentration and salinity result in high vertical overlaps and predation rates, while opposite conditions release cod eggs from clupeid predation (Koester et al. 2005). In addition, egg predation mortality depends on predator abundance. While the stock size of herring decreased throughout the 1980s and 1990s, the sprat stock increased dramatically (Fig. 6b), mainly due to the positive influence of increasing temperatures on sprat reproduction (MacKenzie & Koster 2004), and remains on relatively high levels. The seasonal timing of cod spawning defines the relative predation pressure of the two clupeid species. Sprat is utilizing the same spawning grounds as cod during spring. Thus, early cod spawning times result in a high temporal overlap of eggs with sprat as predators. In contrast, late cod spawning enhances the overlap with herring, returning in early summer from their spawning grounds, while sprat after finishing spawning activity leaves the basin (Koester & Schnack 1994, Koester & Moellmann 2000). In this respect, the observed shift of the cod spawning season from spring to summer (Wieland et al. 2000) has been an advantage for cod reproductive success, especially as the herring stock declined markedly in recent times (Fig. 6b).

However, even though oxygen- and predation-related egg survival are certainly important factors influencing Baltic cod recruitment, considerable explanatory potential remains for other variables and processes. A time series of Baltic cod SSB, oxygen conditions in the spawning grounds, egg predation pressure, egg and larval abundances and recruitment shows several years of low recruitment despite favourable conditions for egg survival (Koester et al. 2005, Koester et al. 2009). High numbers of eggs found in ichthyoplankton surveys after a strong inflow event in 1993 and subsequent years did e.g. not result in increased recruitment levels, despite low clupeid predation pressure. On the other hand, recent estimates of stock biomass and recruitment of Baltic cod suggest improving recruitment despite apparently unchanged environmental conditions for egg survival (Fig. 6a & 10, ICES 2009). Thus, processes after the egg stage must have an additional influence on the fate of a year-class and the recruitment success of Baltic cod.

Cannibalism on juveniles does occur in Baltic cod and has been substantial in periods of high stock size observed in the early 1980’s (Sparholt 1994), but can be regarded to have a minor influence on recruitment regulation at the presently low stock size (Neuenfeldt & Koester 2000, Uzars & Plikshs 2000). Following Paulik’s (1973) framework of studying the recruitment process, Koester et al. (2003a) analysed a time series of abundance data of consecutive life stages. While the relationship between late egg production (stage 3) and larval abundance was weak and not significant, a significant correlation of larval abundance and 0-group recruitment was found (Table 1, from Koester et al. 2003a). This suggests that the larval stage may actually be the most critical phase in determining Baltic cod recruitment variability.

Table 1. Linear regression of abundance or production estimates of individual life stages on the abundance or production of the succeeding life stage of Baltic cod. The table presents r^2-values and significance levels. (from Koester et al. 2003a).



Independent variable	Dependent variable	Sub-division	Time series	r^2	p
cod					
realised egg production (stage I)	late egg production (stage III)	25	1976-96 without 1979-82 & 1984[1)]	0.26	0.044
late egg production (stage III)	larval abundance	25	1976-96 without 1979-82 & 1984[1)]	0.13	0.173
larval abundance	0-group recruitment	25	1976-95	0.64	<0.001
0-group recruitment	1-group recruitment	25	1976-95	0.98	<0.001

2. Rationale for the work and specific issues to be studied

The main aim of this PhD study was to investigate larval stage processes potentially influencing recruitment in Baltic cod. The specific focus was 1) to substantiate the importance of starvation-induced mortality during the larval stage, that was suggested in previous modelling studies, with empirical data from a field setting and 2) assess the potential impact of egg and larval mortality through predation by a new invertebrate ichthyoplankton predator in the Baltic sea ecosystem, the recently introduced invasive alien ctenophore *M. leidyi*.

Despite the apparent influence of processes during the larval stage in shaping the recruitment dynamics of Baltic cod, information on larval survival from field studies is scarce. Exceptions are the studies by Grønkjær et al. (Grønkjær et al. 1997, Grønkjær & Wieland 1997, Grønkjær & Schytte 1999), who found that in order to find sufficient prey, larvae need to conduct an ontogenetic upward migration from hatching depths at ca. 60 m to depths of 20-40 m, and that larvae in this layer showed better condition than larvae at larger depths, and a study by Voss et al. (2001) who investigated larval mortality rates based on abundance data from consecutive ichthyoplankton surveys. Besides, laboratory studies on larval cod behaviour demonstrated that low oxygen concentration has an impact on larval mortality (Nissling 1994) and that egg incubation at low oxygen impacts on larval activity as well (Rohlf 1999). Furthermore, these experiments revealed that vertical migration into upper water layers is not started before day 4 after hatch. Hence, a significant impact of the environment within and below the halocline on larval survival can be expected.

Furthermore, a series of studies approached the issue of larval survival success with several biophysical modelling exercises (Voss et al. 1999, Hinrichsen et al. 2001b, Hinrichsen et al. 2002a, Hinrichsen et al. 2003, Hinrichsen et al. 2005, Schmidt & Hinrichsen 2008). Results from these modelling studies suggested that retention and dispersal of early life stages from the spawning ground and food availability for larvae, especially during the first feeding stage, are influencing survival success. This emphasizes the importance of processes related to the critical period and match-mismatch hypotheses. While Cushings original match-mismatch hypothesis mainly focussed on a temporal overlap of predator and prey, a spatial overlap, both on the horizontal and the vertical plane, is also necessary for a “match” as neither fish larvae nor their zooplankton prey are evenly distributed in space (Letcher & Rice 1997).

As Baltic cod expresses an extremely protracted spawning season and shifts in peak spawning times (Wieland et al. 2000) and the cod spawning grounds in the Baltic show a high degree of environmental heterogeneity (MacKenzie et al. 2000, Hinrichsen et al. 2007), the importance of both spatial and temporal aspects for a match or mismatch situation can not be stressed enough for the larvae of this stock. Especially the spatio-temporal match of abundances of *Pseudocalanus acuspes* nauplii, the preferred prey item of larval Baltic cod (Voss et al. 2003), and of larvae in the critical first feeding stage are likely to be a necessary prerequisite for enhanced larval survival. The lack of inflow events described above did not only have negative effects on the oxygen environment, but also affected the Baltic zooplankton community through associated decreases in salinity. Standing stocks of *Pseudocalanus acuspes*, an oceanic copepod species adapted to higher salinities, were drastically reduced in the past decades, while overall abundances of *Acartia spp.*, a more neritic species, increased due to increasing temperatures (Fig. 11, Moellmann et al. 2000, ICES 2008b).

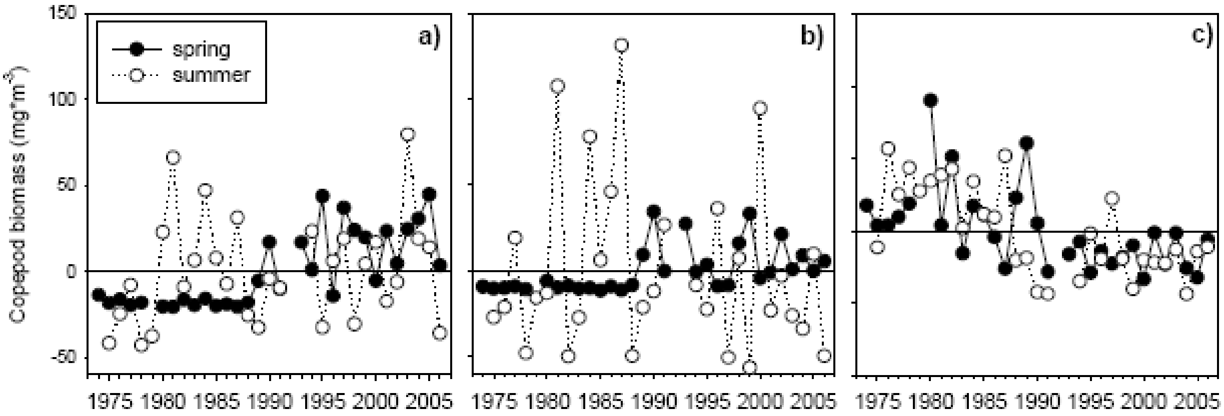


Fig. 11: Changes in zooplankton species composition in the central Baltic Sea: Anomalies of (a) *Acartia spp.*, (b) *Temora longicornis*, and (c) *Pseudocalanus acuspes* in spring and summer (from ICES 2008b).

A biophysical modelling study by Hinrichsen et al. (2002a) suggested that first feeding larvae of Baltic cod have indeed changed from a non-limited to a food-limited stage during the 1990's. If *P. acuspes* was available in the modelled prey fields, food limitation occurred only late in the spawning season. Prey fields without *P. acuspes* resulted in higher survival at the beginning and the end of the spawning season, and at the edges of the spawning ground in the Bornholm Basin. Higher survival early in the spawning season is caused in the model by lower temperatures on average and related lower food requirements for sustaining standard metabolism. Higher survival later in the spawning season is due to an increased abundance of nauplii of other copepod species, and enhanced transport into productive shallow-water areas.

Interannual variability in larval survival from peak spawning activity as derived by coupled model runs (Hinrichsen et al. 2002a) suggested low survival from 1993 to 1997, with the exception of 1996. The latter can be explained by relatively high wind speeds affecting transport and prey encounter via turbulence, below average temperatures, and relatively high availability of *P. acuspes*.

Recent model simulations with directly observed prey fields for 1999 demonstrated that early-hatched cod larvae were not food limited, whereas late hatched survivors were transported to coastal areas because of insufficient food supply in the centre of the basin (Schmidt and Hinrichsen 2008). In general, there was no starvation mortality of individuals spawned in April and May 1999, whereas survival of larvae hatched in June-August decreased to about 60%. The high survival of early-hatched larvae contradicts earlier model results for the 1990s (Hinrichsen et al. 2002a). This may indicate either an improvement of food availability from the mid- to the late-1990s, or that prey fields used in the earlier coupled model runs were underestimated.

At a recent workshop on the Advancements in Modelling Physical-Biological Interactions in Fish Early-Life History (ICES 2006), the tremendous developments in bio-physical models of fish early life, and their contributions to studying recruitment processes, were pointed out (Gallego et al. , Miller 2007). However, emphasis was also put on the issue of an increasing need for model validation, which is especially crucial for any model that will be used for practical applications or to provide advice (Hannah 2007).

Thus, one task of this PhD study was to evaluate the applicability of hydrodynamic modelling to reliably simulate drift patterns of Baltic cod up to the pelagic juvenile stage. This was done by comparing and quantifying the overlap of juvenile distributions from drift simulations with catch distributions from field sampling (paper 1).

Results from previous biophysical model simulations (Hinrichsen et al. 2002) were tested in a field setting by investigating the temporal and spatial origin of actual fish caught in field surveys (paper 1). The approach used is based on a characteristics of survivors analysis (Rice et al. 1987, Fritz et al. 1990, Taggart & Frank 1990). The basic idea of this approach is that survivors are not a random subset of the offspring, but have emerged through selective sources of mortality related to the environment and/or inter-individual variability of certain characteristics that gave them an advantage over their conspecifics during early life. While the vast majority of studies examined survivor characteristics in terms of growth and/or temporal origin (e.g., Rice et al. 1987, Meekan & Fortier 1996, Hare & Cowen 1997, Limburg et al. 1999, Nielsen & Munk 2004, Meekan et al. 2006, Shoji & Tanaka 2006, Fox et al. 2007, Gagliano et al. 2007, Baumann et al. 2008), only relatively few attempts have been made to relate survivors to their spatial origin (e.g., Suthers et al. 1989, Marteinsdottir et al. 2000, Thorrold et al. 2001, Irigoien et al. 2008). However, recent advances in hydrodynamic modelling allow survivors to be connected to certain areas by backtracking their drift routes (e.g., Allain et al. 2003). Such an approach is undertaken in the present study. In particular, analysis of otolith microstructure

(Stevenson & Campana 1992) was combined with hydrodynamic modeling, aiming to track fish that had survived up to the juvenile stage back to their spatio-temporal hatch origin.

The knowledge of age and growth of fishes is fundamental to fishery science. Otoliths came into use to age fish when Reibisch in 1899 first observed annular rings in *Pleuronectes platessa* (Ricker 1975). A major breakthrough in recruitment studies was Pannella's (1971, 1974) detection of a daily increment pattern in otoliths. This enabled age estimations of fishes less than one year of age that had not expressed an annual mark yet. Furthermore, it enabled calculations of growth rates, differences in which may have a profound influence on larval survival (Houde 1987).

Otolith-based growth characteristics of pelagic juveniles were compared with larvae from similar hatching times (paper 2), as larvae after the first feeding stage may be affected by selective processes described in the "growth-mortality hypothesis" (Anderson 1988). Larvae able to exploit superior food resources in terms of number and/or quality are likely to experience a growth advantage which allows them to advance faster to more developed, less vulnerable stages, thereby reducing the risk of mortality due to starvation or predation.

In addition to the known horizontal and long-term variability in the zooplankton community, detailed information on the stage-resolved vertical distribution of major Baltic copepod species has recently become available (Renz & Hirche 2006, Schmidt 2006). The vertical distribution of prey organisms obviously may have a significant influence on larval cod feeding and survival success in dependence of their vertical position in the water column.

Thus, another objective was to resolve the vertical distribution of cod larvae and spatial differences in larval condition and growth in the vertical plane (paper 3). Vertically resolved sampling of larval cod was conducted with multiple opening-closing nets. Condition and growth of individual larvae were determined on the basis of RNA-DNA ratios. Furthermore, growth performance was estimated by relating RNA-DNA derived growth rates to reference growth rates from laboratory studies.

The experiences from previously invaded areas resulted in serious concerns about the impact of *M. leidyi* on the Baltic Sea ecosystem and its fish stocks, especially because semi-enclosed seas like the Baltic are known to have a higher sensitivity to the influence of invasive species (Caddy 1993). Indeed, Haslob et al. (2007) provided first evidence for a vertical overlap of *M. leidyi* and eggs of cod and, to a lesser extent, sprat in the central Bornholm Basin, and for predation of the ctenophore on fish eggs (Fig. 8). They hypothesized that this overlap may result in reduced recruitment success of these fish stocks due to predation by *M. leidyi* on their early life stages, as well as by competition for zooplankton food, influencing the survival success of fish larvae.

However, these overlap calculations need to consider the co-occurrence of predator and prey in time and space, on both the horizontal and the vertical plane. Therefore, studies on the seasonal and spatial abundance and distribution of the new invader *M. leidyi* in relation to the ambient hydrography in the Bornholm Basin were conducted (papers 4-6). Furthermore, the horizontal and vertical overlap with early life stages of the commercially important Baltic fish species cod and sprat were investigated to assess the potential impact on fish recruitment via predation on eggs and larvae (paper 6).

3. Summary of results and conclusions

The suitability of hydrodynamic modeling for drift simulations of early life stages of Baltic cod up to the pelagic juvenile stage was validated, and marked spatial differences in survival depending on larval hatch locations were found (paper 1). Besides, results indicate temporal, but less clear, patterns in larval survival.

Even though it was not possible to directly relate larval survival with zooplankton abundances, the good agreement of results from this field investigation with earlier bio-physical modeling studies allows to conclude that survival was probably related to food availability for early larvae. This provides empirical support for the importance of the critical period and match-mismatch hypotheses in the recruitment process of Baltic cod. Furthermore, it can be concluded that a retrospective analysis of survivor origin by coupling otolith analysis and hydrodynamic modeling provides a valuable tool for recruitment studies and for evaluating the design and performance of Marine Protected Areas established to secure undisturbed spawning of marine fish stocks.

Pelagic juveniles were found to have larger hatch-checks than larvae and to have grown faster during the first weeks of life (paper 2), but the exact mechanisms behind this observation remain elusive. Possible explanations are maternal effects on growth performance, selection for faster growth during early life, or better environmental conditions for individual sub-cohorts. Besides, growth rate estimates for larval and pelagic juvenile cod were obtained, which provide valuable input for modeling studies.

Even though the exact causes and consequences behind the observation of faster growth of pelagic juveniles during the larval stage in Baltic cod could not be clarified, these findings provide empirical indications for the importance of feeding/growth-related processes during the larval stage in shaping recruitment dynamics.

The need for Baltic cod larvae to conduct an ontogenetic vertical migration to depths of peak nauplii abundances was corroborated (paper 3). However, size-dependent vertical distribution suggests that the ontogenetic migration may continue, with larger larvae following increasingly larger prey items to increasing depths.

In comparison with mesocosm and field studies from other areas, Baltic cod larvae expressed generally poor nutritional condition and growth. Furthermore, results show significant growth differences between larvae in relation to their size and their vertical and horizontal catch locations, likely caused by strong vertical and horizontal gradients in ambient temperatures and prey availability. This indicates food limitation and severe starvation, especially for early larvae in the deeper parts of the Bornholm Basin. Estimations of growth performance based on laboratory-derived reference growth rates from the literature likely provide an objective measure for the condition of larval fish and are considered a valuable tool for recruitment studies.

From comparison with results from mesocosms and other field studies, as well as an earlier study on larval Baltic cod growth and condition, it is concluded that starvation-induced larval mortalities have a high potential to regulate recruitment variability in Baltic cod.

The distribution and abundance of the invasive ctenophore *Mnemiopsis leidyi* and thus the predation risk on ichthyoplankton in the Bornholm Basin were found to show strong seasonal variations (papers 4-6). The spatial distribution of *M. leidyi* is probably governed by the ambient environment, in particular by vertical temperature gradients.

Overlap of the ctenophore with fish larvae was generally low due to a vertical mismatch in distributions of predator and potential prey. Concerning the overlap with eggs, comparatively high overlap values with sprat eggs were found in spring. However, *M. leidyi* largely disappeared from the Bornholm Basin during summer, resulting in low overlap values during the peak spawning periods of both sprat and cod. Besides, in comparison with other native and exotic habitats, abundances of *M. leidyi* in the Bornholm Basin were generally low.

It is concluded that the overall predation risk by *M. leidyi* on ichthyoplankton and the influence on the recruitment of Baltic fish stock can presently be regarded as low.

4. General conclusions and perspectives

Previous studies have identified high egg mortalities, caused by unfavourable environmental conditions and fish predation, to influence recruitment success of Baltic cod. This PhD has shown that larval survival has the potential to introduce additional variability in year-class strength, not only during the period of first feeding but also at later larval stages, and it can be concluded that incorporating larval-stage processes into environmentally sensitive stock-recruitment models will likely improve our predictive abilities of the stock development of Baltic cod. However, one future challenge will be to quantify the relative importance of processes during the different egg and larval stages in determining recruitment variability.

Having further shown severe larval starvation as well as spatial and temporal differences in survival, another future aim should be to directly relate larval condition, growth and survival to prey availability. Although such attempts have proven to be difficult, the strong spatio-temporal patterns in both larval vital rates as well as the zooplankton community give reason to hope that it may be possible to find such relationships in the Baltic ecosystem.

Furthermore, spatio-temporal patterns in the survival of different life stages may aid in evaluating and improving the design of management measures such as area- and season-closures (Friedlander et al. 2003, Hinrichsen et al. 2009, Kraus et al. 2009), e.g. to effectively protect those spawning adults that are likely to produce viable offspring (paper 1). In fact, the presently enforced MPA in the Bornholm Basin may not only be ineffective, but even counterproductive in its attempt to ensure undisturbed spawning and enhance recruitment. As shown from Vessel-Monitoring-System (VMS) data (Fig. 12), fishing effort is displaced to areas outside the MPA. However, if survivors actually originate from areas outside the MPA, as shown in paper 1, this may result in increased fishing mortality on fish that contribute proportionally more to successful recruitment than their conspecifics spawning inside the MPA.

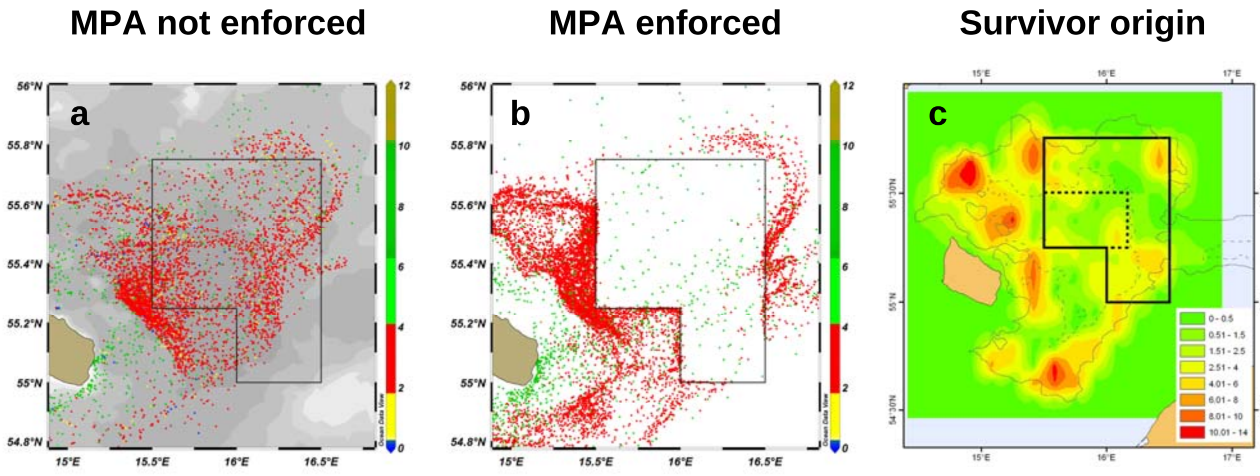


Fig. 12: Possible negative effects of inappropriate MPA placement. The black area marks the extent of the presently enforced MPA in the Bornholm Basin, red dots in a and b denote typical trawling speeds of fishing vessels from VMS data (Boettcher, pers. data), red shading in c shows areas where juvenile survivors originate (paper 1). Inappropriate MPA design may lead to a displacement of fishing effort to areas of high survival probability, e.g. north of Bornholm Island. (Note: survivor origin in c was determined for 2000, while VMS data in a & b are from 2004 as no earlier VMS data are available).

In any case, the study of larval growth performance and especially analyses of survivor characteristics are considered valuable methods for such future investigations and for the study of larval-stage recruitment processes in general. However, in the case of Baltic cod, the applicability of these approaches in practice, i.e. in a field setting, is complicated by the extremely protracted and variable spawning season and the switching from a pelagic to a demersal stage during juvenile life. This causes severe sampling-related problems for birth date analyses. For example, due to the fact that pelagic and demersal juveniles are targeted with different gears having different catchability, the relative importance of early and late survivors for the strength of a year-class is difficult to quantify. Thus, especially the seasonal variability in larval survival awaits further substantiation. Preliminary results show significant differences in larval RNA/DNA ratios between different sampling months (Fig. 13, Huwer & Clemmesen unpubl. data), but it remains to be clarified if these differences persist after conversion of RNA/DNA ratios to specific growth rates and growth performance, and whether they can be related to ambient prey fields.

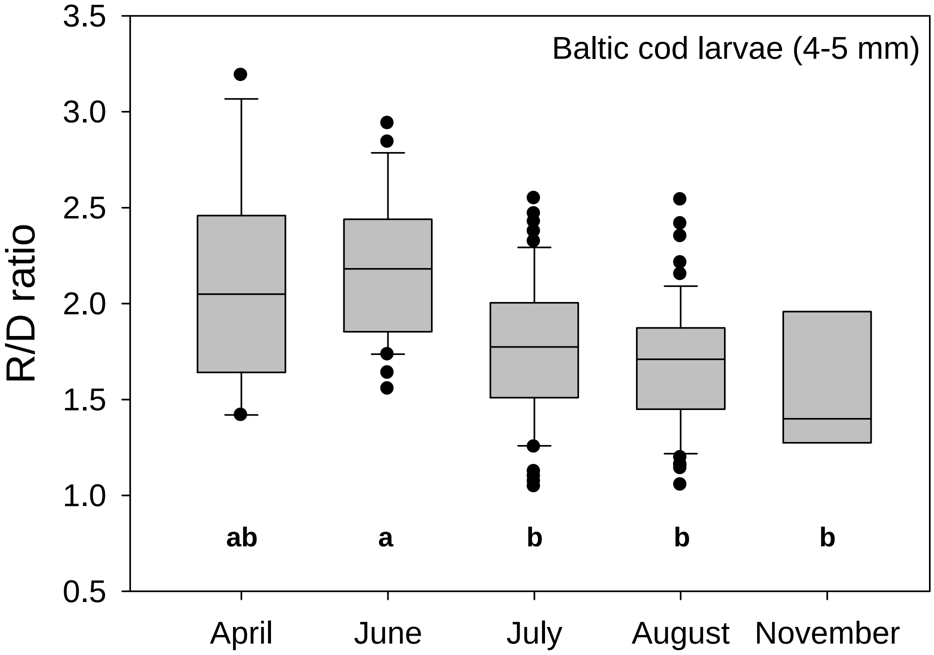


Fig. 13. Seasonal differences in RNA/DNA ratios of Baltic cod larvae (months sharing the same letter are not significantly different from each other).

In addition to food availability, food quality may be of importance for recruitment success. Baltic larval cod are selectively feeding on all stages of *Pseudocalanus acuspes* (Voss et al. 2003) and bio-physical modelling studies suggested food limitation for first feeding larvae due to low abundances of *P. acuspes* nauplii (Hinrichsen et al. 2002a, Hinrichsen et al. 2003, Hinrichsen et al. 2005, Schmidt & Hinrichsen 2008), which was further substantiated by the field studies in this PhD.

Model results further predicted that larger larvae beyond the first feeding stage were not food limited due to the presence of other calanoid copepod species (*Temora longicornis* and *Acartia spp.*) as alternative prey (Hinrichsen et al. 2002a). However, this conclusion may be biased, as *P. acuspes* has a higher nutritional value than the other Baltic calanoid copepods (Peters et al. 2006, Peters 2006), and the sharp reduction in standing stocks of this species (Moellmann et al. 2000, ICES 2008b) might have resulted in a situation were growth and mortality in larval Baltic cod is not only governed by food abundance but also by food quality.

Recently, it was found that food quality for adult Baltic cod impacts gonadal maturation via the lack of essential fatty acids, which is probably mediated through changes in the phyto- and zooplankton community (Tomkiewicz et al. 2009). A lack of essential fatty acids may also affect the development and vital rates of larvae. This quality aspect in larval diets certainly requires further investigation, especially the question if and how essential *P. acuspes* actually is for larval Baltic cod nutrition. Laboratory experiments on this issue have so far been prevented by the inability to maintain cultures of the Baltic *P. acuspes* in the laboratory. Nevertheless, strong correlations between larval cod growth and *Pseudocalanus sp.* in other cod stocks, e.g. on Georges Bank (Buckley & Durbin 2006), indicate that this copepod may represent an essential dietary component for larval cod development, growth and survival.

Furthermore, a back-shift to earlier spawning dates, for which indications were e.g. found in this PhD, and changes in zooplankton bloom timing (Dutz, in prep.) may affect survival chances for early life stages. Also the predation impact by sprat may be subjected to spatio-temporal changes, as there are signs for earlier sprat spawning (Huwer, pers. obs.), earlier sprat migration out of the Bornholm Basin spawning area (Haslob pers. obs.) and an apparent general shift of sprat biomass to eastern and northern areas of the Baltic Sea (ICES 2008a).

Although the influence of cannibalism on juveniles is considered minor at the present low stock-size (Koester et al. 2003a, Koester et al. 2005), spatio-temporal variability in mostly density-dependent processes affecting juvenile survival are also possible. Variable drift during the larval stage results in different juvenile settling areas, and there are indications for spatial differences in settling abilities due to low oxygen concentrations (Hinrichsen et al., in prep.) as well as density-dependent food competition (Huessy et al. 2003) and cannibalism (Uzars & Plikshs 2000). Larval drift to western areas may e.g. lead to density-dependent competition with juveniles of the western stock, which may already occupy the available settling habitats due to their earlier spawning time. Juvenile-stage processes may be additionally affected by habitat characteristics. Bottom types in Swedish coastal areas are e.g. mainly comprised of rock, stone and pebbles, while sandy areas prevail at the Polish coast (Al-Hamdani Z. & Reker J. 2007). This may cause differences in the composition of juvenile prey items, as well as differential possibilities to hide and may thereby lead to variable exposure to predation by adult cod (Lough et al. 1989, Ciannelli et al. 2007). On the temporal scale, later spawned cohorts may experience higher juvenile mortalities due to lower over-winter survival (for review, see Sogard 1997). Such a process may be investigated by comparing otolith-based hatch dates of juveniles caught in fall and in spring, i.e. before and after the potential over-winter mortality.

Even though it was concluded that the overall predation risk by *Mnemiopsis leidyi* on ichthyoplankton and the influence on fish stock recruitment can be regarded as low at present, the unknown further development and effect of *M. leidyi*, and jellyfish in general, should be considered. Summer-time abundances of *Aurelia aurita* seem e.g. to have increased during recent years (Huwer, Haslob and Schaber, pers. obs.). A shift of Baltic cod peak spawning time to earlier months in the season, which was indicated in this PhD, could lead to increasing overlaps between *M. leidyi* and cod early life stages in the future. Besides, ctenophore abundances may have been underestimated as the gears in use, traditional plankton nets, probably lead to mechanical damage and loss of specimens from the samples. Furthermore, gelatinous zooplankton is known to suddenly appear, forming dense patches, and equally rapidly disperse again. For instance, relatively dense aggregations were found in the Bornholmsgatt in immediate vicinity of the Bornholm Basin in August 2007.

While the focus of this work was on spatio-temporal overlap of adult *M. leidyi* as potential direct predator on ichthyoplankton, ctenophores and jellyfish could also indirectly affect larval fish survival via competition for food resources and thus intensify larval starvation. In fact, indications for food limitation in the larval stage exist for both cod (papers 1-3, Hinrichsen et al. 2002) and sprat (Voss et al. 2006), which may be intensified by competition with an additional zooplankton predator. Preliminary results (Huwer, Haslob and Schaber, unpubl. data) show that abundance peaks of ctenophore larvae are found in depth ranges where first feeding cod larvae are aggregating (paper 2, 3 & 6, Grønkjær et al. 1997). However, it remains to be clarified which ctenophore species these larvae actually belong to and if they have a competitive impact on larval fish survival.

Finally, it needs to be pointed out that future mass occurrences of *M. leidyi* in the central Baltic are possible. In the previously invaded Black Sea, the major population outbreak occurred ca. 8 years after the initial introduction, probably mediated by environmental and human disturbances on the ecosystem (Oguz et al. 2008). Thus, a future significant impact of the ctenophore on the recruitment success of the Eastern Baltic cod stock can not be excluded. As the introduction of this alien species into the Baltic Sea occurred only recently, intensive monitoring is suggested to follow the population dynamics of *M. leidyi* in the central Baltic Sea and to timely identify possible population outbreaks with potentially severe impacts on local fish stocks.

Recruitment studies often focus on the relation between the environment and recruitment time series, and although general relations of the plankton biomass and the recruitment of Baltic cod were investigated (Koester et al. 2005), the spatial component was not taken into account. It has always been a wish of fishery scientists to study recruitment by following the life cycle of a cohort from the egg to the adult (Cushing 1985). This is certainly a rather ambitious approach, however, recognizing the importance of spatial and temporal differences in early life stage survival, this may be the only way to advance our understanding of marine fish recruitment (Irigoien et al. 2008). Approaches to elucidate the importance of spatio-temporal origin for the fate of a year class by sampling of consecutive developmental stages have been exemplified in a number of studies (e.g., Meekan & Fortier 1996, Fortier & Quinonez-Velazques 1998, Limburg 2002, Allain et al. 2003, Lapolla & Buckley 2005, Meekan et al. 2006, Irigoien et al. 2008), even though they usually did not have to cope with such extensive spawning seasons as in Baltic cod.

Given the environmental heterogeneity in the Baltic, strong variations in primary and secondary production cycles, the variable and protracted spawning seasons of the main fish species, the multitude of factors potentially important for fish recruitment, as well as their spatial and temporal variability and interaction, a significant improvement in our understanding of their relative influence on recruitment variability can only be achieved by an extensive ecosystem survey. Such an effort should target all consecutive developmental stages from fish eggs to adults, as well as their prey and predators and the ambient environment, with a high temporal, horizontal and vertical resolution to further our understanding of the processes within and between different components of the Baltic Sea ecosystem.

As mentioned above, this would without doubt be an ambitious undertaking. However, a number of survey activities are already taking place in the Baltic Sea, targeting several ecosystem components from hydrography over zoo- and ichthyoplankton to adult fish, but their efficiency and coordination needs improvement. During the course of this PhD, I have e.g. introduced a plankton sampling program in the previously unutilized nighttime of the Danish contribution to the Baltic International Trawl (BITS) surveys. As this survey is conducted annually in March and November, this extended the seasonal coverage of plankton surveys conducted by the Leibniz-Institute of Marine Sciences in Kiel, Germany. Furthermore, I introduced sampling for pelagic juvenile cod on the November survey to re-initiate a series of similar surveys conducted in the 1990's (Boettcher et al. 1998, CORE 1998). Similar improvements on other ongoing surveys are certainly possible and could contribute to an ecosystem survey approach.

However, such a survey program will probably also have to include improvements in sampling strategy and technology. Especially our ability to quantitatively and representatively sample individual developmental stages of fish requires improvement, as they differ in size, motility and aggregation. The Bongo gear is suitable to sample eggs and early larvae, while the Isaacs-Kidd Midwater Trawl (IKMT) has proven to be a suitable gear to target the pelagic juvenile stage. Nevertheless, the catch per unit effort of larvae and pelagic juveniles is low, probably due to the scarcity of individuals surviving to these stages, and may need to be increased by applying new methodology. Larger larval size classes between metamorphosis (> 10-12 mm) and the pelagic juvenile stage (3-5 cm) are very difficult to sample. With the Bongo gear, larvae >10 mm are not sampled representatively. Due to the low abundances of these size classes and their increasing ability to avoid the Bongo gear, a gear sampling larger volumes of water may need to be applied. One possibility might be a large ring net, which has been successfully used to sample all cod size classes from 6 - 60 mm in the North Sea (Nielsen & Munk 2004).

Furthermore, detailed information on juvenile nursery areas is highly desirable but the ability to representatively sample demersal juveniles in the standard BITS surveys is questionable. As pointed out by Methven and Schneider (1998), habitat and size of juvenile cod change substantially after settlement and cohort size cannot be followed using a single gear. In fact, the standard assessment uses 2-group abundances from the BITS surveys as recruitment indicators, because the 0- and 1-groups are not thought to be sampled representatively, although a shift in survey gear in 2001 was introduced to increase catchability of age-group 1 in the BITS survey. Besides, spatial abundance peaks of juveniles may occur in areas that are not at all targeted by this bottom trawl survey, e.g. in coastal areas. As a matter of fact, dense coastal aggregations of juveniles have been reported for cod stocks in several other areas (Methven & Schneider 1998, Bjoernstad et al. 1999, Methven et al. 2003). This will require completely different sampling techniques. In Newfoundland (Methven & Schneider 1998, Methven et al. 2003) and Norway (Bjoernstad et al. 1999), e.g., high numbers of juvenile cod were successfully sampled by gears deployed from the coast, such as beach seines.

Due to the irregular occurrence and patchy distribution of gelatinous plankton, future studies on jellyfish and ctenophores in the Baltic will also need to include more sophisticated monitoring methods. Especially optical gears have the potential to improve the coverage in time and space and the reliability of abundance estimates. In inner Danish waters, e.g., good results were obtained in surveys utilizing a relatively simple towed camera system, the so-called “jelly-counter” (Per Andersen, Orbicon, pers. comm.).

Besides furthering our general understanding of ecosystem functioning, the suggested ecosystem survey could help to identify sensitive habitats and to design effective measures for their protection, such as closed seasons, no-take zones and Marine protected areas. Finally, this could provide important input for modeling studies on individual-, population- and ecosystem-level, which are likely to improve our predictive abilities for medium- to long-term fish stock and ecosystem development.

References

Al-Hamdani Z. and Reker J. 2007. Towards marine landscapes in the Baltic Sea. BALANCE interim report #10. Available at http://balance-eu.org/

Alheit J., Moellmann 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

Allain G., Petitgas P., Grellier P., Lazure P. (2003) The selection process from larval to juvenile stages of anchovy (*Engraulis encrasicolus*) in the Bay of Biscay investigated by Lagrangian simulations and comparative otolith growth. Fisheries Oceanography 12:407-455

Anderson J.T. (1988) A Review of Size Dependent Survival During Pre-Recruit Stages of Fishes in Relation to Recruitment. Journal of Northwest Atlantic Fishery Science 8:55-66

Arai M.N. (1988) Interactions of Fish and Pelagic Coelenterates. Canadian Journal of Zoology - Revue Canadienne de Zoologie 66:1913-1927

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, Finland

Bagge O., Thurow F., Steffensen E., Bay J. (1994) The Baltic cod. Dana 10:1-28

Bailey K.M., Houde E.D. (1989) Predation on eggs and larvae of marine fishes and the recruitment problem. Advances in Marine Biology 25:1-83

Bakun A., Beyer J., Pauly D., Pope J.G., Sharp G.D. (1982) Ocean Sciences in Relation to Living Resources. Canadian Journal of Fisheries and Aquatic Sciences 39:1059-1070

Balon E. K. (1984) Reflections on some decisive events in the early life of fishes. Transactions of the American Fisheries Society 113:178-185

Barz K., Hirche H.J. (2005) Seasonal development of scyphozoan medusae and the predatory impact of *Aurelia aurita* on the zooplankton community in the Bornholm Basin (central Baltic Sea). Marine Biology 147:465-476

Baumann H., Voss R., Hinrichsen H.H., Mohrholz V., Schmidt J.O., Temming A. (2008) Investigating the selective survival of summer- over spring-born sprat, *Sprattus sprattus*, in the Baltic Sea. Fisheries Research 91:1-14

Baumgartner T.R., Soutar A., Riedel W. (1996) Natural time scales of variability in coastal pelagic fish populations of the California Current over the past 1500 years: Response to global climate change and biological interaction. California Sea Grant. Biennial Report of completed Projects 1992-94. pp. 31-37

Beverton R.J.H., Holt S.J. (1957) On the dynamics of exploited fish populations. Fish.Invest.Ser.II Mar.Fish G.B., Ministry of Agriculture, Fisheries and Food, London 19:1-533

Bilio M., Niermann U. (2004) Is the comb jelly really to blame for it all? *Mnemiopsis leidyi* and the ecological concerns about the Caspian Sea. Marine Ecology Progress Series 269:173-183

Bjoernstad O.N., Fromentin J.M., Stenseth N.C., Gjoesaeter J. (1999) A new test for density-dependent survival: The case of coastal cod populations. Ecology 80:1278-1288

Bleil M., Oeberst R. (2002) Spawning areas of the cod stock in the western Baltic Sea and minimum length at maturity. Archive of Fishery and Marine Research 49:243-258

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

Boero F., Bouillon J., Gravili C., Miglietta M.P., Parsons T., Piraino S. (2008) Gelatinous plankton: irregularities rule the world (sometimes). Marine Ecology Progress Series 356:299-310

Boersma M., Malzahn A.M., Greve W., Javidpour J. (2007) The first occurrence of the ctenophore *Mnemiopsis leidyi* in the North Sea. Helgoland Marine Research 61:153-155

Boettcher U., Oeberst R., Mieske B. (1998) Daily vertical migration patterns of Baltic 0-group cod. ICES CM 1998/J:9

Buckley L.J., Durbin E.G. (2006) Seasonal and inter-annual trends in the zooplankton prey and growth rate of Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) larvae on Georges Bank. Deep Sea Research (Part II Topical Studies in Oceanography) 53:2758-244

Caddy J.F. (1993) Toward a comparative evaluation of human impacts on fishery ecosystems of enclosed and semienclosed seas. Reviews in Fisheries Science 1:57-95

Campana S.E. (1996) Year-class strength and growth rate in young Atlantic cod *Gadus morhua*. Marine Ecology Progress Series 135:21-26

Ciannelli L., Dingsor G.E., Bogstad B., Ottersen G., Chan K.S., Gjosaeter H., Stiansen J.E., Stenseth N.C. (2007) Spatial anatomy of species survival: Effects of predation and climate-driven environmental variability. Ecology 88:635-646

Ciechomski J.D., Weiss G. (1974) Studies on the food and feeding habits of larvae of the hake, *Merluccius merluccius hubbsi* and of the anchovy, *Engraulis anchoita* in the sea. Physis 33:199-208

CORE 1998. Mechanisms influencing long time trends in reproductive success and recruitment of Baltic Cod: Implications for fisheries management. EU-Project AIR CT94 1226, Final Report.

Cowan J.H., Houde E.D. (1992) Size-dependent predation on marine fish larvae by ctenophores, scyphomedusae and planktivorous fish. Fisheries Oceanography 1:113-126

Cowan J.H., Houde E.D. (1993) Relative Predation Potentials of Scyphomedusae, Ctenophores and Planktivorous Fish on Ichthyoplankton in Chesapeake Bay. Marine Ecology Progress Series 95:55-65

Cowan J.H.Jr., Shaw R.F. (2002) Recruitment. In: L.A.Fuiman and R.G.Werner (eds) Fishery Science. The Unique Contributions of Early Life Stages. Blackwell Science Ltd., Malden, MA (USA), p 88-111

Cushing D. H. (1974) The possible density-dependence of larval mortality and adult mortality in fishes. The early life history of fish.The Proceedings of an International Symposium held at the Dunstaffnage Marine Research Laboratory of the Scottish Marine Biological Association at Oban, Scotland, from May 17-23, 1973 :103-111

Cushing D.H. (1975) Marine ecology and fisheries. Cambridge Univ.Press, London, UK.

Cushing D. H. (1985) Had I but World Enough and Time…. ICES CM 1985/H:71

Cushing D.H. (1990) Plankton production and year-class strength in fish populations: An update of the match/mismatch hypothesis. Advances in Marine Biology 26:249-294

Daskalov G.M., Mamedov E.V. (2007) Integrated fisheries assessment and possible causes for the collapse of anchovy kilka in the Caspian Sea. ICES Journal of Marine Science 64:503-511

De Silva S.S., Baldontin F. (1974) Laboratory studies on food intake, growth and food conversion of young herring, *Clupea harengus* (L). Journal of Fish Biology 6:645-658

Eero M. (2008) Dynamics of the eastern Baltic cod (*Gadus morhus*) stock in the 20th century under variable climate and anthropogenic forcing. PhD thesis, University of Southern Denmark & National Institute of Aquatic Resources, Technical University of Denmark

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

Eero M., Koester F.W., MacKenzie B.R. (2008) Reconstructing historical stock development of Atlantic cod (*Gadus morhua*) in the eastern Baltic Sea before the beginning of intensive exploitation. Canadian Journal of Fisheries and Aquatic Sciences 65:2728-2741

Faasse M.A., Bayha K.M. (2006) The ctenophore *Mnemiopsis leidyi* A. Agassiz 1865 in coastal waters of the Netherlands: an unrecognized invasion? Aquatic Invasions 1:270-277

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.

Folkvord A. (2005) Comparison of size-at-age of larval Atlantic cod (*Gadus morhua*) from different populations based on size- and temperature-dependent growth models. Canadian Journal of Fisheries and Aquatic Sciences 62:1037-1052

Fortier L., Quinonez-Velazques C. (1998) Dependence of survival on growth in larval pollock *Pollachius virens* and haddock *Melanogrammus aeglefinus*: a field study based on individual hatchdates. Marine Ecology Progress Series 174:1-12

Fox C.J., Geffen A.J., Taylor N., Davison P., Rossetti H., Nash R.D. (2007) Birth-date selection in early life stages of plaice *Pleuronectes platessa* in the eastern Irish Sea (British Isles). Marine Ecology Progress Series 345:255-269

Fraser J.H. (1970) The Ecology of the Ctenophore *Pleurobrachia pileus* in Scottish Waters. ICES Journal du Conseil 33:149-168

Friedlander A., Nowlis J.S., Sanchez J.A., Appeldoorn R., Usseglio P., Mccormick C., Bejarano S., Mitchell-Chui A. (2003) Designing Effective Marine Protected Areas in Seaflower Biosphere Reserve, Colombia, Based on Biological and Sociological Information. Conservation Biology 17:1769-1784

Fritz E.S., Crowder L.B., Francis R.C. (1990) The National Oceanic and Atmospheric Administration plan for recruitment fisheries oceanography research. Fisheries 15:25-31

Gagliano M., McCormick M.I., Meekan M.G. (2007) Survival against the odds: ontogenetic changes in selective pressure mediate growth-mortality trade-offs in a marine fish. Proceedings of the Royal Society of London, Series B: Biological Sciences 274:1575-1582

Gallego A., North E.W., Petitgas P. Introduction: status and future of modelling physical–biological interactions during the early life of fishes. Marine Ecology Progress Series 347:121-126

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

Grønkjær P., Clemmesen C., St.John M.A. (1997) Nutritional condition and vertical distribution of Baltic cod larvae. Journal of Fish Biology 51:352-369

Grønkjær P., Schytte M. (1999) Non-random mortality of Baltic cod larvae inferred from otolith hatch-check sizes. Marine Ecology Progress Series 181:53-59

Hannah C.G. (2007) Future directions in modeling physical-biological interactions. Marine Ecology Progress Series 347:301-306

Hare J.A., Cowen R.K. (1997) Size, growth, development, and survival of the planktonic larvae of *Pomatomus saltatrix* (Pisces: Pomatomidae). Ecology 78:2415-2431

Haslob H., Clemmesen C., Schaber M., Hinrichsen H.H., Schmidt J.O., Voss R., Kraus G., Koester F.W. (2007) Invading *Mnemiopsis leidyi* as a potential threat to Baltic fish. Marine Ecology Progress Series 349:303-306

Hinrichsen H.H., Boettcher U., Oeberst R., Voss R., Lehmann A. (2001a) The potential for advective exchange of the early life stages between the western and eastern Baltic cod (*Gadus morhua* L.) stocks. Fisheries Oceanography 10:249-258

Hinrichsen H.H., St John M.A., Aro E., Grønkjær P., Voss R. (2001b) Testing the larval drift hypothesis in the Baltic Sea: retention versus dispersion caused by wind-driven circulation. ICES Journal of Marine Science 58:973-984

Hinrichsen H.H., Moellmann C., Voss R., Koester F.W., Kornilovs G. (2002a) Biophysical modeling of larval Baltic cod (*Gadus morhua*) growth and survival. Canadian Journal of Fisheries and Aquatic Sciences 59:1858-1873

Hinrichsen H.H., St.John M.A., Lehmann A., MacKenzie B.R., Koester F. (2002b) 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., Lehmann A., Moellmann C., Schmidt J. (2003) Dependency of larval fish survival on retention/dispersion in food limited environments: the Baltic Sea as a case study. Fisheries Oceanography 12:425-433

Hinrichsen H.H., Schmidt J.O., Petereit C., Moellmann C. (2005) Survival probability of Baltic larval cod in relation to spatial overlap patterns with their prey obtained from drift model studies. ICES Journal of Marine Science 62:878-885

Hinrichsen H.H., Voss R., Wieland K., Koester F., Andersen K.H., 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., Bottcher U., Koester F. (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

Hjort J. (1914) Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer 20:1-228

Houde E.D. (1976) Critical food levels for growth and survival of laboratory-reared larvae of three species of subtopical marine fishes. Joint Oceanographic Assembly; Edinburgh (UK); 13 Sep 1976. Book of Abstracts of papers presented at Joint Oceanographic Assembly, Edinburgh, UK, 13-24 Sept 1976.

Houde E.D. (1986) Potential for growth, duration of early life stages and regulation of recruitment in marine fish. ICES CM 1986/L:28

Houde E.D. (1987) Fish early life dynamics and recruitment variability. American Fisheries Society Symposium Series 2:17-29

Houde E.D. (1997) Patterns and trends in larval-stage growth and mortality in teleost fish. Journal of Fish Biology 51:52-83

Huessy K., Mosegaard H., Hinrichsen H.H., Boettcher U. (2003) Using otolith microstructure to analyse growth of juvenile Baltic cod *Gadus morhua*. Marine Ecology Progress Series 258:233-241

Hunter J.R. (1981) Feeding Ecology and Predation of Marine Fish Larvae. In: R.Lasker (ed) Marine Fish Larvae: Morphology, Ecology and Relation to Fisheries. Washington Sea Grant, University of Washington Press, Seattle, WA (USA), p 33-76

Huwer B., Storr-Paulsen M., Riisgård H.U., Haslob H. (2008) Abundance, horizontal and vertical distribution of the invasive ctenophore *Mnemiopsis leidyi* in the central Baltic Sea, November 2007. Aquatic Invasions 3:113-124

ICES (2004) Report of the Study Group on Closed Spawning Areas of Eastern Baltic Cod (SGCSA). ICES Council meeting documents, ICES CM 2004/ACFM:17

ICES 2005. Spawning and life history information for North Atlantic cod stocks. ICES Cooperative Research Report, No. 274. 152 pp.

ICES (2006) Report of the Workshop on Advancements in Modelling Physical-Biological Interactions in Fish Early-Life History: Recommended Practices and Future Directions (WKAMF), 3-5 April, Nantes, France. ICES CM 2006/OCC:05

ICES 2008a. Report of the Baltic International Fish Survey Working Group (WGBIFS). 31 March - 4 April 2008, Gdynia, Poland. ICES CM 2008/LRC:08

ICES 2008b. Report of the Working Group on Integrated Assessment of the Baltic Sea (WGIAB). ICES, Baltic Committee CM 2008/BCC:04

ICES 2009. Report of the Baltic Fisheries Assessment Working Group. Copenhagen, 22-28 April 2009. ICES CM 2009/ACOM:07

Irigoien X., Cotano U., Boyra G., Santos M., Alvarez P., Ibaibarriaga L. (2008) From egg to juvenile in the Bay of Biscay: spatial patterns of anchovy (*Engraulis encrasicolus*) recruitment in a non-upwelling region. Fisheries Oceanography 17:446-462

Ivanov V., Kamakin A.M., Ushivtzev V.B., Shiganova T.A., Zhukova O., Aladin N., Wilson S.I., Harbison G.R., Dumont H.J. (2000) Invasion of the Caspian Sea by the comb jellyfish *Mnemiopsis leidyi* (Ctenophora). Biological Invasions 2:255-258

Javidpour J., Sommer U., Shiganova T. (2006) First record of *Mnemiopsis leidyi* A. Agassiz 1865 in the Baltic Sea. Aquatic Invasions 1:299-302

Kaendler R. (1944) Untersuchungen über den Ostseedorsch während der Forschungsfahrten mit dem R.F.D. „Poseidon" in den Jahren 1925-38. Berichte der Deutschen Wissenschaftlichen Kommission fuer Meeresforschung 11:137-245

Kideys A.E. (2002) Fall and rise of the Black Sea ecosystem. Science 297:1482-1484

Kideys A.E., Niermann U. (1993) Intrusion of *Mnemiopsis mccradyi* (Ctenophora; Lobata) into the Mediterranean Sea. Senckenbergiana Maritima 23:43-47

Kideys A.E., Roohi A., Bagheri S., Finenko G., Kamburska L. (2005) Impacts of Invasive Ctenophores on the Fisheries of the Black Sea and Caspian Sea. Oceanography 18

Kjesbu O.S., Witthames P.R., Solemdal P., Walker M.G. (1990) Ovulatory Rhythm and A Method to Determine the Stage of Spawning in Atlantic Cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciences 47:1185-1193

Koester F.W., Schnack D. (1994) The role of predation on early life stages of cod in the Baltic. Dana 10:179-201

Koester F.W., Moellmann C. (2000) Trophodynamic control by clupeid predators on recruitment success in Baltic cod? ICES Journal of Marine Science 57:310-323

Koester F.W., Hinrichsen H.H., St John M.A., Schnack D., MacKenzie B.R., 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

Koester F.W., Hinrichsen H.H., Schnack D., St John M.A., MacKenzie B.R., Tomkiewicz J., Moellmann C., Kraus G., Plikshs M., Makarchouk A., Aro E. (2003a) Recruitment of Baltic cod and sprat stocks: identification of critical life stages and incorporation of environmental variability into stock-recruitment relationships. Scientia Marina 67:129-154

Koester F.W., Moellmann C., Neuenfeldt S., Vinther M., StJohn M. A., Tomkiewicz J., Voss R., Hinrichsen H. H., Kraus G., Schnack D. (2003b) Fish stock development in the Central Baltic Sea (1976-2000) in relation to variability in the physical environment. ICES Marine Science Symposia 219:294-306

Koester F.W., Moellmann C., Hinrichsen H.H., Wieland K., Tomkiewicz J., Kraus G., Voss R., Makarchouk A., MacKenzie B.R., St.John M.A., Schnack D., Rohlf N., Linkowski T., Beyer J.E. (2005) Baltic cod recruitment - the impact of climate variability on key processes. ICES Journal of Marine Science 62:1408-1425

Koester, F.W., Vinther, M., MacKenzie, B.R., Eero, M., Plikshs, M. (2009) Environmental Effects on Recruitment and Implications for Biological Reference Points of Eastern Baltic Cod (*Gadus morhua*). Journal of Northwest Atlantic Fishery Science 41: 205–220

Kraus G., Mueller A., Trella K., Koester F.W. (2000) Fecundity of Baltic cod: temporal and spatial variation. Journal of Fish Biology 56:1327-1341

Kraus G., Pelletier D., Dubreuil J., Moellmann C., Hinrichsen H.H., Bastardie F., Vermard Y., Mahevas 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

Kube S., Postel L., Honnef C., Augustin C. (2007) *Mnemiopsis leidyi* in the Baltic Sea – distribution and overwintering between autumn 2006 and spring 2007. Aquatic Invasions 2:137-145

Lambert Y., Yaragina N.A., Kraus G., Wright P.J. (2003) Using environmental and biological indices as proxies for egg and larval production of marine fish. Journal of Northwest Atlantic Fishery Science 33:115-159

Lapolla A., Buckley L.J. (2005) Hatch date distributions of young-of-year haddock *Melanogrammus aeglefinus* in the Gulf of Maine/ Georges Bank region: implications for recruitment. Marine Ecology Progress Series 290:239-249

Lasker R. (1975) Field criteria for survival of anchovy larvae - relation between inshore chlorophyll maximum layers and successful first feeding. Fishery Bulletin 73:453-462

Lasker R. (1981) The Role of a Stable Ocean in Larval Fish Survival and Subsequent Recruitment. In: R.Lasker (ed) Marine Fish Larvae - Morphology, Ecology, and Relation to Fisheries. Washington Sea Grant Program, Seattle, WA (USA), p 79-87

Lasker R., Zweifel J.R. (1978) Growth and survival of first-feeding northern anchovy larvae (*Engraulis mordax*) in patches containing different proportions of large and small prey. Spatial pattern in plankton communities. NATO Conf.Ser., pt.4, v.3. Plenum Press, New York, NY (USA), p 329-354

Lasker R., Parsons T.R., Jansson B.O., Longhurst A.R., Saetersdal G. (1978) The relation between oceanographic conditions and larval anchovy food in the California Current: identification of factors contributing to recruitment failure. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer 173:212-230

Lehtiniemi M. (2009a) Arctic comb jelly. The Baltic Sea Portal, p http://www.fimr.fi/en/tietoa/tulokaslajit/en_GB/arktinen-maneetti/.

Lehtiniemi M. (2009b) Last winter's ctenophore identified - they belong to an arctic species. Finnish environment institute (SYKE), http://www.environment.fi/default.asp?contentid=328915 &lan=en.

Lehtiniemi M., Pääkönen J.P., Flinkman J., Katajisto T., Gorokhova E., Karjalainen M., Viitasalo S., Björk H. (2007) Distribution and abundance of the American comb jelly (*Mnemiopsis leidyi*) – A rapid invasion to the northern Baltic Sea during 2007. Aquatic Invasions 2:272-276

Leppaekoski E., Gollasch S., Gruszka P., Ojaveer H., Olenin S., Panov V. (2002) The Baltic - a sea of invaders. Canadian Journal of Fisheries and Aquatic Sciences 59:1175-1188

Leppäranta M., Myrberg K. (2009) Physical Oceanography of the Baltic Sea. Springer, Berlin Heidelberg New York.

Letcher B.H., Rice J.A. (1997) Prey patchiness and larval fish growth and survival: Inferences from an individual-based model. Ecological Modelling 95:29-43

Levine J.M. (2008) Biological invasions. Current Biology 18:R57-R60

Limburg K.E. (2002) Cohort Identification. In: L.A.Fuiman and R.G.Werner (eds) Fishery Science. The Unique Contributions of Early Life Stages. Blackwell Science Ltd., Malden, MA (USA), p 143-160

Limburg K.E., Pace M.L., Arend K.K. (1999) Growth, mortality, and recruitment of larval *Morone spp.* in relation to food availability and temperature in the Hudson River. Fishery Bulletin 97:80-91

Link J.S., Bogstad B., Sparholt H., Lilly G.R. (2009) Trophic role of Atlantic cod in the ecosystem. Fish and Fisheries 10:58-87

Lischka M. (1999) Abundanz, Verteilung und Nahrungsökologie von Scyphomedusen in der zentralen Ostsee. MSc thesis, Christian-Albrechts University, Kiel, Germany

Lough R.G., Valentine P.C., Potter D.C., Auditore P.J., Bolz G.R., Neilson J.D., Perry R.I. (1989) Ecology and distribution of juvenile cod and haddock in relation to sediment type and bottom currents on eastern Georges Bank. Marine Ecology Progress Series 56:1-12

Lynam C.P., Heath M.R., Hay S.J., Brierley A.S. (2005) Evidence for impacts by jellyfish on North Sea herring recruitment. Marine Ecology Progress Series 298:157-167

MacKenzie B., St.John M.A., Wieland K. (1996) 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 B.R., St.John M.A., Plikshs M., Hinrichsen H.H., Wieland K. (1999) Oceanographic processes influencing seasonal and interannual variability in cod spawning habitat in the eastern Baltic Sea. ICES CM 1996/C+J:4

MacKenzie B.R., Hinrichsen H.H., Plikshs M., Wieland K., Zezera A.S. (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 B.R., Koster F.W. (2004) Fish production and climate: Sprat in the Baltic Sea. Ecology 85:784-794

Marteinsdottir G., Gunnarsson B., Suthers I.M. (2000) Spatial variation in hatch date distributions and origin of pelagic juvenile cod in Icelandic waters. ICES Journal of Marine Science 57:1182-1195

Martindale M.Q. (1986) The Ontogeny and Maintenance of Adult Symmetry Properties in the Ctenophore, *Mnemiopsis mccradyi*. Developmental Biology 118:556-576

Martindale M.Q. (1987) Larval Reproduction in the Ctenophore *Mnemiopsis mccradyi* (Order Lobata). Marine Biology 94:409-414

Matthaeus W. (2006) The history of investigation of salt water inflows into the Baltic Sea - from the early beginning to recent results. Meereswissenschaftliche Berichte/Marine scientific reports, No. 65, Institut fuer Ostseeforschung - Warnemuende, Rostock, Germany

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

Matthaeus W., Schinke H. (1994) Mean atmospheric circulation patterns associated with major Baltic inflow. Deutsche Hydrographische Zeitung 46:321-338

Matthaeus W., Nausch G. (2003) Hydrographic-hydrochemical variability in the Baltic Sea during the 1990s in relation to changes during the 20th century. ICES Marine Science Symposia 219:132-143

Meekan M.G., Fortier L. (1996) Selection for fast growth during the larval life of Atlantic cod *Gadus morhua* on the Scotian shelf. Marine Ecology Progress Series 137:25-37

Meekan M.G., Vigliola L., Hansen A., Doherty P.J., Halford A., Carleton J.H. (2006) Bigger is better: size-selective mortality throughout the life history of a fast-growing clupeid, *Spratelloides gracilis*. Marine Ecology Progress Series 317:237-244

Meier H.E.M., Feistel R., Piechura J., Arneborg L., Burchard H., Fiekas V., Golenko N., Kuzmina N., Mohrholz V., Nohr C., Paka V.T., Sellschopp J., Stips A., Zhurbas V. (2006) Ventilation of the Baltic Sea deep water: A brief review of present knowledge from observations and models. Oceanologia 48:133-164

Methven D.A., Schneider D.C. (1998) Gear-independent patterns of variation in catch of juvenile Atlantic cod (*Gadus morhua*) in coastal habitats. Canadian Journal of Fisheries and Aquatic Sciences 55:1430-1442

Methven D.A., Schneider D.C., Rose G.A. (2003) Spatial pattern and patchiness during ontogeny: post-settled *Gadus morhua* from coastal Newfoundland. ICES Journal of Marine Science 60:38-51

Miller T.J., Crowder L.B., Marschall E.A. (1988) Larval Size and Recruitment Mechanisms in Fishes: Toward a Conceptual Framework. Canadian Journal of Fisheries and Aquatic Sciences 45:1657-1670

Miller T.J. (2007) Contribution of individual-based coupled physical-biological models to understanding recruitment in marine fish populations. Marine Ecology Progress Series 347:127-138

Mills C.E. (1995) Medusae, Siphonophores, and Ctenophores As Planktivorous Predators in Changing Global Ecosystems. ICES Journal of Marine Science 52:575-581

Mills C.E. (2001) Jellyfish blooms: are populations increasing globally in response to changing ocean conditions? Hydrobiologia 451:55-68

Moeller H. (1980) Scyphomedusa as predators and food competitors of larval fish. Meeresforschung 28:90-100

Moeller H. (1984) Reduction of a Larval Herring Population by Jellyfish Predator. Science 224:621-622

Moeller L.F., Riisgard H.U. (2007) Feeding, bioenergetics and growth in the common jellyfish *Aurelia aurita* and two hydromedusae, *Sarsia tubulosa* and *Aequorea vitrina*. Marine Ecology Progress Series 346:167-177

Moellmann C., Kornilovs G., Sidrevics L. (2000) Long-term dynamics of main mesozooplankton species in the central Baltic Sea. Journal of Plankton Research 22:2015-2038

Moellmann C., Kornilovs G., Fetter M., Koester F.W. (2005) Climate, zooplankton, and pelagic fish growth in the central Baltic Sea. ICES Journal of Marine Science 62:1270-1280

Mueller A. (1988) Vertical distribution of ichthyoplankton in the Bornholm Basin. Kieler Meeresforschungen, Sonderheft 6:341-347

Muus B.J., Nielsen J.G. (1999) Seafish. Blackwell Science, UK. 340 pp.

Neuenfeldt S., Koester F.W. (2000) Trophodynamic control on recruitment success in Baltic cod: the influence of cannibalism. ICES Journal of Marine Science 57:300-309

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

Nielsen E.E., Grønkjær P., Meldrup D., Paulsen H. (2005) Retention of juveniles within a hybrid zone between North Sea and Baltic Sea Atlantic cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciences 62:2219-2225

Nielsen R., Munk P. (2004) Growth pattern and growth dependent mortality of larval and pelagic juvenile North Sea cod *Gadus morhua*. Marine Ecology Progress Series 278:261-270

Nilsson L.A.F., Thygesen U.H., Lundgren B., Nielsen B.F., Nielsen J.R., Beyer J.E. (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. (1994) Survival of eggs and yolksac larvae of Baltic cod (*Gadus morhua* L.) at low oxygen levels in different salinities. ICES Marine Science Symposia 198:626-631

Nissling A., Kryvi H., Vallin L. (1994) Variation in egg buoyancy of Baltic cod *Gadus morhua* and its implications for egg survival in prevailing conditions in the Baltic Sea. 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

Oguz T., Fach B., Salihoglu B. (2008) Invasion dynamics of the alien ctenophore *Mnemiopsis leidyi* and its impact on anchovy collapse in the Black Sea. Journal of Plankton Research 30:1385-1397

Olenin S., Leppakoski E. (1999) Non-native animals in the Baltic Sea: alteration of benthic habitats in coastal inlets and lagoons. Hydrobiologia 393:233-243

Oliveira O.M.P. (2007) The presence of the ctenophore *Mnemiopsis leidyi* in the Oslofjorden and considerations on the initial invasion pathways to the North and Baltic Seas. Aquatic Invasions 3:185-189

Pannella G. (1971) Fish otoliths: daily growth layers and periodical patterns. Science (Wash.) 173:1124-1127

Pannella G. (1974) Otolith growth pattern: an aid in age determination in temperate and tropical fishes. In: T.B.Bagenal (ed) The aging of fish. Unwin Bros.Ltd.Surrey,England, p 28-39

Paulik G.J. (1973) Studies of the possible form of the stock-recruitment curve. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer 164:302-315

Pedersen T., Falk-Petersen I.B. (1992) Morphological changes during metamorphosis in cod (*Gadus morhua* L.), with particular reference to the development of the stomach and pyloric caeca. Journal of Fish Biology 41:449-461

Petereit C. (2004) Experimente zum Temperatureinfluss auf frühe Entwicklungsstadien des Ostseedorsches *Gadus morhua*. MSc thesis, Leibniz-Institut für Meereswissenschaften an der Christian-Albrechts-Universität zu Kiel, Germany

Peters J. (2006) Lipids in key copepod species of the Baltic Sea and North Sea – implications for life cycles, trophodynamics and food quality. PhD thesis, Department of Marine Zoology, University of Bremen, Germany

Peters J., Renz J., Beusekom J., Boersma M., Hagen W. (2006) Trophodynamics and seasonal cycle of the copepod *Pseudocalanus acuspes* in the Central Baltic Sea (Bornholm Basin): evidence from lipid composition. Marine Biology 149:1417-1429

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

Poulsen E.M. (1931) Biological investigations upon the cod in Danish waters. Meddelelser fra kommissionen for Danmarks Fiskeri- og Havundersøgelser, Serie Fiskeri, Bind IX, Nr. 1:1-148

Purcell J.E. (1997) Pelagic cnidarians and ctenophores as predators: Selective predation, feeding rates, and effects on prey populations. Annales de l'Institut Océanographique 73:125-137

Purcell J.E., Arai M.N. (2001) Interactions of pelagic cnidarians and ctenophores with fish: a review. Hydrobiologia 451:27-44

Purcell J.E., Breitburg D.L., Decker M.B., Graham W.M., Youngbluth M.J., Raskoff K.A. (2001a) Pelagic cnidarians and ctenophores in low dissolved oxygen environments: a review. In: Rablais N.N. and Turner R.E. (eds) Coastal Hypoxia: Consequences for Living Resources and Ecosystems, American Geophysical Union, Coastal and Estuarine Studies, vol 58, pp 77-100

Purcell J.E., Shiganova T.A., Decker M.B., Houde E.D. (2001b) The ctenophore *Mnemiopsis* in native and exotic habitats: US estuaries versus the Black Sea basin. Hydrobiologia 451:145-176

Purcell J.E., Decker M.B. (2005) Effects of climate on relative predation by scyphomedusae and ctenophores on copepods in Chesapeake Bay during 1987-2000. Limnology and Oceanography 50:376-387

Purcell J.E., Uye S., Lo W.T. (2007) Anthropogenic causes of jellyfish blooms and their direct consequences for humans: a review. Marine Ecology Progress Series 350:153-174

Renz J., Hirche H.J. (2006) Life cycle of *Pseudocalanus acuspes* Giesbrecht (Copepoda, Calanoida) in the Central Baltic Sea: I. Seasonal and spatial distribution. Marine Biology 148:567-580

Rice J.A., Crowder L.B., Holey M.E. (1987) Exploration of mechanisms regulating larval survival in Lake Michigan bloater: A recruitment analysis based on characteristics of individual larvae. Transactions of the American Fisheries Society 116:703-718

Ricker W.E. (1954) Stock and recruitment. Journal of the Fisheries Research Board of Canada 11:559-623

Ricker W.E. (1975) Computation and interpretation of biological statistics of fish populations. Bulletin of the Fisheries Research Board of Canada 191, 382 p.

Riisgård H.U., Bøttiger L., Madsen C.V., Purcell J.E. (2007) Invasive ctenophore *Mnemiopsis leidyi* in Limfjorden (Denmark) in late summer 2007 - assessment of abundance and predation effects. Aquatic Invasions 2:395-401

Rohlf N. (1999) Aktivität und Vertikalwanderung der Larven des Ostseedorsches *(Gadus morhua callarias)* während der Dottersackphase. PhD thesis, Institute of Marine Sciences, Kiel. Berichte Institut fuer Meereskunde Kiel 321, 60 pp.

Røllike Ditlefsen C. (2009) Feeding ecology of the american comb jelly *Mnemiopsis leidyi*. MSc thesis, Technical University of Denmark & University of Southern Denmark, 77 pp.

Rothschild B. (1986) Dynamics of marine fish populations. Harvard University Press, Cambridge.

Rothschild B.J., Osborn T.R. (1988) Small-scale turbulence and plankton contact rates. J.Plankton Res. 10:465-474

Rutherford E.S. (2002) Fishery Management. In: L.A.Fuiman and R.G.Werner (eds) Fishery Science. The Unique Contributions of Early Life Stages. Blackwell Science Ltd., Malden, MA (USA), p 206-221

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

Schinke H., Matthaeus W. (1998) On the causes of major Baltic inflows - an analysis of long time series. Continental Shelf Research 18:67-97

Schmidt J.O. (2006) Small and meso-scale distribution patterns of key copepod species in the Central Baltic Sea and their relevance for larval fish survival. PhD thesis, Christian-Albrechts-University, Kiel, Germany

Schmidt J.O., Hinrichsen H.H. (2008) Impact of prey field variability on early cod *Gadus morhua* larval survival: a sensitivity study of a Baltic cod Individual-based Model. Oceanologia 50:205-220

Schnack D. (1972) Nahrungsökologische Untersuchungen an Heringslarven. Berichte der deutschen wissenschaftlichen Kommission fuer Meeresforschung 22:273-343

Schneider G. (1999) Gelatinoeses Zooplankton - Materialsparende Leichtbauweise im Ozean. Biologie in unserer Zeit, 29.Jahrgang, Nr.2

Scura E.D., Jerde C.W. (1977) Various species of phytoplankton as food for larval northern anchovy, *Engraulis mordax*, and relative nutritional value of the dinoflagellates *Gymnodinium splendens* and *Gonyaulax polyedra*. Fishery Bulletin U.S. 75:577-583

Shepherd J.G. (1982) A versatile new stock-recruitment relationship for fisheries, and the construction of sustainable yield curves. ICES Journal of Marine Science (Journal du Conseil) 40:67-75

Shiganova T.A., Mirzoyan Z.A., Studenikina E.A., Volovik S.P., Siokou-Frangou I., Zervoudaki S., Christou E.D., Skirta A.Y., Dumont H.J. (2001) Population development of the invader ctenophore *Mnemiopsis leidyi*, in the Black Sea and in other seas of the Mediterranean basin. Marine Biology 139:431-445

Shoji J., Tanaka M. (2006) Growth-selective survival in piscivorous larvae of Japanese Spanish mackerel *Scomberomorus niphonius*: early selection and significance of ichthyoplankton prey supply. Marine Ecology Progress Series 321:245-254

Sinclair M., Iles T.D. (1985) Atlantic herring (*Clupea harengus*) distributions in the Gulf of Maine-Scotian Shelf area in relation to oceanographic features. Canadian Journal of Fisheries and Aquatic Sciences 42:880-887

Sogard S.M. (1997) Size-selective mortality in the juvenile stage of teleost fishes: A review. Bulletin of Marine Science 60:1129-1157

Soutar A., Isaacs J.D. (1974) Abundance of pelagic fish during the 19th and 20th centuries as recorded in anaerobic sediment off the Californias. Fishery Bulletin U.S. 72:257-273

Sparholt H. (1994) Fish species interactions in the Baltic Sea. Dana 10:131-162

Sparholt H. (1996) Causal correlation between recruitment and spawning stock size of central Baltic cod? ICES Journal of Marine Science 53:771-779

Stepputtis D. (2006) Distribution patterns of Baltic sprat (*Sprattus sprattus* L.) – causes and consequences. PhD thesis, Christian-Albrechts University, Kiel, Germany

Stevenson D.K., Campana S.E. ed. (1992) Otolith microstructure examination and analysis. Canadian Special Publication of Fisheries and Aquatic Sciences 117, 132 pp.

STORE (2003) Environmental and fisheries influences on fish stock recruitment in the Baltic Sea. EU-Project FAIR CT98 3959, Final Report, 401 pp.

Suthers I.M., Frank K.T., Campana S.E. (1989) Spatial Comparison of recent growth in postlarval Atlantic cod (*Gadus morhua*) off southwestern Nova Scotia: Inferior growth in a presumed nursery area. Canadian Journal of Fisheries and Aquatic Sciences 46:113-124

Taggart C.T., Frank K.T. (1990) Perspectives on larval fish ecology and recruitment processes: probing the scales of relationships. In: K.Sherman, L.M.Alexander, and B.D.Gold (eds) Large Marine Ecosystems: Patterns, Processes and Yields. American Association for the Advancement of Science, Washington, DC, p 151-164

Tendal O., Jensen K.R., Riisgard H.U. (2007) Invasive ctenophore *Mnemiopsis leidyi* widely distributed in Danish waters. Aquatic Invasions 2:455-460

Thaulow J. (2009) Genetic population structure of Atlantic cod (*Gadus morhua*) in the Baltic Sea. Msc thesis, Roskilde University, Roskilde, Denmark

Thompson B. M., Riley J. D. (1981) Egg and Larval Development Studies in the North Sea Cod (*Gadus morhua* L.). Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer 178:553-559

Thorrold S.R., Latkoczy C., Swart P.K., Jones C.M. (2001) Natal homing in a marine fish metapopulation. Science 291:297-299

Tomkiewicz J., Støttrup J.G., Jacobsen C., Røjbek M.C., Koester F. (2009) Influence of lipids and fatty acid composition on Baltic cod (*Gadus morhua* L.) maturation and timing of spawning. ICES CM 2009/C:10

Uotani I., Izuha A., Asai K. (1978) Food habits and selective feeding of anchovy larvae (*Engraulis japonica*). Bulletin of the Japanese Society for Fishery Science 44:427-434

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., Westin L. (1999) Potential factors influencing reproductive success of Baltic cod, *Gadus morhua*: a review. Ambio 28:92-99

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

Vinogradov M.E., Shushkina E.A., Musaeva E.I., Sorokin P.Y. (1989) Ctenophore *Mnemiopsis leidyi* (A. Agassiz) (Ctenophora, Lobata) - New Settlers in the Black-Sea. Okeanologiya 29:293-299

Voss R., Hinrichsen H.H., St.john M. (1999) Variations in the drift of larval cod (*Gadus morhua* L.) in the Baltic Sea: combining field observations and modelling. Fisheries Oceanography 8:199-211

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

Voss R., Koester F.W., Dickmann M. (2003) Comparing the feeding habits of co-occurring sprat (*Sprattus sprattus*) and cod (*Gadus morhua*) larvae in the Bornholm Basin, Baltic Sea. Fisheries Research 63:97-111

Voss R., Clemmesen C., Baumann H., Hinrichsen H.H. (2006) Baltic sprat larvae: coupling food availability, larval condition and survival. Marine Ecology Progress Series 308:243-254

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., Zuzarte F. (1991) Vertical distribution of cod and sprat eggs and larvae in the Bornholm Basin (Baltic Sea) 1987-1990. ICES CM 1991/J:37

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., 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 the timing of spawning of Baltic cod: possible causes and implications for recruitment. ICES Journal of Marine Science 57:452-464

Xian W.W., Kang B., Liu R.Y. (2005) Jellyfish blooms in the Yangtze Estuary. Science 307:41

PAPER 1

Characteristics of surviving juvenile Baltic cod I: field evidence for the critical period hypothesis?

B. Huwer[1,5], H.-H. Hinrichsen[2], U. Böttcher[3], R. Voss[4] and F. Köster[1]

[1] Technical University of Denmark, National Institute of Aquatic Resources, Charlottenlund Slot, Jægersborg Allee 1, DK-2920 Charlottenlund, Denmark

[2] Leibniz-Institute of Marine Research, IFM-GEOMAR, Duesternbrooker Weg 20, D-24105 Kiel, Germany

[3] Johann Heinrich von Thünen Institute (vTI), Institute of Baltic Sea Fishery, Alter Hafen Sued, D-18069 Rostock, Germany

[4] Sustainable Fisheries, Department of Economics, University of Kiel, Wilhelm-Seelig-Platz 1, D-24105 Kiel, Germany

[5] Aarhus University, Department of Biological Sciences, Finlandsgade 14, 8200 Aarhus N, Denmark

ABSTRACT

Characteristics of surviving juvenile Baltic cod in terms of their spatio-temporal origins were investigated by coupling otolith microstructure analysis and backtracking drift by hydrodynamic modelling. The suitability of hydrodynamic modeling for drift simulations of early life stages of Baltic cod up to the pelagic juvenile stage was validated by comparing model simulations with the catch distribution from a survey targeting pelagic juveniles. Marked spatial differences in survival in dependence of larval hatch locations were found, while indications for temporal differences in survival are less clear. The good agreement of results from this field investigation with earlier bio-physical modelling studies suggests that survival was related to food availability for first feeding larvae.

Key words: recruitment, otolith, microstructure analysis, age, hatch date, eggs, larvae, ichthyoplankton, hydrodynamic model, drift, spatial origin, MPA, marine protected area, Bornholm Basin

1. INTRODUCTION

Recruitment variability in marine fishes shows tremendous fluctuations (Rothschild 1986), and it is commonly accepted that this variability is caused to a considerable extend by processes during early life (Rothschild 1986, Houde 1987, Houde 1997). A variety of factors are acting on the vulnerable early life stages, including predation, starvation, diseases and advection to unsuitable areas (Houde 1987). Therefore, much fisheries research has focused on recruitment processes and has led to various hypotheses on mechanisms governing these processes. Different hypotheses focus on different processes, e.g. variable larval growth resulting in differential survival (“growth-mortality hypothesis” (Anderson 1988), drift to favourable or unfavourable areas (“member/vagrant hypothesis” (Sinclair & Iles 1985), or variable survival due to prey availability. Two of the most prominent hypotheses of the latter category, the “critical period” (Hjort 1914) and the “match-mismatch” (Cushing 1975) hypotheses, are closely related. While the match-mismatch hypothesis focuses on the temporal overlap of fish larvae and their prey, the critical period hypothesis can be seen as a special case of the former, where the importance of prey availability for first feeding larvae is emphasized. The various recruitment hypotheses should be regarded as different possible components of the recruitment process, with different magnitudes of influence depending on species, stock, area, season, environmental conditions and developmental stage (Anderson 1988).

In the case of Eastern Baltic cod (from now on referred to as Baltic cod), strong differences in recruitment success between the early 1980’s, a period of extremely high stock size, and the following decades, are obvious (Koester et al. 2005). Oxygen-related egg mortality, caused by a lack of formerly regular inflows of oxygen-rich water from the North Sea, is a major source of recruitment variability (Vallin et al. 1999, Koester et al. 2001, Koester et al. 2005). However, high numbers of eggs found in ichthyoplankton surveys after a strong inflow event in 1993 and subsequent years did not result in increased larval abundances and recruitment levels (Koester et al. 2005). Furthermore, recent estimates suggest improving recruitment despite apparently unfavourable environmental conditions for egg survival (ICES 2009). A possible explanation for these observations may be variable survival during the larval stage, and there are indeed indications that the early larval phase from hatch to well-established feeder is a critical early life stage of Baltic cod (Hinrichsen et al. 2002a, Koester et al. 2003).

Despite the apparent influence of processes during the larval stage in shaping the recruitment dynamics of Baltic cod, information on larval survival from field studies is scarce (Grønkjær et al. 1997, Grønkjær & Wieland 1997, Grønkjær & Schytte 1999, Voss et al. 2001). A series of studies approached the issue of larval survival success with biophysical modelling exercises (Voss et al. 1999, Hinrichsen et al. 2001, Hinrichsen et al. 2002a, Hinrichsen et al. 2003b, Hinrichsen et al. 2005, Schmidt & Hinrichsen 2008). Model results suggested that retention and dispersal of early life stages and food availability for larvae, especially during the first feeding stage, are influencing survival success, emphasizing the importance of processes related to the critical period and match-mismatch hypotheses.

While Cushings original match-mismatch hypothesis mainly focussed on a temporal overlap of predator and prey, a spatial overlap is also necessary for a “match”. The importance of both spatial and temporal aspects for a match or mismatch situation can not be stressed enough in the case of Baltic cod, as the cod spawning grounds in the Baltic show a high degree of environmental heterogeneity (MacKenzie et al. 2000, Hinrichsen et al. 2007), and Baltic cod expresses an extremely protracted spawning season with shifts in peak spawning times (Wieland et al. 2000). Especially the spatio-temporal match of abundances of *Pseudocalanus acuspes* nauplii, the preferred prey item of larval Baltic cod (Voss et al. 2003), and of larvae in the critical first feeding stage are likely to be a necessary prerequisite for high larval survival.

Due to a lack of inflow events and the associated decreases in salinity, standing stocks of *Pseudocalanus acuspes* were drastically reduced in the past decades (Moellmann et al. 2000). A biophysical modelling study by Hinrichsen et al. (2002a) suggested that first feeding larvae of Baltic cod have indeed changed from a non-limited to a food-limited stage. In simulations considering a prey field without *Pseudocalanus acuspes* as prey items, larvae that hatched late in the spawning season and at the edges of the spawning ground in the Bornholm Basin had considerably higher survival chances, the reason for this being the availability of nauplii of other copepod species. A more recent study (Hinrichsen et al. 2005) based on spatial overlap patterns of larvae and their prey indicated beneficial feeding conditions in the central spawning ground during summer, while late hatched larvae again had better survival chances at the edges of the basin.

ICES (2006) emphasized the increasing need for validation of coupled bio-physical models, which is especially crucial for any model that will be used for practical applications or to provide advice (Hannah 2007). Thus, the aim of the present study was to test the results from biophysical model simulations in a field setting by investigating the temporal and spatial origin of pelagic juvenile Baltic cod caught in field surveys. Besides, the applicability of the hydrodynamic model in use to reliably simulate drift patterns up to the pelagic juvenile stage was evaluated by comparing drift simulations with the catch distribution of juvenile fish from the field sampling. The approach used is based on a characteristics of survivors analysis (Rice et al. 1987, Fritz et al. 1990, Taggart & Frank 1990), which has gained increasing interest as a tool to investigate recruitment processes (Sogard 1997, Miller 2007). The basic idea of this approach is that survivors are not a random subset of the offspring, but have emerged through selective sources of mortality related to the inter-individual variability of certain characteristics. Thus, instead of trying to find possibly existing links between food availability, growth, predation, mortality and survival of larval fish, which has proven to be extremely difficult (Hunter 1981, Heath 1992), it should be investigated if surviving fish show certain traits that gave them an advantage over their conspecifics during early life. The vast majority of studies examined survivor characteristics in terms of growth and/or temporal origin (e.g., Rice et al. 1987, Hare & Cowen 1997, Limburg et al. 1999, Meekan et al. 2006, Shoji & Tanaka 2006, Fox et al. 2007, Gagliano et al. 2007, Baumann et al. 2008), including investigations on cod (Meekan & Fortier 1996, Nielsen & Munk 2004). Only relatively few attempts have been made to relate survivors to their spatial origin (e.g., Suthers et al. 1989, Marteinsdottir et al. 2000, Thorrold et al. 2001, Irigoien et al. 2008). While we examined growth selective survival during the early life of Baltic cod in a parallel investigation (paper 2), the present study focuses on survivor characteristics in terms of the temporal as well as spatial origin of juveniles. Recent advances in hydrodynamic modelling allow survivors to be connected to certain areas by backtracking their drift routes (e.g., Allain et al. 2003). A similar approach is undertaken in the present study. In particular, we coupled results from analyses of otolith microstructure and hydrodynamic modeling, aiming to track fish that had survived up to the juvenile stage back to their spatio-temporal hatch origin.

Our study investigates 1) the degree of overlap between simulated and observed distributions of juveniles, 2) the temporal origin of juvenile survivors and 3) the spatial origin of juvenile survivors. Hatch origins of survivors in the Bornholm Basin, the presently only spawning ground sustaining regularly successful egg development (Koester et al. 2005), are set in relation to the spawning effort and egg survival as determined by the abundance and distribution of early and late egg development stages and two different measures of egg survival probability. Results are discussed in relation to the recruitment process of Baltic cod, and possible implications for the placement of a Marine protected area in the Bornholm Basin, which was established in the mid 1990s to ensure undisturbed spawning of Baltic cod.

2. MATERIAL AND METHODS

2.1 Sampling procedure and laboratory analyses of ichthyoplankton and pelagic juveniles

Pelagic juvenile cod were sampled during a trawl survey with the German research vessel “Solea” in the southern Baltic Sea (Fig. 1) carried out from October 26 to November 11, 2000 by means of an Isaacs-Kidd-Midwater-Trawl (IKMT). A total of 268 pelagic juveniles were obtained. The catch distribution of these samples is depicted in Fig. 2. Samples were immediately frozen at minus 20°C for later investigation in the laboratory.

Ichthyoplankton samples were collected during cruises with the German research vessel “Alkor” in April, May, July and August 2000 in the Bornholm Basin. To investigate the horizontal distribution and abundance of ichthyoplankton, sampling was conducted with a Bongonet on a station grid with a regular spacing of approximately 10 nautical miles (Fig. 1). On each station a double oblique haul was performed at 3 knots ship speed. The two Bongonets (60 cm diameter each) were equipped with mesh sizes of 335 and 500 µm and with flowmeters to determine the volume of filtered water. The samples were preserved in 4% buffered formaldehyde/seawater solution. To obtain vertical profiles of the ambient environment, CTD casts were conducted on the sampling stations.

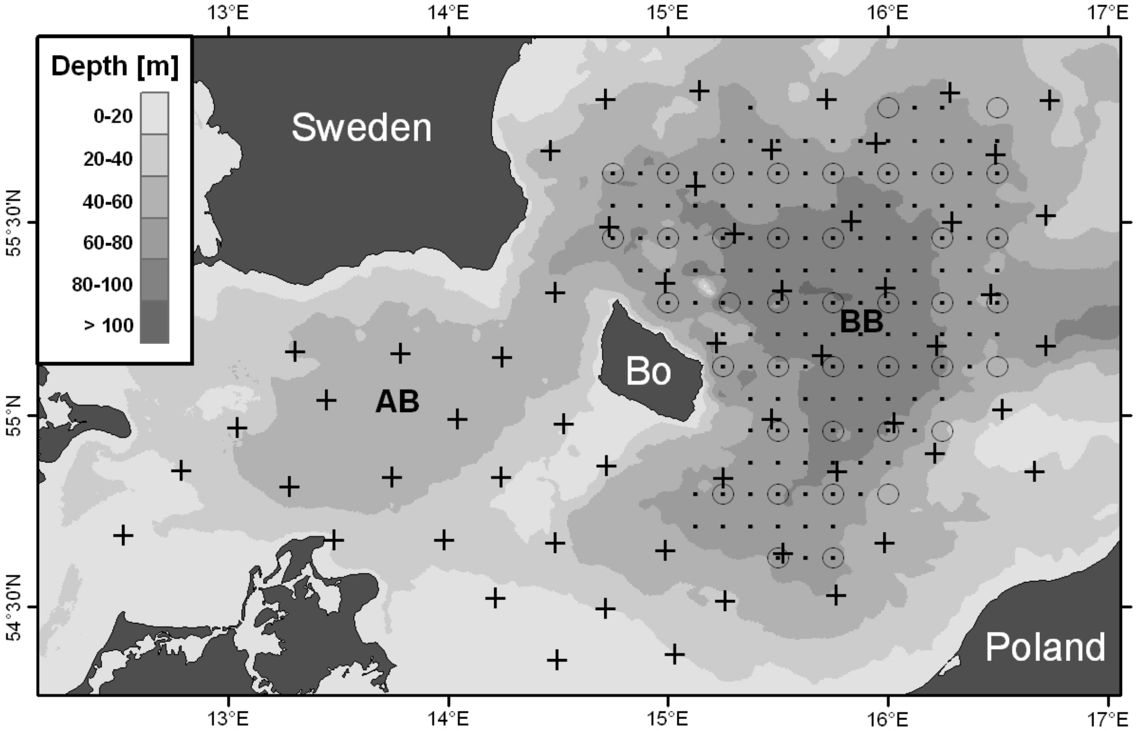


Fig. 1: Overview of the study area in the Baltic Sea. Sampling stations for pelagic juveniles (crosses, Isaacs-Kidd Midwater trawl) and ichthyoplankton (circles, Bongo net). The black dots depict the initial seeding positions for larval drifters in the hydrodynamic model. Bo = Bornholm Island, BB = Bornholm Basin, AB = Arkona Basin.

In the laboratory, standard length (SL), total length (TL) and wet weight of the pelagic juveniles were determined. Ichthyoplankton samples from the 335 µm Bongonets were analysed under a stereo microscope. Cod eggs were sorted from the samples, counted and staged. A subsample of at least 100 specimen was processed for staging using a 4 stage system based on morphological criteria (Thompson & Riley 1981) with stages Ia and Ib combined. The counts were finally standardized to 1 m² sea surface by the volume of filtered water and the maximum depth of the tow (~2 m above the ground).

2.2 Otolith analyses and determination of ages and hatching dates

The backcalculation approach used in the present study is strongly dependent on reliable age estimates. The daily nature of increment formation has been validated for cod (Radtke & Waiwood 1980, Radtke 1984, Campana 1989, Suthers & Sundby 1993, Geffen 1995, Suthers et al. 1999, Buehler 2004), including the stock in the Baltic (Clemmesen & Doan 1996), and daily increment deposition begins at the day of hatch. Thus, enumeration of growth increments in Baltic cod otoliths provides reliable estimates of age and hatch dates.

A subsample of pelagic juveniles was chosen for otolith age determinations to be used for the backcalculation of hatch dates and positions. This subsample (n = 135) was chosen in such a manner that the entire sampling area was covered (Fig. 2) and that the length distribution of the subsample resembled the length distribution of all available samples (Fig. 3). Sagittal otoliths of pelagic juveniles were removed, mounted on glass slides with thermoplastic cement and ground from both sides with different grades of lapping film (12 to 0.05 µm). Growth increments on the otoliths of the subsample were enumerated to determine the age of the fish. To resolve the fine innermost growth increments from the otolith core to the beginning of the secondary primordia, those primary increments were viewed at a magnification of 1512x. For the wider secondary growth increments, lower magnifications (480-960x) were found to be sufficient.

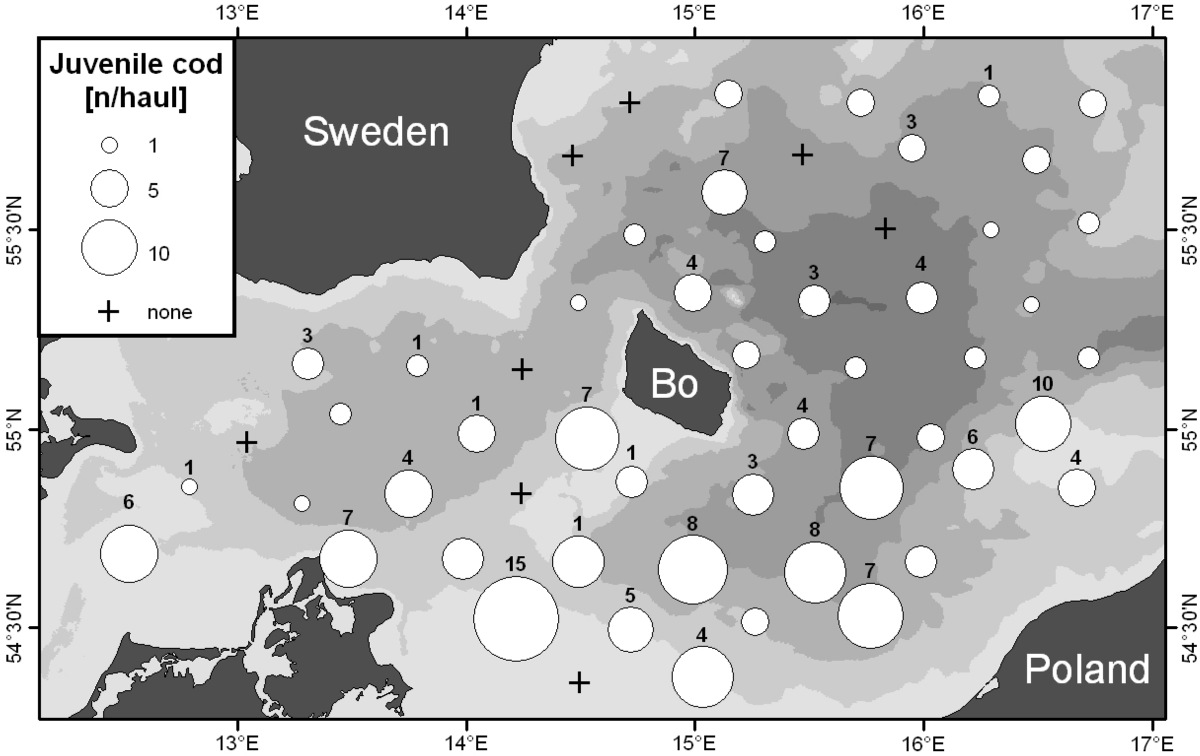


Fig. 2: Catch distribution of pelagic juvenile cod in November 2000. The size of the white circles indicates the number of juvenile cod per haul. Numbers on top of the symbols denote the numbers of juveniles selected for ageing by otolith analysis.

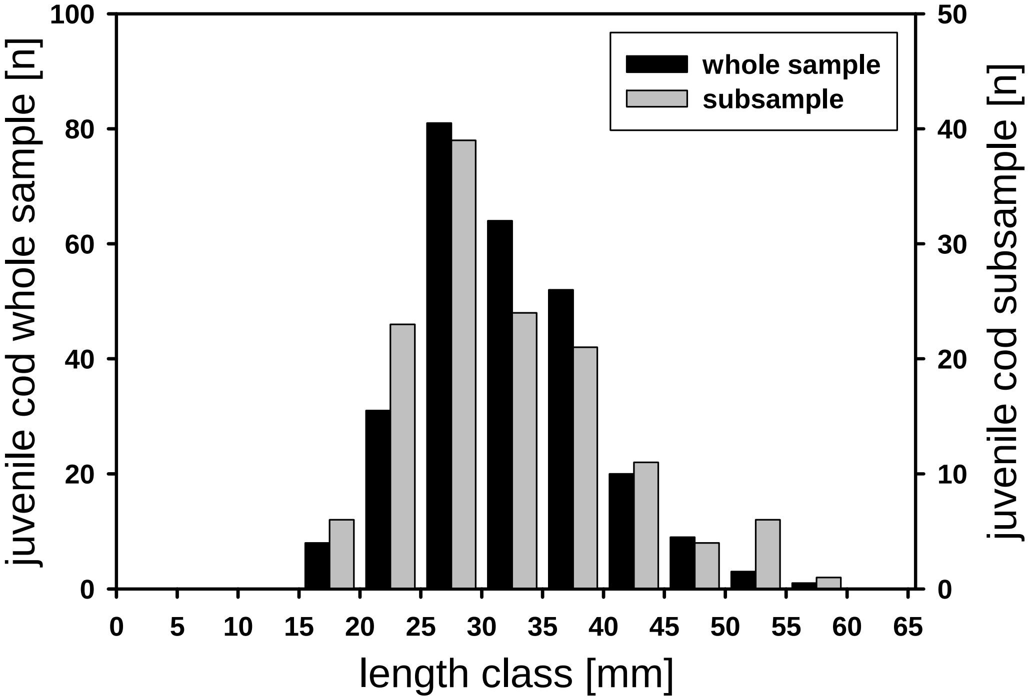


Fig. 3: Length frequency distribution of pelagic juvenile cod sampled in November 2000. Black bars = whole sample, n = 268. Grey bars = subsample that was aged by means of otolith microstructure analysis, n = 135.

The ages of all 268 fish in the entire sample was estimated on the basis of an age-length relationship obtained from the aged subsample (age = 1.1587*SL+34.632, r^2 = 0.786; paper 2). Hatch dates of all pelagic juveniles were calculated by subtracting the age of each fish from its catch date. To obtain the spawning date, an additional 10 days were subtracted to account for the development time of the eggs. This correction factor of 10 days was chosen because the ambient temperature at the usual residence depths of Baltic cod eggs (Wieland & Jarre-Teichmann 1997) in August 2000 was approximately 8°C (paper 2), and according to temperature dependent egg development times the duration from spawning to hatch for this temperature is about 10 to 11 days (Wieland et al. 1994, Petereit 2004).

The survey conducted in November 2000 was targeted at pelagic juveniles. However, at this time of the year part of the 0-group cod have already made the transition to a demersal life stage (Huessy et al. 1997, Huessy et al. 2003, Hinrichsen et al. 2003a). Thus, in order to evaluate the temporal origin of survivors, these fish need to be considered as well. Unfortunately, no otolith samples for demersal juveniles were available for the year 2000. However, length distribution data for demersal 0-group cod caught in November 2000 during the Baltic International Trawl Surveys (BITS) are available from ICES (http://datras.ices.dk/Home/default.aspx). These length distribution data and the established age-length relationship were used to backcalculate the hatch date distribution of demersal juveniles. As the length data from ICES were given in total length (TL), while the age-length key is based on standard length (SL), this was preceded by a conversion from TL to SL, based on a linear relationship obtained from measured TL and SL of pelagic juveniles ($SL=0.9181*TL-0.019$; $r^2 = 0.9978$). Fish with a total length of 4-13 cm were considered to belong to the 0-group. Only data for catch positions in ICES Subdivisions 25 and 26 east of Bornholm were considered, as those fish were assumed to belong to the eastern Baltic cod stock, while catches further west (Subdivision 24) probably mainly consist of fish belonging to the western stock.

An important issue for the back-calculation of birthdate distributions is the influence of age-selective mortality, which can result in a skew of backcalculated hatchdate distributions towards later spawned fish due to higher cumulative mortality of earlier spawned individuals. However, this effect is heavily diminished at older stages, because instantaneous mortalities decline exponentially from eggs to juveniles. Thus, the further the sampling and the spawning period are separated in time, the smaller the effect of differential cumulative mortalities becomes (Campana & Jones 1992). Accordingly, we assumed the bias due to differences in age and thus cumulative mortalities of early vs. late born juveniles to be negligible.

2.3 Baltic Sea model, comparison of pelagic juvenile catch distribution with seasonal larval drift patterns and backcalculation of hatch locations

2.3.1 Baltic sea model

The hydrodynamic model used in this study is based on the free surface Bryan-Cox-Semtner model (Killworth et al. 1991), which is a special version of the Cox numerical ocean general circulation model (Bryan 1969, Semtner 1974, Cox 1984). A detailed description of the equations and modifications required to adapt the model to the Baltic Sea can be found in Lehmann (1995) and Lehmann & Hinrichsen (2000b). A detailed analysis of the Baltic Sea circulation has been performed by Lehmann & Hinrichsen (2000a) and by Lehmann et al. (2002). Physical properties simulated by the hydrodynamic model agree well with known circulation features and observed physical conditions in the Baltic (for further description see Lehmann 1995, Hinrichsen & Voss 1997, Lehmann & Hinrichsen 2000b)). The model domain comprises the entire Baltic Sea including the Gulf of Bothnia, Gulf of Finland, Gulf of Riga as well as the Belt Sea, Kattegat and Skagerrak. The horizontal resolution is 5 km, with 60 vertical levels specified. The thickness of the different levels was chosen to best account for the different sill depths in the Baltic.

The Baltic Sea model is driven by atmospheric data provided by the Swedish Meteorological and Hydrological Institute (SMHI: Norrköping, Sweden) and river runoff taken from a mean runoff database (Bergstroem & Carlsson 1994). The meteorological database covers the whole Baltic Sea drainage basin with a grid of 1° x 1° squares. Meteorological parameters, such as geostrophic wind, 2-m air temperature, 2-m relative humidity, surface pressure, cloudiness and precipitation, are stored with a temporal increment of 3 h. Simulated three-dimensional velocity fields were extracted (at 6-h intervals) to develop a data base for a Lagrangian particle tracking exercise on larval cod. This data set offers the possibility to derive Lagrangian drift routes by calculating the advection of 'marked' water particles. Vertical velocities were calculated from the divergence of the horizontal velocity fields. The drifters were allowed to leave the layers where they were launched. The positions of the drifters varied over time as a result of the threedimensional velocities that they experienced.

To establish a Lagrangian view of the simulated circulation, drifters can be placed in the modelled flow fields at every location within the model domain. Moreover, the initial launch positions can be chosen independent of the vertical resolution of the model's grid. Simulated drift routes were obtained from Eulerian flow fields by utilisation of a Lagrangian particletracking technique. The three-dimensional trajectories of the simulated drifters were computed using a 4th order Runge-Kutta scheme (Hinrichsen & Voss 1997).

2.3.2 Comparison of pelagic juvenile catch distribution with seasonal larval drift patterns

The hydrodynamic model applied in this study has been successfully used for several other purposes, e.g. to investigate the general circulation in the Baltic, meso-scale processes, water mass exchange between North sea and Baltic, ice coverage, and drift studies (Lehmann 1995, Hinrichsen & Voss 1997, Lehmann & Hinrichsen 2000a, Lehmann & Hinrichsen 2000b, Hinrichsen et al. 2001, Hinrichsen et al. 2003b). However, when studying living organisms, hydrodynamic modeling might be complicated by the individual behaviour of the study organisms, i.e. the potential influence of larval and juvenile swimming activity. We hypothesize that individual larval and pelagic juvenile Baltic cod will only conduct small-scale movements in order to obtain prey, which does not have a significant influence on overall drift patterns. To support this hypothesis, we compare the catch distribution of pelagic juveniles from field sampling with spatial juvenile distributions obtained from hydrodynamic modeling exercises (e.g., Hinrichsen et al. 2003a, Hinrichsen et al. 2003b, Hinrichsen et al. 2009).

The hydrodynamic model on Baltic cod larval drift was utilized to investigate larval distribution and transport patterns during the cod spawning season 2000 in order to consider the seasonal variability in larval transports depending on the time of spawning. Lagrangian drifters were released on a regular spaced grid enclosed by the 60 m isobath encompassing the main spawning area in the Bornholm Basin (Fig. 1). A total of 720 drifters were released at 5 depths between 25 and 35 m. These depths were chosen on the basis of investigations on the vertical distribution of Baltic cod larvae, which have shown that the majority of feeding larvae occur at these depths after having conducted an ontogenetic vertical feeding migration (Grønkjær et al. 1997, Grønkjær & Wieland 1997). The grid for drifter release consisted of 144 stations (144 stations*5 depths = 720 drifters). Drifters were inserted into the modeled flow fields at 10-d intervals and tracked for 70 days, as the mean age of pelagic juvenile samples was found to be 72 days (see results). The release dates ranged from April 1 to September 20, thereby encompassing the historical as well as the present main spawning period of Baltic cod (Wieland et al. 2000). A detailed description of these model runs can be found in

In order to obtain an integrated view of drifter end positions after 70 days of drift, the area of the Baltic Sea was divided into a grid of rectangles by sub-dividing the ICES statistical rectangles into 4 smaller rectangles, thus creating rectangles of approximately 15x15 nautical miles. In this way the share of the 720 initially released drifters that ended in a certain rectangle after 70 days of drift could be determined, and this value was assigned to the position in the centre of each rectangle. This information was used to create distribution maps of simulated residence probability of drifter positions after 70 days. These simulation results were also compared with the catch distribution of pelagic juveniles by calculating an overlap-coefficient to quantify the closeness of agreement between simulated and observed distributions. This coefficient C (Horn 1966) is 0 when there is no overlap and 1 at concurrent distributions:

$$C = 2\sum_{i=1}^{n}(A_i \times B_i) \Big/ \left(\sum_{i=1}^{n} A_i^{\,2} + \sum_{i=1}^{n} B_i^{\,2} \right) \qquad (1)$$

where n is the number of strata (in this case the number of rectangles) and A and B are the relative abundances of simulated drifters and pelagic juveniles caught within each stratum. Only rectangles where survey hauls were conducted have been considered in this analysis, and in cases where more than 1 haul was conducted within a rectangle, an effort adjustment was applied by calculating the average number of juveniles caught within the respective rectangles.

2.3.3 Backcalculation of hatch locations

The model runs described in the previous section proved to be sufficient to simulate the general distribution of larvae and pelagic juveniles (see results). However, in order to determine the hatching locations of the aged subsample of pelagic juveniles, a higher temporal match between model start dates and juvenile hatch dates as well as end dates of model runs and juvenile catch dates was needed. Thus, another set of model runs was conducted. Back-calculated hatch dates from otolith analyses were used to define 5-day periods of particle release, while the duration of the model runs was determined by the day of juvenile catch. Back-tracked hatch locations were estimated by determining those drifters that were closest to individual juvenile catch positions at the time of catch. To account for variations of drift routes, the three drifters closest to each juvenile catch position were analysed. In order to obtain an integrated view of the hatch locations of survivors, the study area was divided into a grid of small rectangles by sub-dividing the ICES statistical rectangles into 36 smaller rectangles, thus creating a set of rectangles with a high spatial resolution of approximately 5 x 5 nautical miles. The number of backcalculated survivor hatch locations within each of these rectangles was determined and assigned to the position in the centre of each rectangle.

2.4 Determination of reproductive volume and oxygen-related egg survival

In contrast to other cod stocks, eggs from the Baltic cod stock do not float in the surface waters, but attain neutral buoyancy and peak abundances in the region of the permanent halocline, i.e. usually at depths > 50 meters (Wieland & Jarre-Teichmann 1997). Results from laboratory and field studies have determined salinities > 11 psu, oxygen contents > 2 ml l^{-1} and temperatures > 1.5°C to be the minimum requirements for successful development of Baltic cod eggs (Westin & Nissling 1991, Nissling 1994, Wieland et al. 1994). These minimum requirements form the basis for the calculation of the so called reproductive volume (RV), i.e. the volume of water that meets minimum requirements for successful cod egg development (Plikshs et al. 1993, Nissling et al. 1994). The extent of the RV depends on the frequency and the magnitude of inflows of oxygen rich, highly saline north sea water, as well as on the temperature of the inflowing water which influences oxygen solubility (Hinrichsen et al. 2002b), and oxygen consumption rates by biological processes (MacKenzie et al. 1996).
However, these estimates do not directly consider the environmental conditions inside the water volume that principally sustain egg development. Temperature-controlled laboratory experiments have shown the influence of oxygen concentration on the proportion of viable hatch in relation to the surviving fraction under normoxic conditions (Rohlf 1999). These experiments

confirmed that oxygen concentrations above the threshold level of 2 ml l^{-1} used to define the Baltic cod reproductive volume (RV) have a strong positive impact on egg survival. A sigmoidal oxygen–egg survival relationship can be applied to estimate the fraction of the egg production that will probably survive to the larval stage. Therefore, an index of oxygen-related egg survival (OES) has recently been developed (Koester et al. 2005), which incorporates not only the volume for potentially sustaining egg development, but provides a measure of the oxygen conditions within the salinity range over which cod eggs are neutrally buoyant.

The hydrographic data which provide the basis for the calculation of RV and OES were obtained on the ichthyoplankton sampling stations (Fig. 1). Physical parameters (conductivity, temperature and oxygen) of the water column were measured with CTD/O2 systems. Based on these measurements, we constructed maps of RV and OES by interpolating observed data onto a regular horizontal grid. For a detailed description of this procedure it is referred to Hinrichsen et al. (2007).

2.5 Application of back-calculated hatch positions for the evaluation of Marine protected areas

A marine protected area, in which any fishing activity is prohibited during part of the year, has been established in the Bornholm Basin of the Baltic Sea with the aim of protecting spawning aggregations of Baltic cod. This MPA was initially restricted to the central Bornholm Basin (1995-2003), and after a first enlargement towards the southeast in 2004, a further adaptation was made in 2005 to the presently enforced extent. Back-calculated hatch locations of surviving fish are set in relation to the extent of the MPA to evaluate its efficiency in protecting that part of the spawning stock which likely produces successful offspring.

3. RESULTS

3.1 Size and age of pelagic juveniles

Fish from the entire juvenile sample and the aged subsample had average lengths of 31.96 and 31.76 mm (SL) and 34.84 and 34.15 mm (TL), respectively (Fig. 3). As both the smallest and largest fish were included in the subsample, the length range of fish for both the entire and the subsample was 15.06 – 57.11 mm (SL) and 16.35 – 62.21 mm (TL). The wet weight range was 0.0176 – 1.7452 g, and the average wet weights for the entire and the subsample were 0.3345 and 0.3573 g, respectively. The age range of the subsample was 42 - 105 days, while the average was 71 days. The otolith age readings from the juvenile subsample were used to establish the following age vs. standard length relationship (see also Fig. 6 in paper 2):

$$\text{age} = 1.1587*\text{SL}+34.632 \quad (r^2 = 0.786) \qquad (2)$$

The ages of pelagic juveniles from the entire sample, which were obtained according to this age-length relationship, ranged from 52 – 101 days with an average of 72 days.

3.2 Back-calculated spawning dates of pelagic and demersal juveniles and seasonal egg abundance estimates

The back-calculated spawning date distributions of pelagic and demersal Baltic cod juveniles and seasonal egg stage 1 abundances from ichthyoplankton surveys are presented in Fig. 4. The sampled pelagic juveniles were spawned in the period from day of the year 197 to 248, i.e. from July 15 to September 4, 2000. The median hatch day was on August 14 (day of the year 227). The demersal juveniles originated from day 136 to 222, i.e. from May 15 to August 9, the median spawning day being on day 185 (July 3).

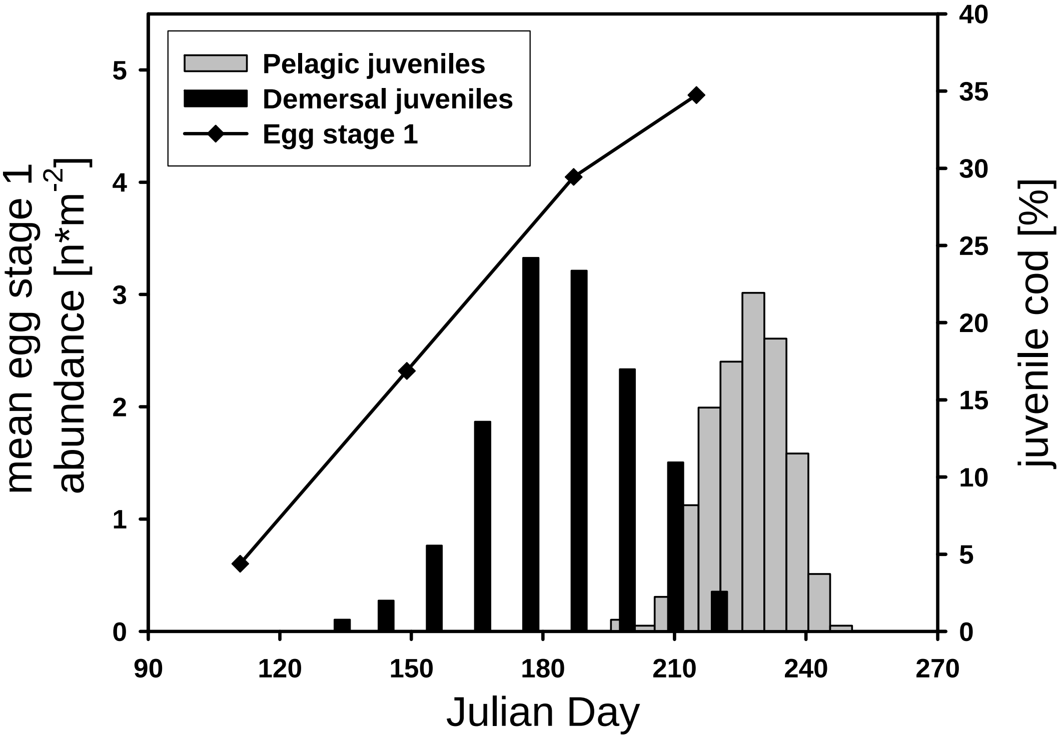


Fig. 4: Back-calculated spawning date distribution of pelagic (grey bars) and demersal (black bars) juveniles (spawning date = hatch date minus 10 days for egg development) in relation to seasonal average egg stage 1 abundance from ichthyoplankton surveys in the Bornholm Basin.

Abundance data of egg stage 1 from April, May, July and August show an increase in spawning effort throughout the season. Unfortunately, no ichthyoplankton sampling was conducted after August, where the highest egg abundances were found. However, results from a timeseries of ichthyoplankton data from the Bornholm Basin suggest that the sampling in august marked the abundance peak, and that spawning activity decreased remarkably shortly thereafter (Wieland et al. 2000, Kraus, pers. comm.).

3.3 Comparison between simulated and observed distribution of pelagic juvenile cod

Figure 5 depicts the simulated residence probabilities of drifters after 70 days drift duration as obtained from the Baltic Sea model simulations. Figures 5 a, b and c show results for drifters released in the early, mid and late spawning season 2000, respectively. In the early spawning season the majority of drifters experienced a slight northward transport towards the Swedish coast (Fig. 5a), while drifters were largely retained on the spawning ground in the Bornholm Basin in mid spawning season (Fig. 5b). Only in the late part of the spawning season were drifters advected into areas south and southwest of Bornholm. The late spawning season corresponds to the period of temporal origin of pelagic juvenile survivors (July 25 – September 14) that were sampled on the survey in November. A high spatial overlap between simulated residence probabilities

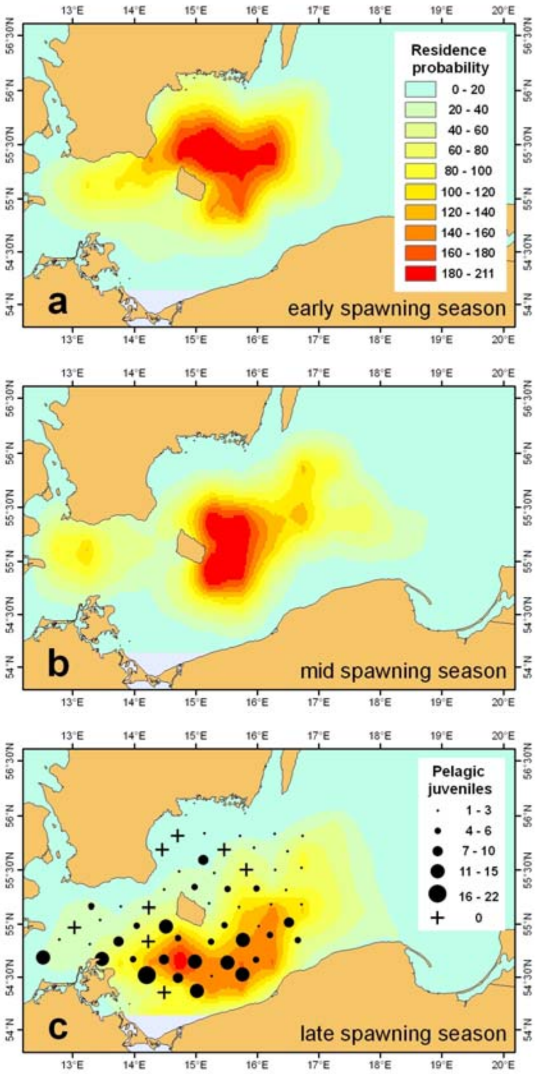


Fig. 5: Ability of the hydrodynamic model to simulate drift of larval and pelagic juvenile Baltic cod. The color scale depicts the simulated residence probability of drifters released on the spawning ground in the Bornholm Basin throughout the spawning season in the year 2000 after 70 days of drift. Drifters released in (a) the early spawning season (April 1 – May 21), (b) the middle of the spawning season (May 31 – July 20) and (c) the late spawning season (July 30 – September 18), corresponding to the period of back-calculated hatch dates of pelagic juveniles, in comparison with the catch distribution of pelagic juveniles from the survey in November 2000 (black circles). A high coefficient of overlap (0.83) shows a good agreement between simulated and observed juvenile distributions for the late spawning season.

of drifters (color scale) and the catch distribution of pelagic juveniles (black symbols) in the late spawning season is evident (Fig. 5c) and corroborated by a high overlap coefficient of 0.83.

3.4 Back-calculated hatch locations, egg distributions, reproductive volume and oxygen-related egg survival probability

Figure 6 shows the back-calculated hatch locations of pelagic juvenile cod in relation to i) depth ii) the simulated larval survival probability from an Individual-based model (Hinrichsen et al. 2002a), iii) abundance estimates of egg stages 1 and 4 from an ichthyoplankton survey in August 2000, iv) the extent of the reproductive volume and the oxygen-related egg survival probability, and v) the extent of a Marine protected area in the Bornholm Basin.

The color scale in Fig. 6a describes the distribution of back-calculated hatching positions of pelagic juveniles. Survivor hatch locations are generally located at the edges of the spawning area in the Bornholm Basin, while only a minor part of fish had hatched in the central deep basin. Only 18 % of survivors originated from the deepest central part of the basin where depths are exceeding 80 meters, while 82 % had hatched in areas with depths between 60 and 80 meters. Centres of survivor origin are located north and east of Bornholm and at the southern edge of the basin.

A comparison of the observed survivor origin in the year 2000 (Fig. 6a) with the modelled average survival probability of cod larvae for a situation of low *Pseudocalanus acuspes* abundance (Fig. 6b, redrawn after Hinrichsen et al. 2002a) shows a high degree of congruence. Especially apparent is the concurrence of high simulated survival probabilities with distinct centres of survivor origin in the northwestern regions of the spawning ground, north and east of Bornholm Island.

Figures 6c and 6d show the horizontal distribution of abundances of egg stages 1 and 4 in August 2000 in relation to the extent of the reproductive volume (RV) and to the oxygen-related egg survival probability (OES), respectively. Egg stage 1, as a proxy for spawning effort, is rather evenly distributed over the entire spawning ground, with slightly higher abundances in the northwestern part and at the southern and eastern edges. In contrast, the distribution of egg stage 4 shows very low abundances in the northwestern part of the area and higher abundances in the central, northeastern and southeastern regions.

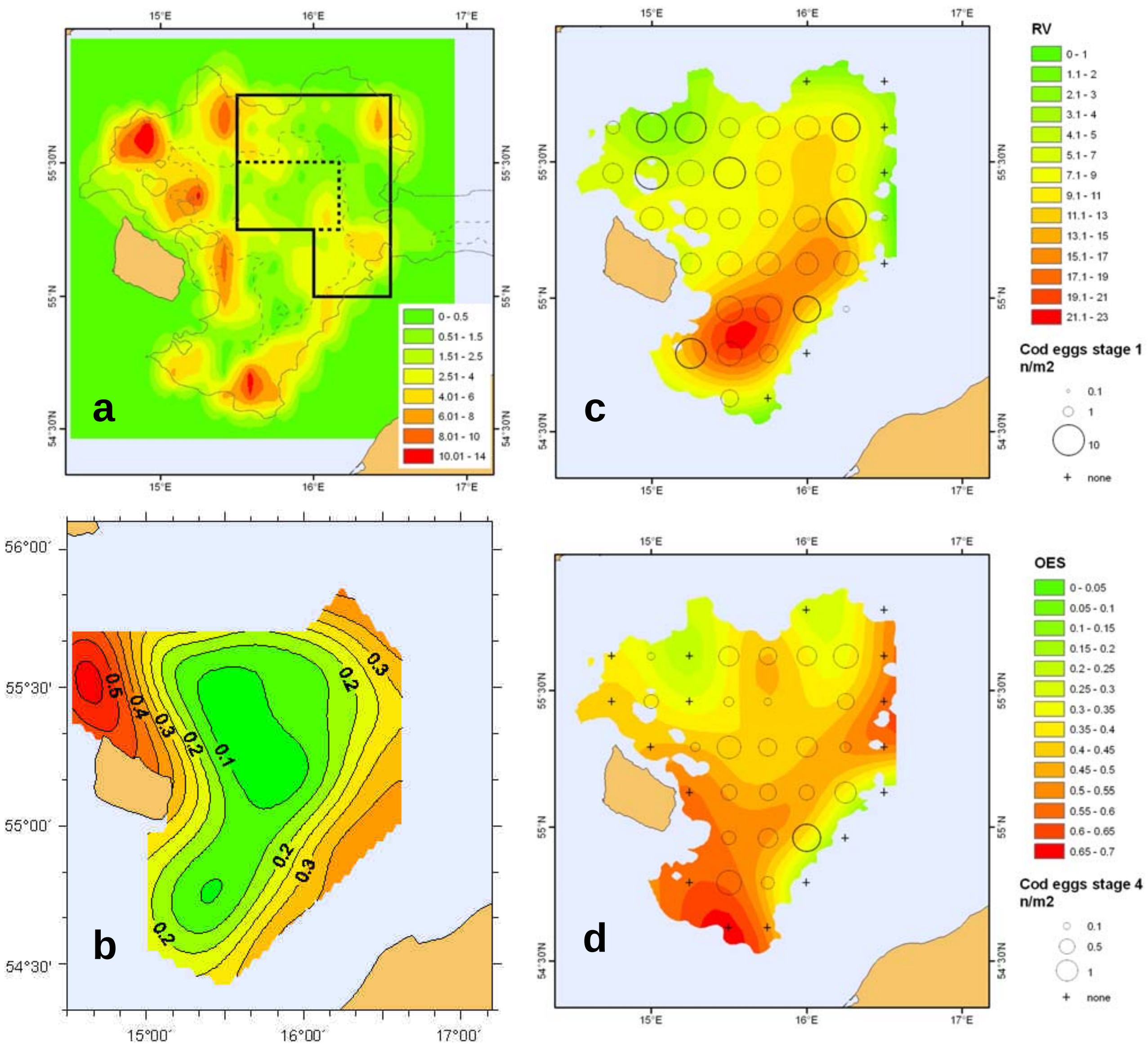


Fig. 6: Spawning activity and survival success of Baltic cod early life stages in the Bornholm Basin. a) Back-calculated hatch positions of pelagic juvenile survivors (color scale) and location of a Marine protected area (thick black lines, solid line = present extent, dashed line = extent in the year 2000). The thin grey lines demark the 60 (solid) and 80 (dashed) meter depth contours. b) Modelled average survival probability of Baltic cod larvae in a situation simulating low abundances of *Pseudocalanus acuspes* nauplii (after Hinrichsen et al. 2002). c) Thickness of the reproductive volume (RV; color scale, meters) and cod egg stage 1 distribution (circles, n*m^{-2}) in August 2000. d) Oxygen related egg survival probability (OES; color scale) and cod egg stage 4 distribution (circles, n*m^{-2}) in August 2000.

The thickness of the RV has its largest extent in the southern and eastern parts of the basin with high values of 15 to 23 meters in the southern and intermediate values between 11 and 15 meters in the northeastern areas (Fig. 7c). In contrast, the vertical extent of the reproductive volume in the northwestern area is considerably lower, ranging only from 1 to 9 meters. The OES shows a slightly different picture (Fig. 6d). Here, highest (0.7) and intermediate (0.4) values are also found in the southern and eastern parts of the spawning area, respectively. However, in contrast to the RV, higher OES values also prevail at the northern and especially eastern coast of Bornholm. Lowest egg survival probabilities of only 0.2-0.35 are consistent with the RV as proxy for egg survival found in the northwestern region.

4. DISCUSSION

We found marked differences in the survival of Baltic cod larvae in dependence of their spawning location, while the importance of temporal origin remains more elusive. Knowledge about the spatio-temporal origin of survivors in a year-class of fish provides important insight into possible factors influencing recruitment success (e.g. Marteinsdottir et al. 2000, Jenkins et al. 2000, Allain et al. 2003, Lapolla & Buckley 2005, Baumann et al. 2008).

4.1 Suitability of the hydrodynamic model to track larval and juvenile drift routes

The hydrodynamic model output was shown to correspond well with observed juvenile catch positions. Hence, there is a clear dependence of juvenile distribution on wind-induced drift, which is mainly controlled by the local atmospheric conditions over the Baltic Sea. This is also in accordance with earlier results by Hinrichsen et al. (2003a). The model appears to be capable of reproducing the drift of larval and pelagic juvenile Baltic cod, and thus appears to be suitable to determine hatch positions back-calculated from hatch dates of field samples.

4.2 Spatial origin of pelagic juvenile survivors

The finding that the vast majority of juveniles originated from areas at the edges of the Bornholm Basin, while only a small part had hatched in the Basin centre, is in good agreement with modeled survival probabilities of early stage larvae. This provides field based evidence that the bio-physical model from Hinrichsen et al. (2002a) is capable of realistically simulating individual larval survival probability.

The study of spatial patterns of fish recruitment presents a challenge to marine science (Irigoien et al. 2008). However, understanding spatial recruitment patterns is important as these patterns offer different combinations of food concentration and predation risk that can be exploited by the fish populations in different ways (Bakun 1996, Bakun & Broad 2003, Irigoien et al. 2007, Irigoien et al. 2008), leading to spatial differences in e.g. feeding rates, growth, condition and, ultimately, survival. A recent field investigation following the spatial recruitment patterns of anchovy from the egg to the juvenile stage, e.g., found marked stage-specific differences in distribution, indicating that transport off the shelf during the larval stage favours good recruitment (Irigoien et al. 2008).

For the Baltic cod stock, Vallin et al. (1999) reviewed potential factors that influence reproductive success. The impact of environmental conditions on egg fertilization and survival (Westin & Nissling 1991, Nissling 1994, Nissling & Vallin 1996, Nissling 2004), egg predation by clupeids (Koester & Schnack 1994, Koester & Moellmann 2000) and decreased larval viability at low oxygen concentrations (Nissling 1994) have been identified as sources of early life stage mortality. In addition, egg quality and fecundity as influenced by (i) fishery induced changes in the age structure of the stock (Vallin & Nissling 2000), (ii) food availability for adults during maturation (Kraus et al. 2002) and (iii) parental effects (Nissling et al. 1998, Vallin & Nissling 2000, Trippel et al. 2005), as well as impacts of pollution and environmental conditions on malformation of eggs and larvae (Grauman & Sukhorukova 1982, Vallin et al. 1999), have been suggested to influence reproductive success, even though evidence for especially the latter factor is inconclusive.

However, egg survival and larval abundance are hardly correlated in Baltic cod, whereas larval abundance is significantly related to year-class strength, indicating that either hatching or the early larval stage, or both, may be the most critical periods for the determination of recruitment strength (Koester et al. 2003). Modelling studies suggested retention and dispersal of larvae from the main spawning area to be key processes influencing recruitment success of the stock (Voss et al. 1999, Hinrichsen et al. 2001). The mechanism behind this observation may confirm Hjort’s (1914) critical period hypothesis, which suggests that variable survival rates are due to variations in food availability at the critical stage when the transition from endogenous (yolk) to exogenous (plankton) feeding occurs.

The observed spatial pattern in the origin of survivors is likely related to spatio-temporal differences in the availability of copepod nauplii for early larvae. Larval cod prey mainly on nauplii of the abundant calanoid copepods in the area, i.e. *Pseudocalanus acuspes, Temora longicornis*, *Acartia* spp., and *Centropages hamatus*. The general distribution and abundance patterns of the dominant copepod species in the Baltic are well known (Moellmann et al. 2000, Moellmann & Koster 2002, Renz & Hirche 2006, Schmidt 2006). According to modeling studies by Hinrichsen et al. (Hinrichsen et al. 2002a, Hinrichsen et al. 2003b, Hinrichsen et al. 2003c), a food limitation for first-feeding cod larvae during the last two decades was caused by a pronounced decline of the copepod *Pseudocalanus acuspes* (Moellmann et al. 2000), which is the preferred prey of larval Baltic cod (Voss et al. 2003). At low abundances of this copepod, first feeding larvae only had higher survival probability when they hatched on the outer edges of the Bornholm Basin at the end of the spawning period or if they were rapidly transported towards shallower areas, because here they could utilise nauplii of other copepod species which are more abundant in shallower water late in the spawning season. In contrast, larvae hatched within the centre of the Bornholm Basin did not encounter sufficient prey for survival along their drift routes. Thus, even though it was not possible in our study to directly relate juvenile survival with zooplankton abundances, the high agreement in patterns of spatial survivor origin from the present observation with model results provides strong empirical support for the importance of the critical period hypothesis in the recruitment process of Baltic cod.

In principal, higher numbers of juveniles originating from the edges of the basin could also simply be related to an increased spawning activity in these areas. However, this possibility can be ruled out, as evidenced by the egg abundance data. Egg stage 1, as a proxy for spawning effort, was relatively evenly distributed over the entire spawning ground. The abundance of stage 4 eggs, i.e. the stage immediately before hatching in the Baltic (Wieland et al. 1994), was lowest in the northwestern basin. While this decrease in abundance from stage 1 to 4 corresponds well to the spatial distribution of egg survival probabilities (RV and OES), it does not match with juvenile hatch locations. The spatial mismatch between late egg stages and survivor origins provides evidence that egg mortality is not the only important source of mortality in the recruitment process of Baltic cod, being consistent with our finding that survival during the first feeding stage is critical.

4.3 Temporal origin of pelagic and demersal juveniles

On the temporal scale, pelagic and demersal juvenile survivors originated mainly from may to august, i.e. from the middle and end of the spawning season, largely following the seasonal development in spawning intensity. However, a “gap” between hatch date distributions of pelagic and demersal juveniles was found in July. This gap may be a consequence of variable catchability for different size classes by the gears used, which may especially affect the abundance estimate of newly settled juveniles in the length range of 4-7 cm (Huessy et al. 1997, ICES 2009).

The observed gap may, however, also be related to lower survival during a time window at peak spawning, lasting from approximately day 180 to 230. Distinct “windows of survival” have been found to be of importance for the recruitment process of other species (e.g., Fortier & Quinonez-Velazques 1998, Limburg 2001, Lapolla & Buckley 2005, Allain et al. 2007, Baumann et al. 2008). Windows of higher survival in the early and late spawning season are in accordance with bio-physical modelling results (Hinrichsen et al. 2002a), even though the model suggested the first period of increased survival to occur considerably earlier in the season (march-april). There are several possible explanations for differences in the timing of high and low survival periods between model and observation. First, the model results describe averages of seasonal survival probabilities for a period of 14 years, and interannual differences in the timing of increased and decreased survival do occur. Second, the model did not account for the marked seasonal differences in spawning effort, which are likely to blur the rather subtle differences in survival probabilities predicted by the model. Finally, ages and spawning dates of demersal juveniles were estimated from an age-length relationship for pelagic juveniles, but demersal juveniles may have grown slower as indicated by an age-length relationship reported in Fey and Linkowski (2006) and, thus, have earlier birthdates than the pelagic ones. Even though this effect can not be ruled out, its magnitude is regarded as minor, as the application of Fey and Linkowski's age-length relationship developed specifically for demersal juvenile Baltic cod results only in a small (ca. 10 days) shift of the spawning date distribution to earlier dates. This shift is not large enough to change the spawning date distribution to much earlier dates, thus being unlikely to mask an even more pronounced decline in survival during mid spawning season.

Still the possibility of decreased survival at peak spawning time exists and is also supported by an earlier study (Hinrichsen et al. 2003a). In summary, decreasing availability of *Pseudocalanus acuspes* nauplii for first feeding larvae in mid-season may reduce larval survival, while later hatched larvae may profit from increasing abundances of nauplii of other copepod species if they are hatched in or transported to shallower coastal areas, as evidenced by the spatial origin of survivors in the present study.

We conclude that the temporal aspect in determining survivorship remains more elusive than the spatial influence. This is associated with sampling-related problems for the birth date analyses, especially when investigating a stock with a very protracted spawning season, as is the case with Baltic cod, a species with the additional awkwardness of switching from a pelagic to a demersal stage during juvenile life. For example, due to the fact that pelagic and demersal juveniles were caught with different gears having different catchability, the relative importance of early and late survivors for the strength of the year-class could not be quantified. To further elucidate the importance of temporal origin for the fate of a year class of Baltic cod, high frequency, quantitative sampling of consecutive developmental stages and their prey, both in space and time, seems mandatory to be able to follow different sub-cohorts from the egg to at least the juvenile stage. Such an approach has been exemplified in a number of studies (Meekan & Fortier 1996, Fortier & Quinonez-Velazques 1998, Limburg 2002, Allain et al. 2003, Lapolla & Buckley 2005, Meekan et al. 2006, Irigoien et al. 2008), even though they usually did not have to cope with such extensive spawning seasons as in Baltic cod.

4.4 Evaluation of the presently enforced MPA in the Bornholm Basin

Marine protected areas as tools in fisheries management have recently received increasing interest, especially due to the fact that traditional management efforts have largely failed to effectively prevent overexploitation of target species (Beverton 1998, Buckworth 1998, Gell & Roberts 2003, Roberts et al. 2005), and the depletion of nontarget species, habitat degradation and associated disruption of the food web (Roberts & Polunin 1993, Dayton et al. 1995, Pitcher & Pauly 1998). Even though increases of fish abundance and size in such areas have been documented (Pulunin & Roberts 1993, Roberts 1995, Mosqueira et al. 2001, Cote et al. 2001), a wider application of MPA's has so far been impeded by design issues related to the placement and extent of such areas, uncertainties concerning the effectiveness of such measures in terms of increased yield, and by opposition from the fishing industry (Apostolaki et al. 2002).

The approach of back-calculating the spatial origin of survivors presented in the present study can be applied to evaluate the location of Marine Protected Areas. As shown in Fig. 6a, only few juvenile survivors (26%) originated from the presently enforced MPA, and especially few (6%) from the central part which was protected in 2000, i.e. at the time where fish for the present analysis were collected. Accordingly, at the present environmental situation in the Baltic characterized by stagnation and declining salinities, the current location of the MPA in the Bornholm Basin seems to have a low potential of effectively contributing to the enhancement of the Baltic cod stock by protecting spawning aggregations. Offspring with a high survival probability are actually not spawned in the protected area. Instead, locations outside the MPA, especially in the northwestern part of the Bornholm Basin, seem to yield the highest probability for enhanced survival of larvae and, eventually, subsequent recruitment. However, our results only cover one year, and additional years need to be included in this analysis to determine if the observed spatial survival patterns are stable or varying between years, due to variable environmental forcing conditions, e.g. after inflow situations. Besides, the influence of the MPA on other factors, such as egg production (Hinrichsen et al. 2007) or fishing mortality of adults (Kraus et al. 2009), as well as interactions with other measures, e.g. seasonal closures, need to be considered. Nevertheless, it is our opinion that this type of analysis provides a valuable tool for the evaluation of the performance of Marine Protected Areas designed to secure undisturbed spawning and to promote recruitment of marine fish stocks.

4.5 Utility of the characteristics of survivors approach to study recruitment processes in Baltic cod

Recruitment success in marine fish is mainly determined through variable mortality during early life, but reliable mortality estimates from field sampling are difficult to obtain (Houde 1987). In contrast, the analysis of survivor characteristics has the advantage of analyzing fish that have already proven to belong to the successful fish of a year-class, and thus provides important indications for possible factors influencing the recruitment process in fish populations. In fact, Limburg et al. (1999) stated that they probably would have drawn erroneous conclusions about the recruitment potential of different cohorts, had they not included a retrospective analysis based on the characteristics of survivors. By applying survivor analysis to field samples of Baltic cod, we found strong empirical evidence for the importance of processes during the larval stage in shaping recruitment dynamics, as suggested by previous results from time-series analysis (Koester et al. 2003) and bio-physical modeling (Hinrichsen et al. 2002a). In combination with results from a parallel study, we suggest that the process of survivor selection in Baltic cod larvae may be (at least) twofold: while the period at first feeding is a first major bottleneck, otolith-based growth characteristics indicate additional recruitment regulation during the later larval stage (paper 2).

Recruitment is routinely estimated for most commercially important fish stocks. However, in most stocks the mechanisms determining recruitment variability are still poorly understood and are usually limited to general concepts such as food availability or relations with environmental factors without an understanding of the underlying mechanisms (Leggett & Deblois 1994, Cowan & Shaw 2002). Especially processes operating with high spatial variability are normally poorly resolved (Irigoien et al. 2008). Our study is the first one to provide empirical evidence from field samples for spatial differences in larval survival of Baltic cod. From the results, we conclude that addressing spatio-temporal variability in survival of early life stages has a high potential to improve our understanding of acting and interacting processes affecting recruitment and to construct environmentally sensitive stock-recruitment models. Besides, such dynamics need to be considered in spatial and temporal management measures, e.g. the design of protected seasons and areas.

References

Allain G., Petitgas P., Grellier P., Lazure P. (2003) The selection process from larval to juvenile stages of anchovy (Engraulis encrasicolus) in the Bay of Biscay investigated by Lagrangian simulations and comparative otolith growth. Fisheries Oceanography 12:407-455

Allain G., Petitgas P., Lazure P. (2007) The influence of environment and spawning distribution on the survival of anchovy (*Engraulis encrasicolus*) larvae in the Bay of Biscay (NE Atlantic) investigated by biophysical simulations. Fisheries Oceanography 16:506-514

Anderson J.T. (1988) A Review of Size Dependent Survival During Pre-Recruit Stages of Fishes in Relation to Recruitment. Journal of Northwest Atlantic Fishery Science 8:55-66

Apostolaki P., Milner-Gulland E.J., McAllister M.K., Kirkwood G.P. (2002) Modelling the effects of establishing a marine reserve for mobile fish species. Canadian Journal of Fisheries and Aquatic Sciences 59:405-415

Bakun A. (1996) Patterns in the ocean: Ocean processes and marine population dynamics. California Sea Grant/CIB

Bakun A., Broad K. (2003) Environmental 'loopholes' and fish population dynamics: comparative pattern recognition with focus on El Nino effects in the Pacific. Fisheries Oceanography 12:458-473

Baumann H., Voss R., Hinrichsen H.H., Mohrholz V., Schmidt J.O., Temming A. (2008) Investigating the selective survival of summer- over spring-born sprat, *Sprattus sprattus*, in the Baltic Sea. Fisheries Research 91:1-14

Bergstroem S., Carlsson B. (1994) River runoff to the Baltic Sea:1950- 1990. Ambio 23:280-287

Beverton R. (1998) Fish, fact and fantasy: a long view. Reviews in Fish Biology and Fisheries 8:229-249

Bryan K. (1969) A numerical method for the study of the circulation of the world ocean. Journal of Physical Oceanography 15:1312-1324

Buckworth R.C. (1998) World fisheries are in crisis? We must respond! Reinventing fisheries management, Chapman & Hall fish and fisheries series No.23, pp. 3-17.

Buehler V. (2004) Influence of maternal effects and environmental conditions on growth and survival of Atlantic cod (*Gadus morhua* L.). PhD thesis, Leibniz-Institut für Meereswissenschaften an der Christian-Albrechts-Universität zu Kiel, Germany

Campana S.E. (1989) Otolith microstructure of three larval gadids in the Gulf of Maine, with inferences on early life history. Canadian Journal of Zoology - Revue Canadienne de Zoologie 67:1401-1410

Campana S.E., Jones C.M. (1992) Analysis of otolith microstructure data. In: D.K.Stevenson and S.E.Campana (eds) Otolith microstructure examination and analysis. Canadian Special Publication of Fisheries and Aquatic Sciences 117. p 73-100

Clemmesen C., Doan T. (1996) Does otolith structure reflect the nutritional condition of a fish larva? - Comparison of otolith structure and biochemical index (RNA/DNA ratio) determined on cod larvae. Marine Ecology Progress Series 138:33-39

Cote I.M., Mosqueira I., Reynolds J.D. (2001) Effects of marine reserve characteristics on the protection of fish populations: a meta-analysis. Journal of Fish Biology 59:178-189

Cowan J.H.Jr., Shaw R.F. (2002) Recruitment. In: L.A.Fuiman and R.G.Werner (eds) Fishery Science. The Unique Contributions of Early Life Stages. Blackwell Science Ltd., Malden, MA (USA), p 88-111

Cox M.D. (1984) A primitive equation 3-dimensional model of the ocean. GFDL Ocean Group Tech.Rep.No.1, GFDL/Princeton University.

Cushing D.H. (1975) Marine ecology and fisheries. Cambridge Univ.Press, London, UK.

Dayton P.K., Thrush S.F., Agardy M.T., Hofman R.J. (1995) Environmental effects of marine fishing. Aquatic Conservation: Marine and Freshwater Ecosystems 5:205-232

Fey D.P., Linkowski T.B. (2006) Predicting juvenile Baltic cod (*Gadus morhua*) age from body and otolith size measurements. ICES Journal of Marine Science 63:1045-1052

Fortier L., Quinonez-Velazques C. (1998) Dependence of survival on growth in larval pollock *Pollachius virens* and haddock *Melanogrammus aeglefinus*: a field study based on individual hatchdates. Marine Ecology Progress Series 174:1-12

Fox C.J., Geffen A.J., Taylor N., Davison P., Rossetti H., Nash R.D. (2007) Birth-date selection in early life stages of plaice *Pleuronectes platessa* in the eastern Irish Sea (British Isles). Marine Ecology Progress Series 345:255-269

Fritz E.S., Crowder L.B., Francis R.C. (1990) The National Oceanic and Atmospheric Administration plan for recruitment fisheries oceanography research. Fisheries 15:25-31

Gagliano M., McCormick M.I., Meekan M.G. (2007) Survival against the odds: ontogenetic changes in selective pressure mediate growth-mortality trade-offs in a marine fish. Proceedings of the Royal Society of London, Series B: Biological Sciences 274:1575-1582

Geffen A.J. (1995) Growth and otolith microstructure of cod (*Gadus morhua* L.) larvae. Journal of Plankton Research 17:783-800

Gell F.R., Roberts C.M. (2003) Benefits beyond boundaries: the fishery effects of marine reserves. Trends in Ecology and Evolution 18:448-455

Grauman G., Sukhorukova L. (1982) On the emergence of sprat and cod abnormal embryos in the open Baltic. ICES CM1982/J:7

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

Grønkjær P., Clemmesen C., St.John M.A. (1997) Nutritional condition and vertical distribution of Baltic cod larvae. Journal of Fish Biology 51:352-369

Grønkjær P., Schytte M. (1999) Non-random mortality of Baltic cod larvae inferred from otolith hatch-check sizes. Marine Ecology Progress Series 181:53-59

Hannah C.G. (2007) Future directions in modeling physical-biological interactions. Marine Ecology Progress Series 347:301-306

Hare J.A., Cowen R.K. (1997) Size, growth, development, and survival of the planktonic larvae of *Pomatomus saltatrix* (Pisces: Pomatomidae). Ecology 78:2415-2431

Heath M.R. (1992) Field investigations of the early life stages of marine fish. Advances in Marine Biology 28:1-178

Hinrichsen H.H., Voss R. (1997) The influence of variations of meteorological forcing on larval drift and retention of Baltic cod - a modelling approach. Ichthyoplankton Ecology, Annual International Symposium of the Fisheries Society of the British Isles, Galway (Ireland), 8-11 Jul 1997, 21 pp.

Hinrichsen H.H., St John M.A., Aro E., Grønkjær P., Voss R. (2001) Testing the larval drift hypothesis in the Baltic Sea: retention versus dispersion caused by wind-driven circulation. ICES Journal of Marine Science 58:973-984

Hinrichsen H.H., Moellmann C., Voss R., Koster F.W., Kornilovs G. (2002a) Biophysical modeling of larval Baltic cod (*Gadus morhua*) growth and survival. Canadian Journal of Fisheries and Aquatic Sciences 59:1858-1873

Hinrichsen H.H., St.John M.A., Lehmann A., MacKenzie B.R., Koester F. (2002b) 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., Boettcher U.Y., Koester F.W., Lehmann A., St.John M. (2003a) Modelling the influences of atmospheric forcing conditions on Baltic cod early life stages: distribution and drift. Journal of Sea Research 49:187-201

Hinrichsen H.H., Lehmann A., Moellmann C., Schmidt J. (2003b) Dependency of larval fish survival on retention/dispersion in food limited environments: the Baltic Sea as a case study. Fisheries Oceanography 12:425-433

Hinrichsen H.H., Schmidt J.O., Moellmann C. (2003c) Spatial overlap patterns between Baltic larval cod and its prey obtained from drift model studies. Theme Session O. Transport of Eggs and Larvae Relevant to Cod Stocks of the North Atlantic. ICES CM 2003/O:01

Hinrichsen H.H., Schmidt J.O., Petereit C., Moellmann C. (2005) Survival probability of Baltic larval cod in relation to spatial overlap patterns with their prey obtained from drift model studies. ICES Journal of Marine Science 62:878-885

Hinrichsen H.H., Voss R., Wieland K., Koester F., Andersen K.H., 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., Boettcher U., Koester F. (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

Hjort J. (1914) Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer 20:1-228

Horn H.S. (1966) Measurement of Overlap in Comparative Ecological Studies. American Naturalist 100:419-424

Houde E.D. (1987) Fish early life dynamics and recruitment variability. American Fisheries Society Symposium Series 2:17-29

Houde E.D. (1997) Patterns and trends in larval-stage growth and mortality in teleost fish. Journal of Fish Biology 51:52-83

Huessy K., St.John M.A.S., Boettcher U. (1997) Food resource utilization by juvenile Baltic cod *Gadus morhua*: A mechanism potentially influencing recruitment success at the demersal juvenile stage? Marine Ecology Progress Series 155:199-208

Huessy K., Mosegaard H., Hinrichsen H.H., Boettcher U. (2003) Using otolith microstructure to analyse growth of juvenile Baltic cod *Gadus morhua*. Marine Ecology Progress Series 258:233-241

Hunter J. (1981) Feeding ecology and predation of marine fish larvae. In: R.Lasker (ed) Marine fish larvae: morphology, ecology, and relation to fisheries. Univ. Washington Press., p 34-77

ICES 2009. Report of the Baltic Fisheries Assessment Working Group. Copenhagen, 22-28 April 2009. ICES CM 2009/ACOM:07

Irigoien X., Fiksen O., Cotano U., Uriarte A., Alvarez P., Arrizabalaga H., Boyra G., Santos M., Sagarminaga Y., Otheguy P., Etxebeste E., Zarauz L., Artetxe I., Motos L. (2007) Could Biscay Bay Anchovy recruit through a spatial loophole? Progress in Oceanography 74:132-133

Irigoien X., Cotano U., Boyra G., Santos M., Alvarez P., Ibaibarriaga L. (2008) From egg to juvenile in the Bay of Biscay: spatial patterns of anchovy (*Engraulis encrasicolus*) recruitment in a non-upwelling region. Fisheries Oceanography 17:446-462

Jenkins G.P., Black K.P., Hamer P.A. (2000) Determination of spawning areas and larval advection pathways for King George whiting in southeastern Australia using otolith microstructure and hydrodynamic modelling. 1. Victoria. Marine Ecology Progress Series 199:231-242

Killworth P.D., Stainforth D., Webbs D.J., Paterson S.M. (1991) The development of a free-surface Bryan-Cox-Semtner ocean model. Journal of Physical Oceanography 21:1333-1348

Koester F.W., Schnack D. (1994) The role of predation on early life stages of cod in the Baltic. Dana 10:179-201

Koester F.W., Moellmann C. (2000) Trophodynamic control by clupeid predators on recruitment success in Baltic cod? ICES Journal of Marine Science 57:310-323

Koester F.W., Hinrichsen H.H., St.John M.A., Schnack D., MacKenzie B., 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

Koester F.W., Hinrichsen H.H., Schnack D., St John M.A., MacKenzie B.R., Tomkiewicz J., Moellmann C., Kraus G., Plikshs M., Makarchouk A., Aro E. (2003) Recruitment of Baltic cod and sprat stocks: identification of critical life stages and incorporation of environmental variability into stock-recruitment relationships. Scientia Marina 67:129-154

Koester F.W., Moellmann C., Hinrichsen H.H., Wieland K., Tomkiewicz J., Kraus G., Voss R., Makarchouk A., MacKenzie B.R., St.John M.A., Schnack D., Rohlf N., Linkowski T., Beyer J.E. (2005) Baltic cod recruitment - the impact of climate variability on key processes. ICES Journal of Marine Science 62:1408-1425

Kraus G., Tomkiewicz J., Koester F.W. (2002) Egg production of Baltic cod (*Gadus morhua*) in relation to variable sex ratio, maturity, and fecundity. Canadian Journal of Fisheries and Aquatic Sciences 59:1908-1920

Kraus G., Pelletier D., Dubreuil J., Moellmann C., Hinrichsen H.H., Bastardie F., Vermard Y., Mahevas 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

Lapolla A., Buckley L.J. (2005) Hatch date distributions of young-of-year haddock *Melanogrammus aeglefinus* in the Gulf of Maine/ Georges Bank region: implications for recruitment. Marine Ecology Progress Series 290:239-249

Leggett W.C., Deblois E. (1994) Recruitment in marine fishes: is it regulated by starvation and predation in the egg and larval stages? Netherlands Journal of Sea Research 32:119-134

Lehmann A. (1995) A three-dimensional baroclinic eddy-resolving model of the Baltic Sea. Tellus 47a:1013-1031

Lehmann A., Hinrichsen H.H. (2000a) On the wind driven and thermohaline circulation of the Baltic Sea. Physics and Chemistry of the Earth (B) 25:183-189

Lehmann A., Hinrichsen H.H. (2000b) On the thermohaline variability of the Baltic Sea. Journal of Marine Systems 25:333-357

Lehmann A., Krauss W., Hinrichsen H.H. (2002) Effects of remote and local atmospheric forcing on circulation and upwelling in the Baltic Sea. Tellus 54a:299-316

Limburg K.E. (2001) Through the gauntlet again: Demographic restructuring of American shad by migration. Ecology 82:1584-1596

Limburg K.E. (2002) Cohort Identification. In: L.A.Fuiman and R.G.Werner (eds) Fishery Science. The Unique Contributions of Early Life Stages. Blackwell Science Ltd., Malden, MA (USA), p 143-160

Limburg K.E., Pace M.L., Arend K.K. (1999) Growth, mortality, and recruitment of larval *Morone spp.* in relation to food availability and temperature in the Hudson River. Fishery Bulletin 97:80-91

MacKenzie B., St.John M.A., Wieland K. (1996) 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 B.R., Hinrichsen H.H., Plikshs M., Wieland K., Zezera A.S. (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

Marteinsdottir G., Gunnarsson B., Suthers I.M. (2000) Spatial variation in hatch date distributions and origin of pelagic juvenile cod in Icelandic waters. ICES Journal of Marine Science 57:1182-1195

Meekan M.G., Fortier L. (1996) Selection for fast growth during the larval life of Atlantic cod *Gadus morhua* on the Scotian shelf. Marine Ecology Progress Series 137:25-37

Meekan M.G., Vigliola L., Hansen A., Doherty P.J., Halford A., Carleton J.H. (2006) Bigger is better: size-selective mortality throughout the life history of a fast-growing clupeid, *Spratelloides gracilis*. Marine Ecology Progress Series 317:237-244

Miller T.J. (2007) Contribution of individual-based coupled physical-biological models to understanding recruitment in marine fish populations. Marine Ecology Progress Series 347:127-138

Moellmann C., Kornilovs G., Sidrevics L. (2000) Long-term dynamics of main mesozooplankton species in the central Baltic Sea. Journal of Plankton Research 22:2015-2038

Moellmann C., Koester F.W. (2002) Population dynamics of calanoid copepods and the implications of their predation by clupeid fish in the Central Baltic Sea. Journal of Plankton Research 24:959-978

Mosqueira I., Cote I. M., Jennings S., Reynolds J. D. (2001) Conservation benefits of marine reserves for fish populations. Annual Symposium of the Fisheries Society of the British Isles, Leicester (UK)

Nielsen R., Munk P. (2004) Growth pattern and growth dependent mortality of larval and pelagic juvenile North Sea cod *Gadus morhua*. Marine Ecology Progress Series 278:261-270

Nissling A. (1994) Survival of eggs and yolksac larvae of Baltic cod (*Gadus morhua* L.) at low oxygen levels in different salinities. ICES Marine Science Symposia 198:626-631

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. Hydrobiologia115-123

Nissling A., Kryvi H., Vallin L. (1994) Variation in egg buoyancy of Baltic cod *Gadus morhua* and its implications for egg survival in prevailing conditions in the Baltic Sea. 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

Nissling A., Larsson R., Vallin L., Frohlund K. (1998) Assessment of egg and larval viability in cod, *Gadus morhua*: methods and results from a experimental study. Fisheries Research 38:169-186

Petereit C. (2004) Experimente zum Temperatureinfluss auf frühe Entwicklungsstadien des Ostseedorsches *Gadus morhua*. MSc thesis, Leibniz-Institut für Meereswissenschaften an der Christian-Albrechts-Universität zu Kiel, Germany

Pitcher T.J., Pauly D. (1998) Rebuilding ecosystems, not sustainability, as the proper goal of fishery management. Reinventing fisheries management. Chapman & Hall Fish and Fisheries Series No.23

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

Pulunin N.V.C., Roberts C.M. (1993) Greater biomass and value of target coral-reef fishes in two small Caribbean marine reserves. Marine Ecology Progress Series 167-176

Radtke R. L. (1984) Cod fish otoliths: Information storage structures. The Propagation of Cod *Gadus morhua* L. An International Symposium., Arendal (Norway), 14-17 Jun 1983. Floedevigen Rapportserie 1, 1984:273-289

Radtke R.L., Waiwood K.G. (1980) Otolith formation and body shrinkage due to fixation in larval cod. (*Gadus morhua* L.). Canadian Technical Report of Fisheries and Aquatic Sciences 929:1-10

Renz J., Hirche H.J. (2006) Life cycle of *Pseudocalanus acuspes* Giesbrecht (Copepoda, Calanoida) in the Central Baltic Sea: I. Seasonal and spatial distribution. Marine Biology 148:567-580

Rice J.A., Crowder L.B., Holey M.E. (1987) Exploration of mechanisms regulating larval survival in Lake Michigan bloater: A recruitment analysis based on characteristics of individual larvae. Transactions of the American Fisheries Society 116:703-718

Roberts C.M. (1995) Rapid build-up of fish biomass in a Caribbean marine reserve. Conservation Biology 9:816-826

Roberts C.M., Polunin N.V.C. (1993) Marine reserves: Simple solutions to managing complex fisheries? Ambio 22:363-368

Roberts C.M., Hawkins J.P., Gell F.R. (2005) The role of marine reserves in achieving sustainable fisheries. Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences 360:123-132

Rohlf N. (1999) Aktivität und Vertikalwanderung der Larven des Ostseedorsches *(Gadus morhua callaris)* während der Dottersackphase. PhD thesis, Institute of Marine Sciences, Kiel. Berichte Institut fuer Meereskunde Kiel 321, 60 pp.

Rothschild B. (1986) Dynamics of marine fish populations. Harvard University Press, Cambridge.

Schmidt J.O. (2006) Small and meso-scale distribution patterns of key copepod species in the Central Baltic Sea and their relevance for larval fish survival. PhD thesis, Christian-Albrechts-University, Kiel, Germany

Schmidt J.O., Hinrichsen H.H. (2008) Impact of prey field variability on early cod *Gadus morhua* larval survival: a sensitivity study of a Baltic cod Individual-based Model. Oceanologia 50:205-220

Semtner A.J. (1974) A general circulation model for the World Ocean. UCLA Department of Meteorology Technical Report No. 8. 99 pp.

Shoji J., Tanaka M. (2006) Growth-selective survival in piscivorous larvae of Japanese Spanish mackerel *Scomberomorus niphonius*: early selection and significance of ichthyoplankton prey supply. Marine Ecology Progress Series 321:245-254

Sinclair M., Iles T.D. (1985) Atlantic herring (*Clupea harengus*) distributions in the Gulf of Maine-Scotian Shelf area in relation to oceanographic features. Canadian Journal of Fisheries and Aquatic Sciences 42:880-887

Sogard S.M. (1997) Size-selective mortality in the juvenile stage of teleost fishes: A review. Bulletin of Marine Science 60:1129-1157

Suthers I.M., Frank K.T., Campana S.E. (1989) Spatial Comparison of recent growth in postlarval Atlantic cod (*Gadus morhua*) off southwestern Nova Scotia: Inferior growth in a presumed nursery area. Canadian Journal of Fisheries and Aquatic Sciences 46:113-124

Suthers I.M., Sundby S. (1993) Dispersal and growth of pelagic juvenile Arcto-Norwegian cod (*Gadus morhua*), inferred from otolith microstructure and water temperature. ICES Journal of Marine Science 50:261-270

Suthers I.M., van der Meeren T., Jørstad K.E. (1999) Growth histories derived from otolith microstructure of three Norwegian cod stocks co-reared in mesocosms; effect of initial size and prey changes. ICES Journal of Marine Science 56:658-672

Taggart C.T., Frank K.T. (1990) Perspectives on larval fish ecology and recruitment processes: probing the scales of relationships. In: K.Sherman, L.M.Alexander, and B.D.Gold (eds) Large Marine Ecosystems: Patterns, Processes and Yields. American Association for the Advancement of Science, Washington, DC, p 151-164

Thompson B. M., Riley J. D. (1981) Egg and Larval Development Studies in the North Sea Cod (*Gadus morhua* L.). Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer 178:553-559

Thorrold S.R., Latkoczy C., Swart P.K., Jones C.M. (2001) Natal homing in a marine fish metapopulation. Science 291:297-299

Trippel E.A., Kraus G., Koester F.W. (2005) Maternal and paternal influences on early life history traits and processes of Baltic cod *Gadus morhua*. Marine Ecology Progress Series 303:259-267

Vallin L., Nissling A., Westin L. (1999) Potential factors influencing reproductive success of Baltic cod, *Gadus morhua*: a review. Ambio 28:92-99

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

Voss R., Hinrichsen H.H., St.john M. (1999) Variations in the drift of larval cod (*Gadus morhua* L.) in the Baltic Sea: combining field observations and modelling. Fisheries Oceanography 8:199-211

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

Voss R., Koester F.W., Dickmann M. (2003) Comparing the feeding habits of co-occurring sprat (*Sprattus sprattus*) and cod (*Gadus morhua*) larvae in the Bornholm Basin, Baltic Sea. Fisheries Research 63:97-111

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

Wieland K., Jarre-Teichmann A. (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 the timing of spawning of Baltic cod: possible causes and implications for recruitment. ICES Journal of Marine Science 57:452-464

PAPER 2

Characteristics of surviving juvenile Baltic cod II: field evidence for the growth-mortality hypothesis?

B. Huwer[1,5], H.-H. Hinrichsen[2], U. Böttcher[3], R. Voss[4] and F. Köster[1]

[1] Technical University of Denmark, National Institute of Aquatic Resources, Charlottenlund Slot, Jægersborg Allee 1, DK-2920 Charlottenlund, Denmark

[2] Leibniz-Institute of Marine Research, IFM-GEOMAR, Duesternbrooker Weg 20, D-24105 Kiel, Germany

[3] Johann Heinrich von Thünen Institute (vTI), Institute of Baltic Sea Fishery, Alter Hafen Sued, D-18069 Rostock, Germany

[4] Sustainable Fisheries, Department of Economics, University of Kiel, Wilhelm-Seelig-Platz 1, D-24105 Kiel, Germany

[5] Aarhus University, Department of Biological Sciences, Finlandsgade 14, 8200 Aarhus N, Denmark

ABSTRACT

There is evidence from both field and laboratory studies for an inverse relationship between growth and mortality during the larval stage in Atlantic cod. For the Eastern Baltic cod, information on processes affecting the larval stage from field studies is scarce. Especially mortality rates are difficult to examine in the field. In contrast, growth can be accurately determined by otolith microstructure analysis, but relating growth of larval fish to their experienced environment has proven to be difficult. The analysis of growth characteristics of surviving fish before and after an assumed selection for faster growth can provide important insight into factors influencing recruitment. By comparing otolith characteristics of pelagic juveniles of eastern Baltic cod with larvae from a similar hatch origin, we found faster growth of pelagic juveniles during the larval stage. Possible reasons for this observation are discussed, with several indications that selection for faster growth was caused by starvation rather than by predation. Comparison of larval growth rates from our study in 2000 with data from the mid 1990’s, a period of low recruitment despite high abundances and survival of eggs, indicates that growth/feeding-related processes during the larval stage have a high potential of influencing the recruitment dynamics of Baltic cod.

Key words: larvae, pelagic juveniles, otolith, microstructure analysis, growth, selection, recruitment, vertical distribution, Bornholm Basin

1. INTRODUCTION

Survival during the highly vulnerable early life stages is of critical importance to the recruitment success of marine fish (Houde 1987, Anderson 1988, Leggett & Deblois 1994, Chambers & Trippel 1997). Numerous biotic and abiotic influences are acting on marine fishes during early life, leading to exceptionally high mortality rates (Houde 1987, Houde 1989). Predation and starvation are thought to be the major mortality agents (Bailey & Houde 1989). Growth rate is thought to be a major factor influencing larval survival, as faster growing fish spend less time in vulnerable size classes (Houde 1987, Beyer 1989) and larger larvae have e.g. better prey capture and predator avoidance abilities than smaller larvae (Hunter 1981, Miller et al. 1988). While some recruitment hypotheses emphasized the importance of either food abundance, feeding success and starvation (Hjort 1914, Lasker et al. 1978) or predation (Houde 1987), the “growth-mortality hypothesis” addresses feeding success and predation in an integrated framework: growth increases with increasing feeding success, while mortality due to starvation or predation decreases (Anderson 1988).

Both field (Campana 1996) and laboratory studies (Buckley et al. 1993) have demonstrated an inverse relationship between growth and mortality of cod during the first months of life. While mortality is very difficult to determine in the field, especially down to a level of accuracy that allows to derive any implications for recruitment (Houde 1986), growth rates of larval fish can be accurately determined by otolith microstructure analysis (Stevenson & Campana 1992, Campana 2001). The two major environmental factors that influence growth are temperature and food availability. However, linking prey availability to larval fish growth in the field has proven difficult, and the literature is roughly evenly divided between studies that do find such a relationship and studies that do not (Buckley & Durbin 2006). Prey abundances in the field are often found to be too low to support the energetic demands of larvae determined in the laboratory. The reason for this apparent feeding paradox may be that the usual field sampling techniques for larval prey organisms integrate over large spatial and temporal scales, unable to resolve down to scales which are important for individual larval fish (Heath 1992). Nevertheless, by combining two data sets of larval cod growth estimates and of zooplankton abundances from spatially and temporally explicit field sampling programs on Georges Bank, Buckley and Durbin (Buckley & Durbin 2006) recently provided strong evidence for such a linkage. They particularly found abundances of *Pseudocalanus spp.* to be highly correlated with larval cod growth, which is in good accordance with studies on prey selection of larval cod. While larvae of most North Atlantic cod stocks prey predominantly on *Calanus finmarchicus* (Sundby 2000), *Pseudocalanus spp.* was identified to be the preferred prey item for larval cod in a number of southern stocks, such as the ones on Georges Bank (Kane 1984, Buckley & Lough 1987, Lough et al. 1996, Lough et al. 2005), on the Scotian Shelf (McLaren & Avendano 1995, McLaren et al. 1997) and in the North Sea (Munk 1997).

Also for larval Baltic cod have the various life stages of *Pseudocalanus acuspes* been identified as essential prey items (Voss et al. 2003). However, standing stocks of *P. acuspes* in the Baltic have dramatically decreased over the past decades in concert with decreasing salinities (Moellmann et al. 2000, ICES 2008), caused by a lack of inflows of highly saline, oxygen-rich water from the North Sea (Matthaeus & Franck 1992, Leppäranta & Myrberg 2009). While such inflow events occurred frequently in former times, only two major inflows have been observed since the late 1980's, in 1993 and 2003. A bio-physical modelling study by Hinrichsen et al. (2002) suggested that the decrease of *P. acuspes* had a strong influence on the recruitment success of Baltic cod. In particular, due to the low abundances of *P. acuspes* nauplii, first feeding larvae were found to have changed from a non-limited to a food-limited stage from the 2nd half of the 1980's to the mid 1990's. We provide empirical support for this model result in a parallel, process-oriented field study (paper 1). However, the model suggested food limitation only to occur in the first-feeding stage, whereas later larval stages where not food limited (Hinrichsen et al. 2002). In contrast to that, Buckley and Durbin (Buckley & Durbin 2006) found larval cod growth to be strongly related to *Pseudocalanus spp.* abundances throughout the larval stage, and this relation became first weaker after metamorphosis. This is in good agreement with the finding that starvation resistance does not improve much during the larval phase (Miller et al. 1988, Jordaan & Brown 2003). Thus, low abundances of suitable prey may also influence growth and survival of older larvae in the well established feeding stage.

Meekan and Fortier (1996) found a strong selection for faster growth in Atlantic cod larvae in one out of two years investigated. They hypothesized that selection for fast growth may be particularly strong in poor environmental conditions for growth (e.g., feeding success, growth potential or temperature). If this is true, one should expect a selection for fast growth during the larval stage of Baltic cod, considering the presently low abundances of *P. acuspes*, i.e. the preferred larval prey item. To test this hypothesis, we conducted a field study based on a characteristics of survivors approach (Rice et al. 1987, Fritz et al. 1990, Taggart & Frank 1990) to determine if growth-selective mortality occurs during early life of Baltic cod. The basic idea of this approach is that survivors are not a random subset of the offspring, but have emerged through selective sources of mortality related to the inter-individual variability of certain characteristics, e.g. growth rate. While early stage larvae constitute a mixture of potential survivors and non-survivors, fish sampled at a later stage, e.g. as juveniles, are the subset of the initial population that survived to that date. Thus, analyzing differences in the growth of the two groups during the larval stage will give an indication of which growth characteristics are most favourable for survival. As otoliths are continuously recording growth throughout the life of a fish (Stevenson & Campana 1992, Campana 2001), otolith microstructure analysis has been widely used to investigate growth-selective survival during early life stages of many fish species, (e.g. Hare & Cowen 1997, Limburg et al. 1999, Baumann et al. 2008), including cod (Meekan & Fortier 1996, Nielsen & Munk 2004).

The present study presents the first comparative analysis of larval and pelagic juvenile growth for the Eastern Baltic cod stock. After increasing to historically high levels in the mid 1980's (Eero et al. 2008), stock size rapidly decreased, and strong differences in recruitment success are apparent (Koester et al. 2005). A combination of fishery pressure and environmental factors was found to be influencing recruitment. In particular, egg mortality due to predation and low ambient oxygen concentration, caused by the lack of formerly regular inflows of oxygen-rich water from the North Sea (Matthaeus & Franck 1992, Leppäranta & Myrberg 2009), were identified as major sources of recruitment variability (Koester et al. 2001, Koester et al. 2005). However, while a strong inflow event in 1993 resulted in high egg abundances and favorable conditions for egg survival in the following years, the improved environmental situation was not reflected in increased larval abundances and recruitment levels (Koester et al. 2005). Moreover, recent estimates of stock biomass and recruitment of Baltic cod suggest improving recruitment despite overall relatively unfavourable environmental conditions (ICES 2009). These observations indicate that additional recruitment regulation is likely to occur during the larval stage.

Despite this obvious influence of processes during the larval stage in shaping the recruitment dynamics of Baltic cod, information on larval survival from field studies is limited (Grønkjær et al. 1997, Grønkjær & Wieland 1997, Grønkjær & Schytte 1999), but several biophysical modelling studies addressed the issue of larval survival success (Voss et al. 1999, Hinrichsen et al. 2001, Hinrichsen et al. 2002, Hinrichsen et al. 2003b, Hinrichsen et al. 2005, Schmidt & Hinrichsen 2008). While results from these modeling exercises and our parallel field study (paper 1) indicate food limitation for first-feeding larvae, the present study focuses on survivor characteristics during later life, as well established feeders and at the transition from larvae to pelagic juveniles. In particular, we compared otolith-based growth characteristics of pelagic juveniles with larvae from similar hatching times, as larvae after the first feeding stage may be affected by processes described in the "growth-mortality hypothesis" (Anderson 1988). In addition, we provide information on the vertical distribution of larvae and on larval and pelagic juvenile growth rates. Results are discussed with respect to the ambient environment and are set in relation to earlier field studies during a period of apparently low larval survival.

2. MATERIAL AND METHODS

2.1 Sampling procedure and laboratory analyses of larvae and pelagic juveniles

Due to environmental limitations for successful reproduction in the more eastern historical spawning grounds in the Gdansk Deep and the Gotland Basin, the Bornholm Basin (Fig. 1) has become the most important spawning area for the Eastern Baltic cod stock in recent years (Koester et al. 2005). Therefore, our study focuses on this area.

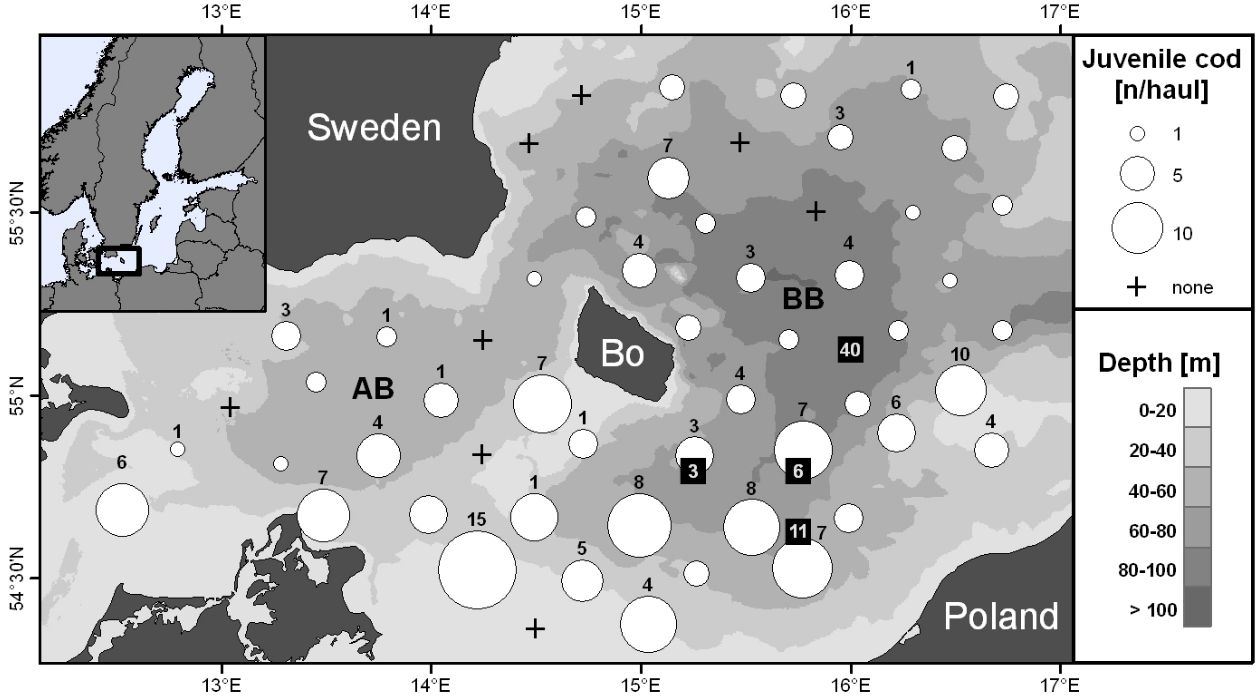


Fig. 1: Overview of the study area in the Baltic Sea and sampling positions. White circles depict the catch distribution of pelagic juvenile cod sampled with an Isaacs-Kidd-Midwater trawl in November 2000, numbers on top of the symbols denote the numbers of juveniles selected for ageing by otolith analysis (n=135). Black squares and numbers indicate the catch positions and numbers of larvae used for otolith analyses (n = 60, note that at the station in the central Bornholm Basin, 36 of the 40 larvae were from a BIOMOC haul, while all other larvae were from Bongo net hauls). Bo = Bornholm Island, BB = Bornholm Basin, AB = Arkona Basin.

In April, May, July and August 2000, samples of Baltic cod larvae were collected during cruises with the German research vessel “Alkor” by means of a Bongo net. For sampling details see Huwer et al. (paper 1). Cod larvae were immediately sorted from samples collected with a 500 µm net and stored in 96% alcohol.

In addition to the Bongonet sampling, hauls with a multiple opening and closing net (1 m² opening, 335 µm mesh size) were conducted in August 2000 at a station in the central Bornholm Basin (Fig. 1) to resolve the vertical distribution of larvae. The net, a so called BIOMOC, was equipped with 9 net bags, allowing sampling of a profile of the entire water column from 5 to 80 m with a resolution of 5 m depth intervals with two hauls. A total of 8 profiles (16 hauls) were conducted from august 5 to august 6, at time intervals of 2 to 3 hours.

The nets were towed at a definite depth for 3.5 minutes at a speed of 3 knots. A total number of 205 cod larvae were obtained. Larvae were immediately sorted from the samples and stored in 96% alcohol. To obtain a vertical profile of the ambient environment, a CTD cast was conducted on the sampling station.

In addition, to analyse the vertically resolved temperature development in the Bornholm Basin from July to September 2000, temperature data in the Baltic Sea were compiled from the International Council for the Exploration of the Sea (ICES) Oceanographic Database (http://www.ices.dk/ocean/) containing depth-specific CTD (conductivity-temperature-depth) and bottle measurements. From the database, all available temperature measurements were selected for the area of the Bornholm Basin between July and September 2000. Data were subsequently aggregated to obtain monthly means per 5 m depth stratum.

From October 26 to November 11, 2000, samples of pelagic juvenile Baltic cod were obtained during a trawl survey with the German research vessel “Solea” in the southern Baltic Sea carried out by means of an Isaacs-Kidd-Midwater-Trawl (IKMT). A total number of 268 pelagic juveniles were caught. The catch distribution of these samples is shown in Fig. 1. Samples were immediately frozen at minus 20°C for later investigation in the laboratory.
In the laboratory, standard length (SL) of the larvae and standard length (SL), total length (TL), and wet weight of the pelagic juveniles were determined. No corrections for shrinkage of larvae and juveniles due to the preservation procedure were applied.

2.2 Otolith microstructure examination and statistical analyses

The principal aim of this study was to compare growth characteristics of juvenile survivors with larvae from a similar hatching origin. Age determination of the pelagic juveniles sampled in October/November suggested that the majority of survivors originated from August 2000 (paper 1). Thus, larvae collected during the sampling in August (1st - 4th) were chosen for this analysis, as they were expected to have hatched closest to the juvenile hatch dates.

Subsamples of larvae (n=60) from the BIOMOC (n=36) and the Bongo samples (n=24) and of pelagic juveniles (n=135) were selected for age determinations and growth rate analyses (for sampling stations and numbers of larvae and juveniles used in this analysis, see Fig. 1). Otoliths of larvae and juveniles were removed with fine insect needles and tweezers and mounted on glass slides with thermoplastic cement (Buehler). Sagittal otoliths were ground and polished from both sides with different grades of lapping film (3 µm and 0.05 µm for larval otoliths, 12 to

0.05 µm for juvenile otoliths) until the core region was visible. Daily growth increments were enumerated to determine the age of larvae and juveniles.

In many fish species, otolith size shows a strong correlation with fish size, indicating that size and growth of the otoliths are good descriptors of the somatic size and growth pattern of the fish. If such a correlation exists, otolith growth can be used as a proxy for somatic growth (Campana & Jones 1992). A highly significant relationship between otolith and fish size was found for the larvae and juveniles of Baltic cod in the present study (see results), and the daily nature of increment formation has been validated for cod (Radtke & Waiwood 1980, Campana 1989, Geffen 1995), including the stock in the Baltic (Clemmesen & Doan 1996). Therefore, we used otolith increment widths at age as proxies for fish growth performance to investigate possible growth-selective survival during the larval stage of Baltic cod. Besides, we compared otolith hatch check sizes between larvae and juveniles, as they have the potential to link survivors to maternal or intrinsic factors (Grønkjær & Schytte 1999, Bang et al. 2004, Bang & Grønkjær 2005).

Otolith pictures were taken with an image analysis system, consisting of a digital camera (Leica DFC 320) connected to a compound microscope (Leica DM LB 100T) and a computer with an image analysis software (Image Pro Plus, Version 5.0). For each otolith a series of pictures was taken, as increments became visible at different focal planes depending on their distance from the otolith centre. Pictures of larval otoliths (n=60) were taken at a magnification of 1512x. As otoliths of juveniles were too large to entirely fit onto the visible area at this magnification, they had to be repositioned, and several series of pictures were taken. Pictures in the centre of the juvenile otoliths (n=33) were taken at the same magnification as for larvae to resolve the finer innermost growth increments from the otolith core to the beginning of the secondary primordia. For the wider secondary growth increments, lower magnifications (480-960x) were found to be sufficient. Up to five series of pictures were taken for juvenile otoliths to obtain a transect from the centre to the edge. To assure comparability of increment measurements, pictures were taken at the same location on all otoliths, resulting in images showing a transect of increments from the otolith centre to the edge in the region of the rostrum. The otolith images were analysed with an image analysis software. The otolith radius, hatch check radius and individual increment widths of the otoliths were measured on a transect on the radius of maximum length between centre and edge of the otolith in rostral direction. The final increment at the edge of each otolith was regarded as incomplete and thus was excluded from further analyses. Possible differences in otolith hatch-check radius and otolith increment width at age between larvae and pelagic juveniles were investigated with Kolmogorov-Smirnov tests.

3. RESULTS

3.1 Vertical distribution of cod larvae in relation to ambient temperatures

The vertical distribution of cod larvae in relation to ambient temperatures in the central Bornholm Basin in the beginning of August 2000 is presented in Fig. 2. The majority of larvae were found in a depth range between 20 and 30 meters. At these depths, the larvae experienced temperatures between 6 and 14°C. The size range of these larvae was 3.8-11.7 mm SL. Additionally, small numbers of larvae of a smaller size range (4.0-6.8 mm SL) were found at larger depths between 50 and 80 meters.

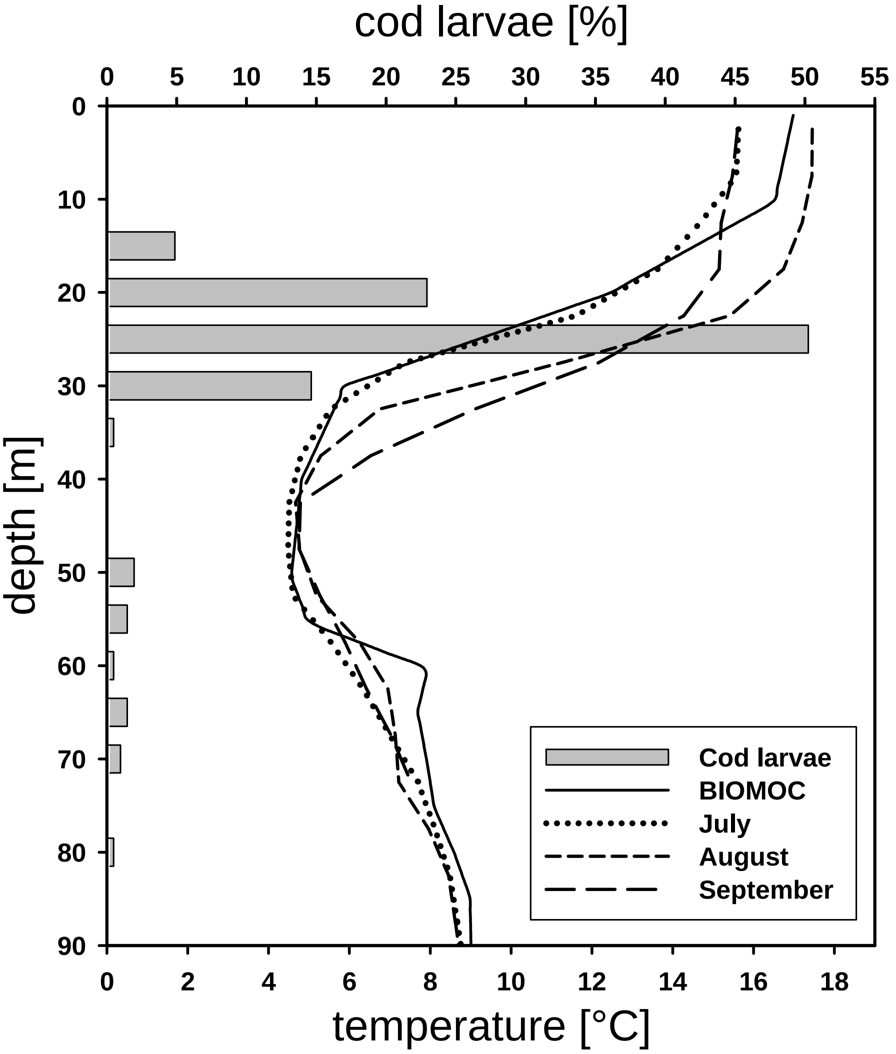


Fig. 2: Vertical distribution of Baltic cod larvae (bars, n=205) and temperature (solid line) at the BIOMOC station in the central Bornholm Basin in the beginning of August 2000 and temperature development from July (dotted line) to August (short dashed line) and September (long dashed line) 2000 as averages of stations in the Bornholm Basin from the ICES Oceanographic database (http://www.ices.dk/ocean/). The majority of larvae were found in a depth range between 20 and 30 meter, where they experienced temperatures between 6 and 14°C. Temperatures in this depth range in August and September were 2-4°C warmer than in July and at the time of larval sampling in early August.

Figure 2 also shows the temperature development in the Bornholm Basin from July to September 2000 (averages of stations in the Bornholm Basin from the ICES Oceanographic database). Temperatures in the larval dwelling depths in August and September were 2-4°C warmer than in July and at the time of larval sampling in early August.

3.2 Growth and otolith characteristics of larvae and pelagic juveniles

3.2.1 Otolith-standard length relationship, hatch dates and growth estimates of larvae and juveniles

A highly significant allometric relationship between otolith radius and fish size was found for the larvae and juveniles analysed in this study (Fig. 3). The hatch date distributions of larvae and juveniles used for the otolith comparisons are depicted in Fig. 4. Even though we selected larvae from the latest ichthyoplankton sampling available, only very few of the youngest larvae had hatch dates that overlapped with the hatch dates of the juveniles. Larval hatch dates ranged from day of the year 183 to 213 (average 202, median 204), while juvenile hatch dates ranged from day 206 to 259 (average 236, median 238).

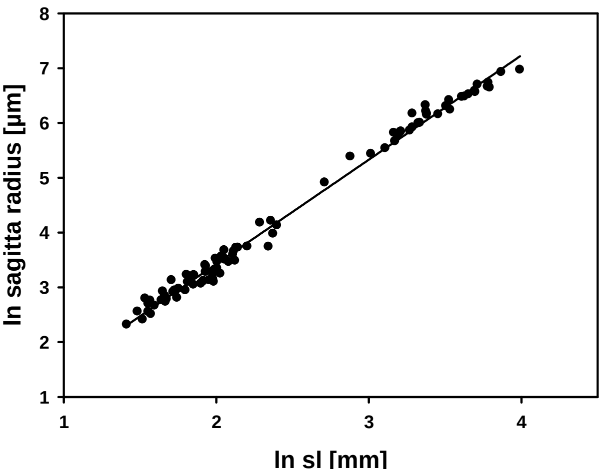


Fig. 3: A strong relationship between sagitta radius and standard length was found for larval and juvenile Baltic cod (n = 93). Due to the allometric nature of the relationship, data were ln-ln transformed. Linear regression equation: ln radius = 1.9037*ln sl – 0.3814 (r^2 = 0.9923).

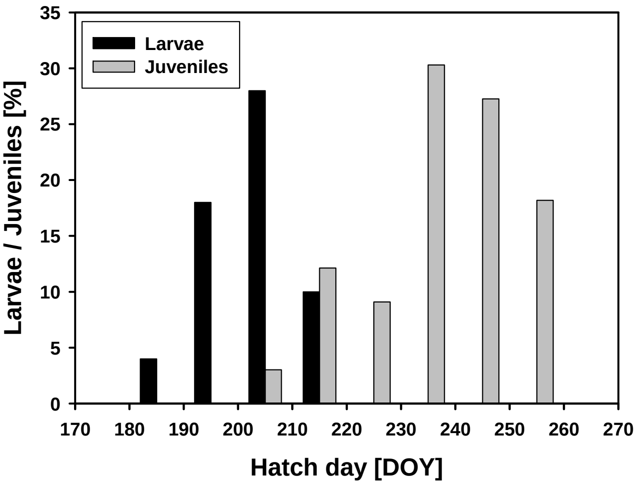


Fig. 4: Hatch date distribution of larvae (black bars) and juveniles (grey bars) used for comparison of otolith characteristics (DOY = day of the year).

Figures 5 and 6 show size-at-age of larvae and pelagic juveniles, respectively. The data for larvae and juveniles were both described well by linear relationships, yielding average growth rate estimates of 0.2058 and 0.6783 mm/day for larvae and pelagic juveniles, respectively.

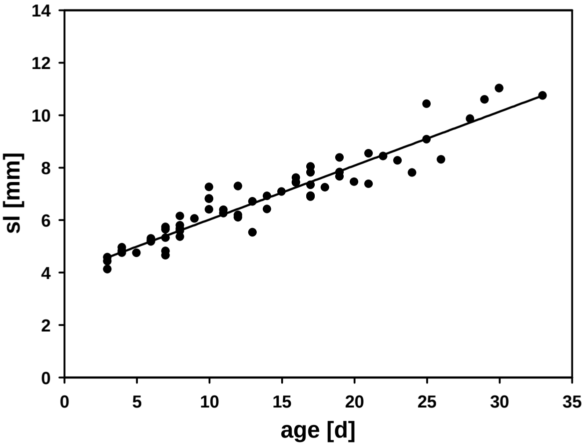


Fig. 5: Standard length vs. age of larval Baltic cod (n = 60). Linear regression equation: sl = 0.2057*age+3.9652 (r^2 = 0.9032)

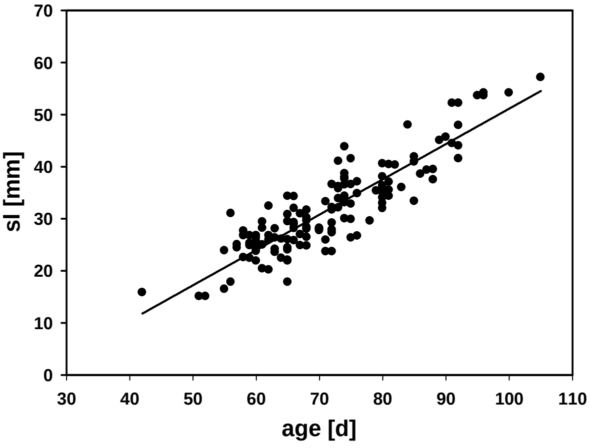


Fig. 6: Standard length vs. age of pelagic juvenile Baltic cod (n = 135). Linear regression equation: sl = 0.6783*age – 16.6942 (r^2 = 0.7860)

3.2.2 Otolith characteristics and comparison of increment widths and hatch-check sizes between larvae and juveniles

Sagittal otoliths of Baltic cod larvae and juveniles showed a distinct hatch check, which was surrounded by a number of fainter initial increments (here termed type 1 increments) with weak contrast before increments started to become more contrasted in appearance (type 2 increments). This change of otolith increment appearance occurred approximately at increment number 20. With an increase in increment width followed the occurrence of sub-daily increments. Another marked change in increment appearance occurred at the transition to secondary growth increments on accessory growth centres. Here, increments became considerably broader and heavier in appearance (type 3 increments). Secondary increment formation began at increment number 42-71, with an average of 55.8 (+- 6.7 sd). In the majority of cases (>73%), secondary increment formation occurred between increment number 50 and 65. These results are largely in accordance with earlier studies on the otolith microstructure of juvenile Baltic cod, which used transverse otolith sections (Boettcher & Oeberst 1996, Oeberst & Boettcher 1998). However, in our study a larger number of primary increments were found, indicating that the method applied in the present study was better suited to resolve this type of increments.

The comparison of increment widths of the first 24 increments of larvae vs. pelagic juveniles is shown in Fig. 7. Comparison of older ages was not possible, as only 2 larvae older than 24 days were available. Besides, increments of type 2 were excluded from this analysis, as the markedly different appearance of these increments suggested that a direct comparison with increments of type 1 is not applicable. Even though increment widths showed a large variability between individuals, otoliths of pelagic juveniles showed on average larger increment widths than larvae. Note that the number of increment observations decreases with increasing increment number due to i) the decreasing number of older larvae and ii) the removal of increments of type 2 from the analysis. Statistically significant differences ($p < 0.05$; Kolmogorv-Smirnov test) were found between the widths of all increments except for increment numbers 18 and 22 ($p = 0.0838$ and 0.1859, respectively). For increment numbers 1-12, 15 and 19, differences were highly significant ($p < 0.01$).

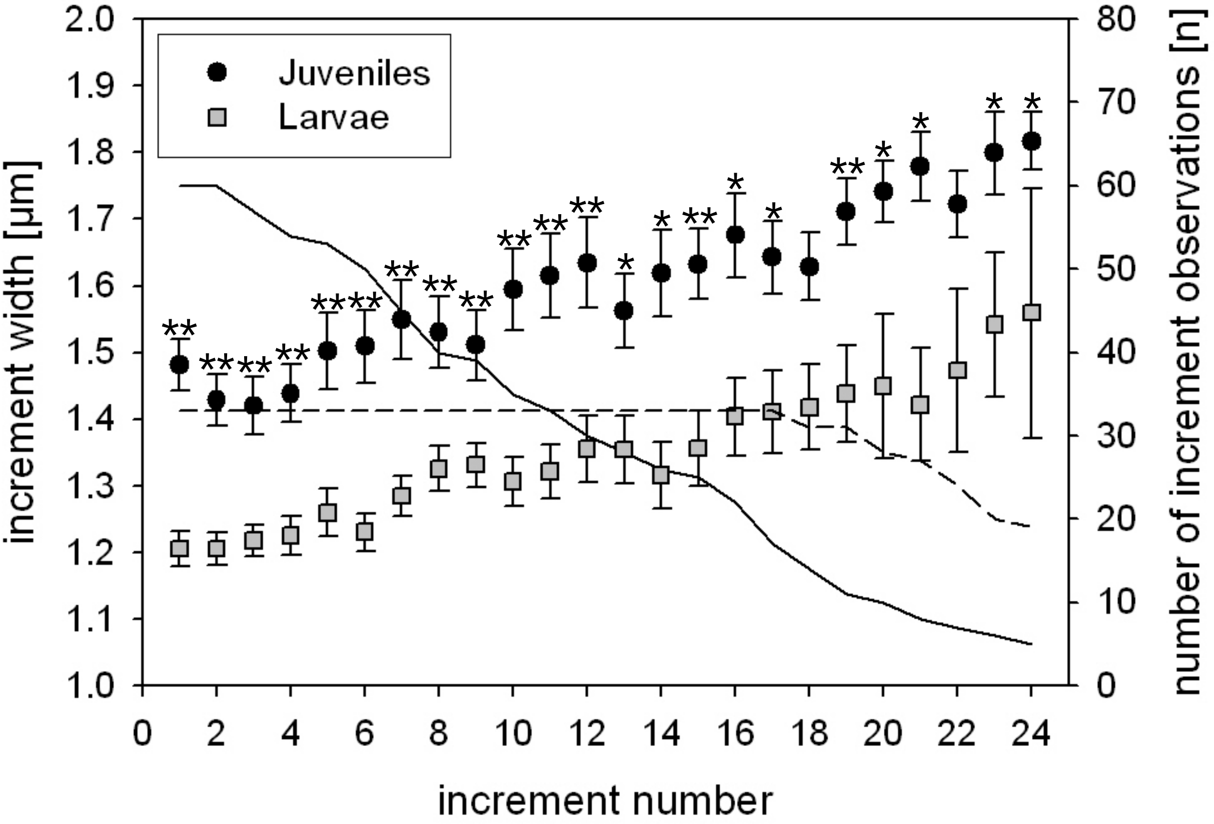


Fig. 7: Comparison of otolith increment widths of the first 24 increments of larvae vs. pelagic juveniles. Grey squares = larvae (n = 60), black dots = pelagic juveniles (n = 33), symbols = averages, error bars = standard error, solid line = number of increment observations for larvae, stippled line = number of increment observations for pelagic juveniles; note that the number of increment observations decreases with increasing increment number due to the decreasing number of older larvae and the removal of increments of type 2 from the analysis; see text for further details. Statistically significant differences (* <= 0.05; ** <= 0.01; Kolmogorov-Smirnov-test) between larvae and juveniles were found for the widths of all increment numbers with the exception of increment numbers 18 (p = 0.0838) and 22 (p = 0.1859). Comparison of older ages was regarded as inappropriate, as only 2 larvae older then 24 days were available.

The hatch checks of larvae and juveniles were found at radii ranging from 7 to 12 µm from the otolith centre (Fig. 8). A statistically significant difference in otolith hatch-check radius between larvae and juveniles was found (Kolmogorov-Smirnov test, $p < 0.05$).

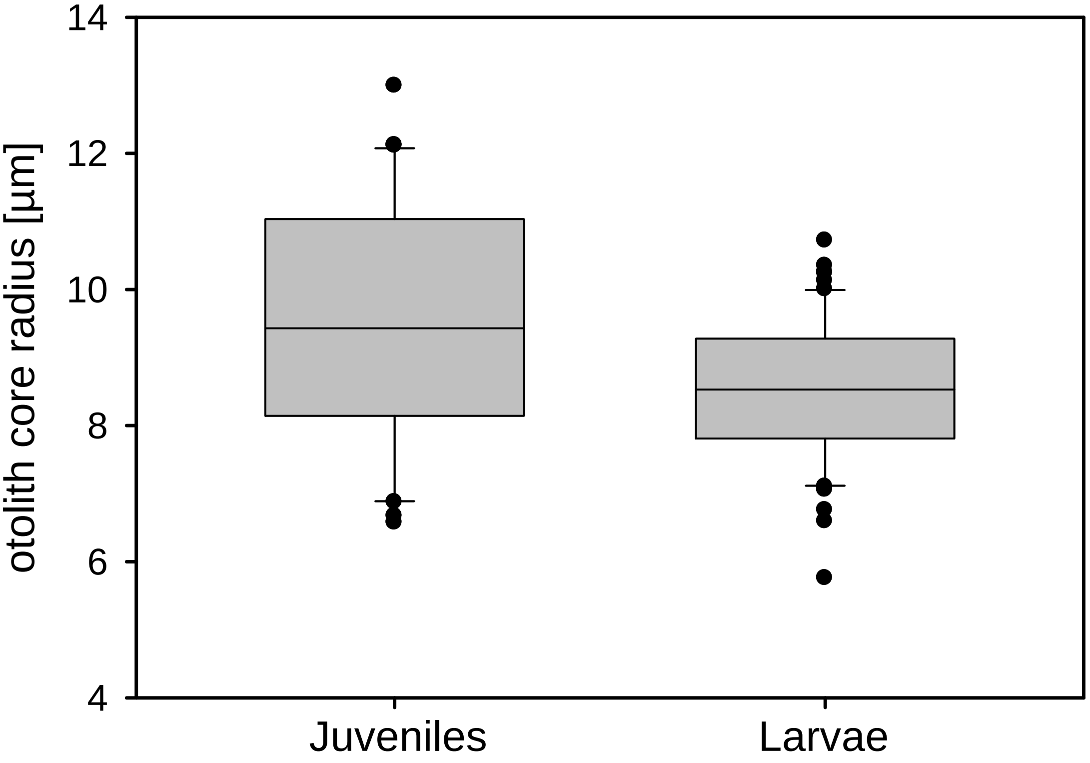


Fig. 8: Comparison of otolith core radii between larvae and juveniles. The lines in the middle and at the lower and upper end of the boxes show the median, 25th and 75th percentiles, the whiskers show the 10th and 90th percentiles, points are outliers. A statistically significant difference was found ($p < 0.05$, Kolmogorov-Smirnov test).

4. DISCUSSION

We found pelagic juvenile Baltic cod to have grown faster during the early larval stage than larvae from a similar hatching origin. Unfortunately, our sampling did not allow us to compare larvae and juveniles from the same cohort, as the larvae analysed in our study had hatched about one month earlier than the juveniles. The finding of faster growth of pelagic juveniles in the larval phase may indicate either a generally higher growth potential of juvenile survivors caused by e.g. maternal or intrinsic factors, selection for faster growing fish during the larval stage, or a generally better environment for growth of the later hatched cohort. In any case, there are several indications that the observed growth differences were caused by food-limitation rather than by predation. In the following, we discuss different possible hypotheses for this observation.

Hypothesis 1: Maternal or intrinsic effects on growth performance

Superior feeding conditions should only result in better growth, i.e. broader otolith increment widths, when the larva is relying on exogenous food. In contrast, during the yolk-sac stage, when the larva is relying on endogenous food, such differences should not occur. Nevertheless, also the very first increments representing the yolk-sac phase were significantly broader in juvenile fish. This may be related to metabolic factors. In fact, otolith size was hypothesized to reflect metabolic rate rather than growth per se, even though a high metabolic rate is a prerequisite for fast growth (Mosegaard 1990, Titus & Mosegaard 1991).

This possible explanation receives support from the analysis of hatch check sizes. Grønkjær and Schytte (1999) found hatch check areas of larger, older Baltic cod larvae to be significantly larger than those of smaller, younger larvae, indicating higher survival of larvae with large hatch checks. This finding is confirmed in the present study. Grønkjær and Schytte hypothesized that intrinsic factors (e.g. metabolic rate) or maternal effects (e.g. larger egg size) may control otolith size at hatch and, thus, influence the survival of Baltic cod larvae.

In Baltic cod, larger females produce larger eggs than smaller females (Grauman 1964, Vallin & Nissling 2000) and larval size at hatching and at yolk sac depletion is significantly correlated with egg size (Nissling et al. 1998). However, otolith size-at-hatch does not appear to be a good measure of larval size-at-hatch in both cod (Geffen 1995, Miller et al. 1999) and other species (Hoeie et al. 1999, Bang & Grønkjær 2005). In contrast, otolith size-at-hatch can be used as a proxy for the predetermined standard metabolic rate of the embryo (Bang et al. 2004, Bang & Grønkjær 2005), and a recent study on Atlantic herring (Bang A. et al. 2007) provides support for faster growth in larvae with larger otoliths at hatch (as a proxy for high standard metabolic rate). Furthermore, Trippel et al. (2005) found embryo survival, larval standard length, yolk-sac area, yolk utilization and resistance to starvation in Baltic cod to be significantly influenced by maternal and paternal (i.e., interaction between both parents) effects. Thus, larger otolith hatch check sizes and larger increment widths during the yolk-sac stage in juvenile vs. larval Baltic cod may be related to parental effects on endogenously predetermined metabolic rates and larval condition which influence growth.

Hypothesis 2: Growth-selective survival during the larval stage

Generally, survival chances of marine fish larvae are increasing with age or size (Pepin 1991, Houde 1997b). Survivors of Atlantic cod on the Scotian Shelf expressed higher growth rates, larger size-at-age and larger hatch-check diameters (Meekan & Fortier 1996). While selection for faster growth in that investigation did not seem to occur until the late larval stage, pelagic juveniles in our study expressed significantly larger hatch-check sizes and significantly larger increment widths than larvae during the first 3 weeks of life. This is far beyond the first-feeding stage, which usually is terminated within ca. 10 days after hatching (Ellertsen et al. 1980, Fossum 1986, Grønkjær & Wieland 1997). Accordingly, surviving fish may have experienced a growth advantage during larval life after first feeding.

The most likely reasons for growth-selective survival are the removal of slower growing individuals due to starvation or predation, as suggested in the “growth-mortality” hypothesis (see (Anderson 1988). There is increasing evidence that in many marine fish species, predation may have a by far greater influence on early life stage mortality than starvation (Bailey & Houde 1989, Houde 1997a, Houde 2002). In the species poor Baltic, though, the only identified potential predators on larval Baltic cod are the clupeids sprat and herring as well as the scyphomedusa *Cyanea capillata* (CORE 1998). However, while predation on cod eggs can reach substantial levels, predation on cod larvae can be regarded as negligible due to a very limited vertical overlap between the larvae and their potential predators (Koester & Schnack 1994, Koester & Moellmann 2000). Thus, predation is unlikely to be the driving factor for a selection process of Baltic cod larvae.

In contrast to adult fish, larvae are usually not storing significant amounts of energy in liver and muscle, and resilience to starvation is therefore not improving much during the larval phase (Miller et al. 1988, Jordaan & Brown 2003). Food shortage can therefore rapidly lead to high starvation mortalities, especially at relatively high ambient temperatures. In order to initiate first feeding, Baltic cod larvae have to conduct an ontogenetic vertical migration (Grønkjær et al. 1997, Grønkjær & Wieland 1997, paper 3) from hatching depths to shallower waters, as it is here their principal prey items, i.e. copepod nauplii, are most abundant (Renz & Hirche 2006, Schmidt 2006). Thus, the larvae are usually dwelling in the region of the summer thermocline (cf. Fig. 2, Grønkjær et al. 1997, Grønkjær & Wieland 1997, paper 3), at least during their first weeks of life. Here, the warm temperatures probably allow relatively fast growth, but may also result in high mortalities due to increasing energy demands and in a selection for fast growing fish. This may be amplified by the negative long-term trend in the abundance of *Pseudocalanus acuspes* (Moellmann et al. 2000, Moellmann & Koster 2002), the preferred larval Baltic cod prey item (Voss et al. 2003), as it has been suggested that selection for fast growth may be especially pronounced in unfavourable feeding conditions (Meekan & Fortier 1996).

Thus, the observed growth differences between larvae and surviving juveniles during early life may reflect growth-selective survival related to better feeding abilities of larvae that are larger-at-age, mediated through advantages such as faster swimming speed and larger search volume (Blaxter 1986), larger reactive distances (Miller et al. 1988) and generally better physical abilities to catch prey (Pepin & Penney 1997, Puvanendran et al. 2002).

Hypothesis 3: Better environmental conditions for growth of the later hatched cohort

The most influential environmental factors on growth are food availability and temperature, and differences in these two factors between the larval and juvenile hatch dates may be a possible explanation for the observed growth differences.

Larval cod are preying on the different developmental stages of the dominant calanoid copepods in the Baltic, i.e. *Pseudocalanus acuspes, Temora longicornis*, *Acartia* spp., and *Centropages hamatus*, but show a strong selective feeding on *P. acuspes* (Voss et al. 2003). Unfortunately, no zooplankton data for the larval and juvenile hatch periods are available, but the general distribution and abundance patterns of the dominant copepod species in the Baltic are known (Moellmann et al. 2000, Moellmann & Koster 2002, Renz & Hirche 2006, Schmidt 2006). After peaking in spring, the abundance of *P. acuspes* is sharply decreasing throughout the summer, while abundances of all other copepod species are increasing from late summer to fall (Fig. 9, Moellmann et al. 2000).

This may have lead to a situation where the earlier cohort (the larvae) had less favourable feeding conditions, i.e. did not enjoy a relatively high production of *P. acuspes* nauplii occurring early in the spawning season and faced lower availability of other nauplii species than the later cohort (the juveniles). This would correspond well with the finding of higher larval survival probabilities in the early and late spawning season from both modeling (Hinrichsen et al. 2002, Hinrichsen et al. 2003b) and field studies (Hinrichsen et al. 2003a), paper 1).

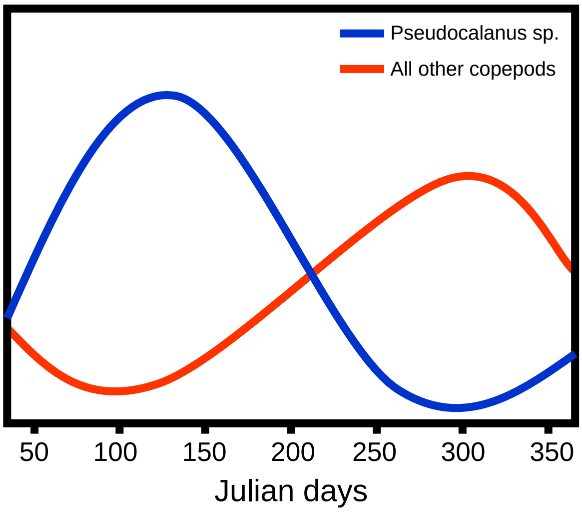


Fig. 9: Schematic of seasonal copepod abundance development in the central Baltic (after Moellmann et al. 2000).

Temperature has pronounced effects on metabolism and growth rates of larval fish (Blaxter 1992). A laboratory study by Otterlei et al. (1999) suggests a temperature optimum for growth at 14-16°C for cod larvae fed ad libitum. In contrast, Buckley et al. (2004) reported a dome-shaped relationship between growth of larval cod and water temperature in field samples, with a maximum at temperatures around 7°C. They interpreted this discrepancy as evidence for food-limited growth at higher temperatures in the field, as the optimum for growth shifts to lower temperatures when food ration is restricted (Brett 1979).

As mentioned in the previous section, feeding Baltic cod larvae are usually found in and at the lower end of the summer thermocline, where they can experience considerable differences in ambient temperatures. From the data provided by Otterlei et al. (1999), assuming a hatch length of 4 mm, we estimated average growth rates of larvae < 10-11 mm to be 0.20, 0.22, 0.29, 0.31 and 0.35 mm d^{-1} for temperatures of 6, 8, 10, 12 and 14°C, respectively. Similar sized larvae in the present study expressed an average growth rate of 0.21 mm d^{-1}. This corresponds best to the laboratory values at 6 and 8°C, despite a much broader range of temperatures (6-14°C) experienced by our field-caught larvae. This suggests that the Baltic cod larvae in the present study may have experienced food-limited growth.

The temperature development in the usual larval dwelling depths showed a further warming and a more pronounced thermocline from July, i.e. the main hatch period of larvae, to August and September, i.e. the juvenile hatch months. Thus, different ambient temperatures could have caused the observed growth differences between the early (larvae) and late (juveniles) cohort, but the suggested food-limited growth is also indicative of growth-selective survival, as weaker larvae may be rapidly removed from the system through starvation. In any case, possible food-limited growth is a further indication that the hypothesized growth-selective survival between different individuals or different cohorts was governed by prey availability rather than by predation. On the other hand, significant differences were already observed in the widths of the very first increments. These increments correspond to the first days after hatching, when both larvae and juveniles can be expected to have experienced very similar temperatures, as temperatures at hatching depths in the halocline region show very little variability. Thus, intrinsic effects can neither be ruled out.

Environmental effects on larval growth and importance for recruitment

By actively seeking or avoiding certain depths ranges, larvae may actually be able to choose different survival strategies. In modeling studies on larval Northeast Arctic cod, feeding vs. predation based trade-off rules resulted in large survival differences dependent on vertical migration behaviour (Vikebø et al. 2007, Kristiansen et al. 2009). As described above, predation risk for Baltic cod larvae is low and independent of larval dwelling depths, and a predation related trade-off situation is therefore unlikely. However, for this stock, a bioenergetic feeding-starvation trade-off may exist, i.e. larvae may need to choose between combinations of (i) high or (ii) low temperature and food abundance, leading to faster growth but also high energetic demands and higher starvation risk for (i) or the opposite for (ii). Such a possible trade-off may have significant influences on the recruitment regulation of Baltic cod.

For cod larvae on Georges Bank, which like Baltic cod also aggregate in the summer thermocline (Lough & Potter 1993), Buckley et al. (2004) estimated that a 1.5°C deviation from the optimum temperature for growth would result in a five-fold decrease in survival to the pelagic juvenile stage. Information on the vertical distribution and migration of Baltic cod larvae is limited, but the few published field studies give no indications for extended diel vertical migrations (Wieland & Zuzarte 1991, Grønkjær & Wieland 1997). However, these observations were largely conducted on small larval size groups, and larvae may first begin to conduct diel vertical migrations upon reaching larger sizes, as e.g. observed for cod larvae on Georges Bank (Lough & Potter 1993). Besides, in the highly stratified Baltic, a temperature difference of 1.5°C may be achieved by moving as little as 2-3 meters in vertical direction (cf. Fig. 2), a distance that even small larvae should be able to complete within few hours (MacKenzie & Kiørboe 1995, Peck et al. 2006).

Food shortage related to the Baltic zooplankton dynamics was hypothesized to be the reason for observed lower larval survival during summer (Hinrichsen et al. 2003a, paper 1). The interplay of prey abundance, temperature and starvation could be a further reason for these observations. This may also give an additional explanation for the pronounced decline in overall recruitment levels (Koester et al. 2001, Koester et al. 2005) after a shift in peak spawning time of Baltic cod from spring to summer (Wieland et al. 2000). In this respect, the issue of climate change may also be of importance. The relationship of cod recruitment and temperature is positive for stocks in cold waters, while negative for stocks in warm waters (Planque & Fredou 1999). In the Baltic, a general increase of water temperatures and a decline in salinity has been observed over the past decades (Moellmann et al. 2000, The BACC Author Team 2008). In fact, in a time series from 1961 to 1997, high positive temperature and negative salinity anomalies were coupled with highest negative anomalies of *Pseudocalanus acuspes* in the first half of the 1990’s (Moellmann et al. 2000), a period characterized by extremely low larval abundances and recruitment levels despite favourable environmental conditions for egg survival after the 1993 inflow, record high egg abundances and low egg mortality due to predation (Koester et al. 2005).

An indication for the importance of prey availability and temperature for larval survival and subsequent recruitment during this period is provided by a comparison of larval growth rates. Estimated recruitment originating from the years 1994 and 1995 was lower than for 2000, the year of the present investigation ($116*10^6$, $89*10^6$ and $127*10^6$ recruits at age 2, respectively; (ICES 2009). Baltic cod larvae sampled in 1994 and 1995 showed very poor nutritional condition and an average growth rate of only 0.12 mm d^{-1} (Grønkjær et al. 1997), which is considerably lower than the 0.20 mm d^{-1} found in our study. In conjunction with the estimates of egg abundance and recruitment strength, this is an indication for extremely poor larval survival in the mid 1990’s, probably due to severe food limitation, as previously suggested (Koester et al. 2005).

Juvenile growth

The possibility of growth-selective survival during the larval stage of Baltic cod is partly in contrast to studies on other cod stocks, who found selection for faster growth not to occur until the pelagic juvenile stage and therefore suggested a minor influence of the early larval phase in determining adult cohort abundance (Campana 1996, Meekan & Fortier 1996). Even though not investigated in the present study, growth-selective survival may also occur during the juvenile stage of Baltic cod. Starvation is less likely to be of importance during this life stage due to more efficient prey catching abilities and larger energy reserves of juvenile fish, but density-dependent recruitment regulation in the juvenile stage due to food competition, slower growth and longer cumulative predation mortality has been suggested (Sissenwine 1984, Myers & Cadigan 1993). The average growth rate for pelagic juveniles found in our study compares relatively well with previously reported growth estimates for similar sized Baltic cod (Boettcher & Oeberst 1996, Fey & Linkowski 2006) but marked inter-annual differences in growth and size-at-age are certainly possible, especially in the light of the very protracted spawning season of this stock. However, the only potential source of predation mortality for Baltic cod juveniles is cannibalism by adult cod, i.e. cannibalism is unlikely to occur in the pelagic juvenile stage due to the demersal life style of the adults. On the other hand, slower growth of pelagic juveniles will result in later settling and may lead to higher over-winter mortality (Sogard 1997), and Campana (1996) found a significant correlation between size-at-age and year-class strength of Atlantic cod on Georges Bank. Besides, cannibalism on demersal juveniles can reach considerable levels (Neuenfeldt & Koester 2000), and even though this possibility of recruitment regulation was considered unlikely to have a major influence at the presently low stock size of Baltic cod (Neuenfeldt & Koester 2000, Uzars & Plikshs 2000), growth dependent regulation during this stage can not be entirely excluded.

Conclusion

Whereas most early recruitment hypotheses related year-class success or failure to more or less catastrophic, episodic processes, eliminating entire cohorts, the hypotheses related to the “growth-mortality” idea suggest that relatively subtle changes in rates of growth and mortality result in tremendous differences in survival and recruitment (Anderson 1988, Leggett & Deblois 1994, Cowan & Shaw 2002).

Even though the exact causes and consequences behind the observation of faster growth of pelagic juveniles during the larval stage in Baltic cod remain elusive, our findings provide empirical support for the importance of processes during the larval stage in shaping recruitment dynamics. In conjunction with results from a parallel investigation, our study suggests that (at least) two processes may determine survival in the larval stage of Baltic cod: while food availability for early larvae in the first feeding period is a major initial bottleneck (paper 1) which may result in episodic removal of entire cohorts, growth differences between larvae and juveniles indicate additional recruitment regulation by more continuous, growth related processes during the later larval stage. Clearly, processes in the larval and juvenile stages of Baltic cod require additional investigations and one of the future challenges will be to resolve the relative importance of processes during the egg, larval and juvenile stage in shaping Baltic cod recruitment dynamics. In any case, having provided empirical support for the potentially high influence of food availability for larval cod growth and survival, we conclude that the incorporation of larval stage processes has a high potential of explaining recruitment variability and improving the predictive abilities of environmentally sensitive stock-recruitment models of Baltic cod.

References

Anderson J.T. (1988) A Review of Size Dependent Survival During Pre-Recruit Stages of Fishes in Relation to Recruitment. Journal of Northwest Atlantic Fishery Science 8:55-66

Bailey K.M., Houde E.D. (1989) Predation on eggs and larvae of marine fishes and the recruitment problem. Advances in Marine Biology 25:1-83

Bang A., Grønkjær P., Malte H. (2004) Individual variation in the rate of oxygen consumption by zebrafish embryos. Journal of Fish Biology 64:1285-1296

Bang A., Grønkjær P. (2005) Otolith size-at-hatch reveals embryonic oxygen consumption in the zebrafish, *Danio rerio*. Marine Biology 147:1419-1423

Bang A., Grønkjær P., Folkvord A. (2007) Possible fitness costs of high and low standard metabolic rates in larval herring *Clupea harengus*, as determined by otolith microstructure. Marine Ecology Progress Series 331:233-242

Baumann H., Voss R., Hinrichsen H.H., Mohrholz V., Schmidt J.O., Temming A. (2008) Investigating the selective survival of summer- over spring-born sprat, *Sprattus sprattus*, in the Baltic Sea. Fisheries Research 91:1-14

Beyer J.E. (1989) Recruitment stability and survival - simple size-specific theory with examples from the early life dynamics of marine fish. Dana 7:45-147

Blaxter J.H.S. (1986) Development of sense organs and behaviour of teleost larvae with special reference to feeding and predator avoidance. Transactions of the American Fisheries Society 115:98-114

Blaxter J.H.S. (1992) The effect of temperature on larval fishes. Netherlands Journal of Zoology 42:336-357

Boettcher U., Oeberst R. (1996) Investigations to the otolith-microstructure of juvenile Baltic cod in the phase of the settling. ICES CM 1996/J:9

Brett J.R. (1979) Environmental factors and growth. In: W.S.Hoar, D.J.Randall, and J.R.e.Brett (eds) Fish physiology. Volume 8. Bioenergetics and growth. Academic Press, New York, p 599-675

Buckley L.J., Lough R.G. (1987) Recent growth, biochemical composition, and prey field of larval haddock (*Melanogrammus aeglefinus*) and Atlantic cod (*Gadus morhua*) on Georges Bank. Canadian Journal of Fisheries and Aquatic Sciences 44:14-25

Buckley L.J., Smigielski A.S., Halavik T.A., Burns B.R., Laurence G.C. (1993) Growth and survival of the larvae of three temperate marine fish species at discrete prey densities. II. Cod (*Gadus morhua*), winter flounder (*Pseudopleuronectes americanus)*, and silver hake (*Merluccius bilinearis*). In: B.T.Walther and H.J.Fyhn (eds) Physiological and Biochemical Aspects of Fish Development. University of Bergen, Bergen, p 183-195

Buckley L.J., Caldarone E.M., Lough R.G. (2004) Optimum temperature and food-limited growth of larval Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) on Georges Bank. Fisheries Oceanography 13:134-140

Buckley L.J., Durbin E.G. (2006) Seasonal and inter-annual trends in the zooplankton prey and growth rate of Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) larvae on Georges Bank. Deep Sea Research (Part II Topical Studies in Oceanography) 53:2758-244

Campana S.E. (1989) Otolith microstructure of three larval gadids in the Gulf of Maine, with inferences on early life history. Canadian Journal of Zoology - Revue Canadienne de Zoologie 67:1401-1410

Campana S.E., Jones C.M. (1992) Analysis of otolith microstructure data. In: D.K.Stevenson and S.E.Campana (eds) Otolith microstructure examination and analysis. Canadian Special Publication of Fisheries and Aquatic Sciences 117. p 73-100

Campana S.E. (1996) Year-class strength and growth rate in young Atlantic cod *Gadus morhua*. Marine Ecology Progress Series 135:21-26

Campana S.E. (2001) Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. Journal of Fish Biology 59:197-242

Chambers R.C., Trippel E.A. (1997) Early Life History and Recruitment in Fish Populations. Chapman & Hall.

Clemmesen C., Doan T. (1996) Does otolith structure reflect the nutritional condition of a fish larva? - Comparison of otolith structure and biochemical index (RNA/DNA ratio) determined on cod larvae. Marine Ecology Progress Series 138:33-39

CORE 1998. Mechanisms influencing long time trends in reproductive success and recruitment of Baltic Cod: Implications for fisheries management. EU-Project AIR CT94 1226, Final Report.

Cowan J.H.Jr., Shaw R.F. (2002) Recruitment. In: L.A.Fuiman and R.G.Werner (eds) Fishery Science. The Unique Contributions of Early Life Stages. Blackwell Science Ltd., Malden, MA (USA), p 88-111

Eero M., Koster F.W., MacKenzie B.R. (2008) Reconstructing historical stock development of Atlantic cod (*Gadus morhua*) in the eastern Baltic Sea before the beginning of intensive exploitation. Canadian Journal of Fisheries and Aquatic Sciences 65:2728-2741

Ellertsen B., Moksness E., Solemdal P., Stroemme T., Tilseth S., Westgard T., Oiestad V. (1980) Some biological aspects of cod larvae (*Gadus morhua*). Fiskeridirektoratets Skrifter, Serie Havundersoekelser 17:29-47

Fey D.P., Linkowski T.B. (2006) Predicting juvenile Baltic cod (*Gadus morhua*) age from body and otolith size measurements. ICES Journal of Marine Science 63:1045-1052

Fossum P. (1986) A staging system for larval cod (*Gadus morhua* L.). Fiskeridirektoratets Skrifter, Serie Havundersoekelser 18:69-76

Fritz E.S., Crowder L.B., Francis R.C. (1990) The National Oceanic and Atmospheric Administration plan for recruitment fisheries oceanography research. Fisheries 15:25-31

Geffen A.J. (1995) Growth and otolith microstructure of cod (*Gadus morhua* L.) larvae. Journal of Plankton Research 17:783-800

Grauman G. (1964) The importance of the size of the eggs of the Baltic cod for the survival of foetuses. ICES CM 1964 (Gadoid Fish Committee) 85:1-5

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

Grønkjær P., Clemmesen C., St.John M.A. (1997) Nutritional condition and vertical distribution of Baltic cod larvae. Journal of Fish Biology 51:352-369

Grønkjær P., Schytte M. (1999) Non-random mortality of Baltic cod larvae inferred from otolith hatch-check sizes. Marine Ecology Progress Series 181:53-59

Hare J.A., Cowen R.K. (1997) Size, growth, development, and survival of the planktonic larvae of *Pomatomus saltatrix* (Pisces: Pomatomidae). Ecology 78:2415-2431

Heath M.R. (1992) Field investigations of the early life stages of marine fish. Advances in Marine Biology 28:1-178

Hinrichsen H.H., St John M.A., Aro E., Grønkjær P., Voss R. (2001) Testing the larval drift hypothesis in the Baltic Sea: retention versus dispersion caused by wind-driven circulation. ICES Journal of Marine Science 58:973-984

Hinrichsen H.H., Moellmann C., Voss R., Koester F.W., Kornilovs G. (2002) Biophysical modeling of larval Baltic cod (*Gadus morhua*) growth and survival. Canadian Journal of Fisheries and Aquatic Sciences 59:1858-1873

Hinrichsen H.H., Boettcher U.Y., Koester F.W., Lehmann A., St.John M. (2003a) Modelling the influences of atmospheric forcing conditions on Baltic cod early life stages: distribution and drift. Journal of Sea Research 49:187-201

Hinrichsen H.H., Lehmann A., Moellmann C., Schmidt J. (2003b) Dependency of larval fish survival on retention/dispersion in food limited environments: the Baltic Sea as a case study. Fisheries Oceanography 12:425-433

Hinrichsen H.H., Schmidt J.O., Petereit C., Moellmann C. (2005) Survival probability of Baltic larval cod in relation to spatial overlap patterns with their prey obtained from drift model studies. ICES Journal of Marine Science 62:878-885

Hjort J. (1914) Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer 20:1-228

Hoeie H., Folkvord A., Johannessen A. (1999) Maternal, paternal and temperature effects on otolith size of young herring (*Clupea harengus* L.) larvae. Journal of Experimental Marine Biology and Ecology 234:167-184

Houde E.D. (1986) Potential for growth, duration of early life stages and regulation of recruitment in marine fish. ICES CM 1986/L:28

Houde E.D. (1987) Fish early life dynamics and recruitment variability. American Fisheries Society Symposium Series 2:17-29

Houde E.D. (1989) Comparative growth, mortality, and energetics of marine fish larvae: Temperature and implied latitudinal effects. Fishery Bulletin U.S. 87:471-495

Houde E.D. (1997a) Patterns and consequencs of selective processes in teleost early life histories. In: R.C.Chambers and E.A.Trippel (eds) Early Life History and Recruitment in Fish Populations. p 173-196

Houde E.D. (1997b) Patterns and trends in larval-stage growth and mortality in teleost fish. Journal of Fish Biology 51:52-83

Houde E.D. (2002) Mortality. In: L.A.Fuiman and R.G.Werner (eds) Fishery Science. The Unique Contributions of Early Life Stages. Blackwell Science Ltd., Malden, MA (USA), p 64-87

Hunter J.R. (1981) Feeding Ecology and Predation of Marine Fish Larvae. In: R.Lasker (ed) Marine Fish Larvae: Morphology, Ecology and Relation to Fisheries. Washington Sea Grant, University of Washington Press, Seattle, WA (USA), p 33-76

ICES 2008. Report of the Working Group on Integrated Assessment of the Baltic Sea (WGIAB). ICES, Baltic Committee CM 2008/BCC:04, 145 pp.

ICES 2009. Report of the Baltic Fisheries Assessment Working Group. Copenhagen, 22-28 April 2009. ICES CM 2009/ACOM:07

Jordaan A., Brown J.A. (2003) The risk of running on empty: The influence of age on starvation and gut fullness in larval Atlantic cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciences 60:1289-1298

Kane J. (1984) The feeding habits of co-occurring cod and haddock larvae from Georges Bank. Marine Ecology Progress Series 16:9-22

Koester F.W., Schnack D. (1994) The role of predation on early life stages of cod in the Baltic. Dana 10:179-201

Koester F.W., Moellmann C. (2000) Trophodynamic control by clupeid predators on recruitment success in Baltic cod? ICES Journal of Marine Science 57:310-323

Koester F.W., Hinrichsen H.H., St.John M.A., Schnack D., MacKenzie B., 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

Koester F.W., Moellmann C., Hinrichsen H.H., Wieland K., Tomkiewicz J., Kraus G., Voss R., Makarchouk A., MacKenzie B.R., St.John M.A., Schnack D., Rohlf N., Linkowski T., Beyer J.E. (2005) Baltic cod recruitment - the impact of climate variability on key processes. ICES Journal of Marine Science 62:1408-1425

Kristiansen T., Jorgensen C., Lough R.G., Vikebo F., Fiksen O. (2009) Modeling rule-based behavior: habitat selection and the growth-survival trade-off in larval cod. Behavioral Ecology 20:490-500

Lasker R., Parsons T.R., Jansson B.O., Longhurst A.R., Saetersdal G. (1978) The relation between oceanographic conditions and larval anchovy food in the California Current: identification of factors contributing to recruitment failure. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer 173:212-230

Leggett W.C., Deblois E. (1994) Recruitment in marine fishes: is it regulated by starvation and predation in the egg and larval stages? Netherlands Journal of Sea Research 32:119-134

Leppäranta M., Myrberg K. (2009) Physical Oceanography of the Baltic Sea. Springer, Berlin Heidelberg New York.

Limburg K.E., Pace M.L., Arend K.K. (1999) Growth, mortality, and recruitment of larval *Morone spp.* in relation to food availability and temperature in the Hudson River. Fishery Bulletin U.S. 97:80-91

Lough R.G., Potter D.C. (1993) Vertical distribution patterns and diel migrations of larval and juvenile haddock *Melanogrammus aeglefinus* and Atlantic cod *Gadus morhua* on Georges Bank. Fishery Bulletin U.S. 91:281-303

Lough R.G., Caldarone E.M., Rotunno T.K., Broughton E.A., Burns B.R., Buckley L.J. (1996) Vertical distribution of cod and haddock eggs and larvae, feeding and condition in stratified and mixed waters on southern Georges Bank, May 1992. Deep-Sea Research II 43:1875-1904

Lough R.G., Buckley L.J., Werner F.E., Quinlan J.A., Pehrson Edwards K. (2005) A general biophysical model of larval cod (*Gadus morhua*) growth applied to populations on Georges Bank. Fisheries Oceanography 14:241-262

MacKenzie B.R., Kiørboe T. (1995) Encounter rates and swimming behaviour of pause-travel and cruise larval fish predators in calm and turbulent laboratory environments. Limnology and Oceanography 40:1278-1289

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

McLaren I.A., Avendano P. (1995) Prey field and diet of larval cod on Western Bank, Scotian Shelf. Canadian Journal of Fisheries and Aquatic Sciences 52:448-463

McLaren I.A., Avendano P., Taggart C.T., Lochmann S.E. (1997) Feeding by larval cod in different water-masses on Western Bank, Scotian Shelf. Fisheries Oceanography 6:250-265

Meekan M.G., Fortier L. (1996) Selection for fast growth during the larval life of Atlantic cod *Gadus morhua* on the Scotian shelf. Marine Ecology Progress Series 137:25-37

Miller T.J., Crowder L.B., Marschall E.A. (1988) Larval Size and Recruitment Mechanisms in Fishes: Toward a Conceptual Framework. Canadian Journal of Fisheries and Aquatic Sciences 45:1657-1670

Miller T.J., Herra T., Leggett W.C. (1999) The relation between otolith size and larval size at hatching for Atlantic cod, *Gadus morhua*. Fishery Bulletin 97:294-305

Moellmann C., Kornilovs G., Sidrevics L. (2000) Long-term dynamics of main mesozooplankton species in the central Baltic Sea. Journal of Plankton Research 22:2015-2038

Moellmann C., Koster F.W. (2002) Population dynamics of calanoid copepods and the implications of their predation by clupeid fish in the Central Baltic Sea. Journal of Plankton Research 24:959-978

Mosegaard H. (1990) What Is Reflected by Otolith Size at Emergence - A Reevaluation of the Results in West and Larkin (1987). Canadian Journal of Fisheries and Aquatic Sciences 47:225-228

Munk P. (1997) Prey size spectra and prey availability of larval and small juvenile cod. Journal of Fish Biology 51:340-351

Myers R.A., Cadigan N.G. (1993) Density-dependent juvenile mortality in marine demersal fish. Canadian Journal of Fisheries and Aquatic Sciences 50:1576-1590

Neuenfeldt S., Koester F.W. (2000) Trophodynamic control on recruitment success in Baltic cod: the influence of cannibalism. ICES Journal of Marine Science 57:300-309

Nielsen R., Munk P. (2004) Growth pattern and growth dependent mortality of larval and pelagic juvenile North Sea cod *Gadus morhua*. Marine Ecology Progress Series 278:261-270

Nissling A., Larsson R., Vallin L., Frohlund K. (1998) Assessment of egg and larval viability in cod, *Gadus morhua*: methods and results from a experimental study. Fisheries Research 38:169-186

Oeberst R., Boettcher U. (1998) Development of juvenile Baltic cod described with meristic, morphometric and sagitta otolith parameters. ICES CM 1998/CC:15

Otterlei E., Nyhammer G., Folkvord A., Stefansson S.O. (1999) Temperature- and size-dependent growth of larval and early juvenile Atlantic cod (*Gadus morhua*): a comparative study of Norwegian coastal cod and northeast Arctic cod. Canadian Journal of Fisheries and Aquatic Sciences 56:2099-2111

Peck M.A., Buckley L.J., Bengtson D.A. (2006) Effects of temperature and body size on the swimming speed of larval and juvenile Atlantic cod (*Gadus morhua*): implications for individual-based modelling. Environmental Biology of Fishes 75:419-429

Pepin P. (1991) Effect of Temperature and Size on Development, Mortality, and Survival Rates of the Pelagic Early Life-History Stages of Marine Fish. Canadian Journal of Fisheries and Aquatic Sciences 48:503-518

Pepin P., Penney R.W. (1997) Patterns of prey size and taxonomic composition in larval fish: are there general size-dependent models? Journal of Fish Biology 51:84-100

Planque B., Fredou T. (1999) Temperature and the recruitment of Atlantic cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciences 56:2069-2077

Puvanendran V., Leader L.L., Brown J.A. (2002) Foraging behaviour of Atlantic cod (*Gadus morhua*) larvae in relation to prey concentration. Canadian Journal of Zoology-Revue Canadienne de Zoologie 80:689-699

Radtke R.L., Waiwood K.G. (1980) Otolith formation and body shrinkage due to fixation in larval cod. (*Gadus morhua* L.). Canadian Technical Report of Fisheries and Aquatic Sciences 929:1-10

Renz J., Hirche H.J. (2006) Life cycle of *Pseudocalanus acuspes* Giesbrecht (Copepoda, Calanoida) in the Central Baltic Sea: I. Seasonal and spatial distribution. Marine Biology 148:567-580

Rice J.A., Crowder L.B., Holey M.E. (1987) Exploration of mechanisms regulating larval survival in Lake Michigan bloater: A recruitment analysis based on characteristics of individual larvae. Transactions of the American Fisheries Society 116:703-718

Schmidt J.O. (2006) Small and meso-scale distribution patterns of key copepod species in the Central Baltic Sea and their relevance for larval fish survival. PhD thesis, Christian-Albrechts-University, Kiel, Germany

Schmidt J.O., Hinrichsen H.H. (2008) Impact of prey field variability on early cod *Gadus morhua* larval survival: a sensitivity study of a Baltic cod Individual-based Model. Oceanologia 50:205-220

Sissenwine M.P. (1984) Why do fish populations vary? In: R.M.May (ed) Exploitation of marine communities. Springer Verlag, New York, p 59-94

Sogard S.M. (1997) Size-selective mortality in the juvenile stage of teleost fishes: A review. Bulletin of Marine Science 60:1129-1157

Stevenson D.K., Campana S.E.ed. (1992) Otolith microstructure examination and analysis. Canadian Special Publication of Fisheries and Aquatic Sciences 117, 132 pp.

Sundby S. (2000) Recruitment of Atlantic cod stocks in relation to temperature and advection of copepod populations. Sarsia 85:277-298

Taggart C.T., Frank K.T. (1990) Perspectives on larval fish ecology and recruitment processes: probing the scales of relationships. In: K.Sherman, L.M.Alexander, and B.D.Gold (eds) Large Marine Ecosystems: Patterns, Processes and Yields. American Association for the Advancement of Science, Washington, DC, p 151-164

The BACC Author Team (2008) Assessment of Climate Change for the Baltic Sea Basin. Springer, Berlin, Heidelberg.

Titus R.G., Mosegaard H. (1991) Selection for growth-potential among migratory Brown Trout (*Salmo trutta*) fry competing for territories - Evidence from Otoliths. Canadian Journal of Fisheries and Aquatic Sciences 48:19-27

Trippel E.A., Kraus G., Koester F.W. (2005) Maternal and paternal influences on early life history traits and processes of Baltic cod *Gadus morhua*. Marine Ecology Progress Series 303:259-267

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

Vikebø F., Jørgensen C., Kristiansen T., Fiksen Ø. (2007) Drift, growth, and survival of larval Northeast Arctic cod with simple rules of behaviour. Marine Ecology Progress Series 347:207-219

Voss R., Hinrichsen H.H., St.john M. (1999) Variations in the drift of larval cod (*Gadus morhua* L.) in the Baltic Sea: combining field observations and modelling. Fisheries Oceanography 8:199-211

Voss R., Koester F.W., Dickmann M. (2003) Comparing the feeding habits of co-occurring sprat (*Sprattus sprattus*) and cod (*Gadus morhua*) larvae in the Bornholm Basin, Baltic Sea. Fisheries Research 63:97-111

Wieland K., Zuzarte F. (1991) Vertical distribution of cod and sprat eggs and larvae in the Bornholm Basin (Baltic Sea) 1987-1990. ICES CM1991/J:37

Wieland K., Jarre-Teichmann A., Horbowa K. (2000) Changes in the timing of spawning of Baltic cod: possible causes and implications for recruitment. ICES Journal of Marine Science 57:452-464

PAPER 3

Vertical distribution and growth of Baltic Cod larvae - field evidence for a spatial match-mismatch hypothesis?

B. Huwer[1,3], C. Clemmesen[2], and P. Grønkjær[3]

[1] Technical University of Denmark, National Institute of Aquatic Resources, Charlottenlund Slot, Jægersborg Allee 1, DK-2920 Charlottenlund, Denmark

[2] Leibniz-Institute of Marine Research, IFM-GEOMAR, Duesternbrooker Weg 20, D-24105 Kiel, Germany

[3] Aarhus University, Department of Biological Sciences, Finlandsgade 14, 8200 Aarhus N, Denmark

ABSTRACT

Besides variable egg survival, previous studies suggested that the larval stage may be the most critical phase in determining Baltic cod recruitment variability, and that larvae need to conduct an ontogenetic vertical migration from hatching depths (> 50 m) to upper layers with increased food availability in order to initiate first feeding, improve their nutritional condition and growth, and avoid starvation. Recently, detailed information on the stage-resolved vertical distribution of *Pseudocalanus acuspes*, the preferred larval Baltic cod prey item, has become available. Therefore, the vertical distribution of Baltic cod larvae, as well as their depth-dependent nutritional condition and growth, were investigated in August 2007 by sampling with multiple opening-closing nets and RNA-DNA based estimations of specific growth rates and growth performance. The need for early larvae to migrate to shallower layers was corroborated, however, larger larvae were found at larger depths, indicating a continuation of the ontogenetic vertical migration in order to follow increasingly larger prey items at larger depths and to save energy in cooler waters below the thermocline. Larval growth declined with increasing depth, however, this tendency became less pronounced with larger size, indicating that larger larvae were better in coping with the environment at larger depths. Besides, differences in larval growth between sampling stations were observed, which may be related to horizontal differences in zooplankton composition. Generally, larval Baltic cod grew poorly in comparison with larvae from other studies. Comparison with earlier results from 1994 and 1995, a period of low recruitment despite favourable conditions for egg survival, showed a higher frequency of starving larvae and lower frequencies of larger larvae after the first-feeding stage in those years. It is concluded that larval starvation mortality has a high potential to contribute to recruitment variability in Baltic cod.

Key words: Bornholm Basin, recruitment, vertical migration, condition, RNA, DNA, standardized RNA/DNA ratio, specific growth rate, growth performance, survival

INTRODUCTION

The Eastern Baltic cod stock (in the following referred to as Baltic cod) has shown large fluctuations in both stock size and recruitment success. After being on historically high levels in the early 1980's (Eero et al. 2008), stock size rapidly declined and remained below average, although the latest assessments show a slow recovery in recent years (ICES 2009). A combination of high fishing pressure and unfavourable environmental conditions has influenced recruitment, presumably via high egg mortalities due to predation and detrimental ambient oxygen concentrations, caused by a lack of formerly regular inflows of oxygen-rich water from the North Sea to the spawning areas in the Baltic Sea basins (Koester et al. 2001, Koester et al. 2005). However, following Paulik's framework of studying the recruitment process, the analysis of a time series of abundance data of consecutive life stages suggested that the larval stage may be the most critical phase in determining Baltic cod recruitment variability (Koester et al. 2003).

Several biophysical modeling studies addressed the issue of larval survival success (Voss et al. 1999, Hinrichsen et al. 2001, Hinrichsen et al. 2002, Hinrichsen et al. 2003b, Hinrichsen et al. 2005, Schmidt & Hinrichsen 2008), but information on larval-stage processes from field studies is limited. Exceptions are studies by Grønkjær and Wieland (1997) and Grønkjær et al. (1997), who investigated the vertical distribution and depth-dependent nutritional condition and growth of cod larvae in the Bornholm Basin (Fig. 1). This area is the most important Baltic cod spawning ground in the present environmental situation, as the lack of inflows caused severe oxygen depletion in the more eastern historical spawning areas, i.e. the Gdansk Deep and Gotland Basin (Bagge et al. 1994).

In contrast to most other cod stocks (ICES 2005), Baltic cod larvae hatch in deeper layers > 50 m, because eggs are neutrally buoyant in the region of the permanent halocline (Mueller 1988, Wieland & Jarre-Teichmann 1997). As this is a region of low light and prey availability, Grønkjær and Wieland (1997) hypothesized that larvae need to conduct an ontogenetic vertical migration from hatching depths to upper layers with increased food availability in order to initiate first feeding, improve their nutritional condition and avoid starvation. This hypothesis was corroborated by RNA/DNA based growth and condition estimates (Grønkjær et al. 1997), which have proven to be a valuable tool in larval growth and recruitment studies (e.g., (Clemmesen 1996, Buckley et al. 1999, Buckley et al. 2006, Malzahn et al. 2007, Chicharo & Chicharo 2008). Even though larvae were generally in very poor condition, individuals above the halocline expressed better growth than those caught at larger depths, indicating a vertical match-mismatch situation related to the availability of zooplankton prey organisms (Grønkjær et al. 1997).

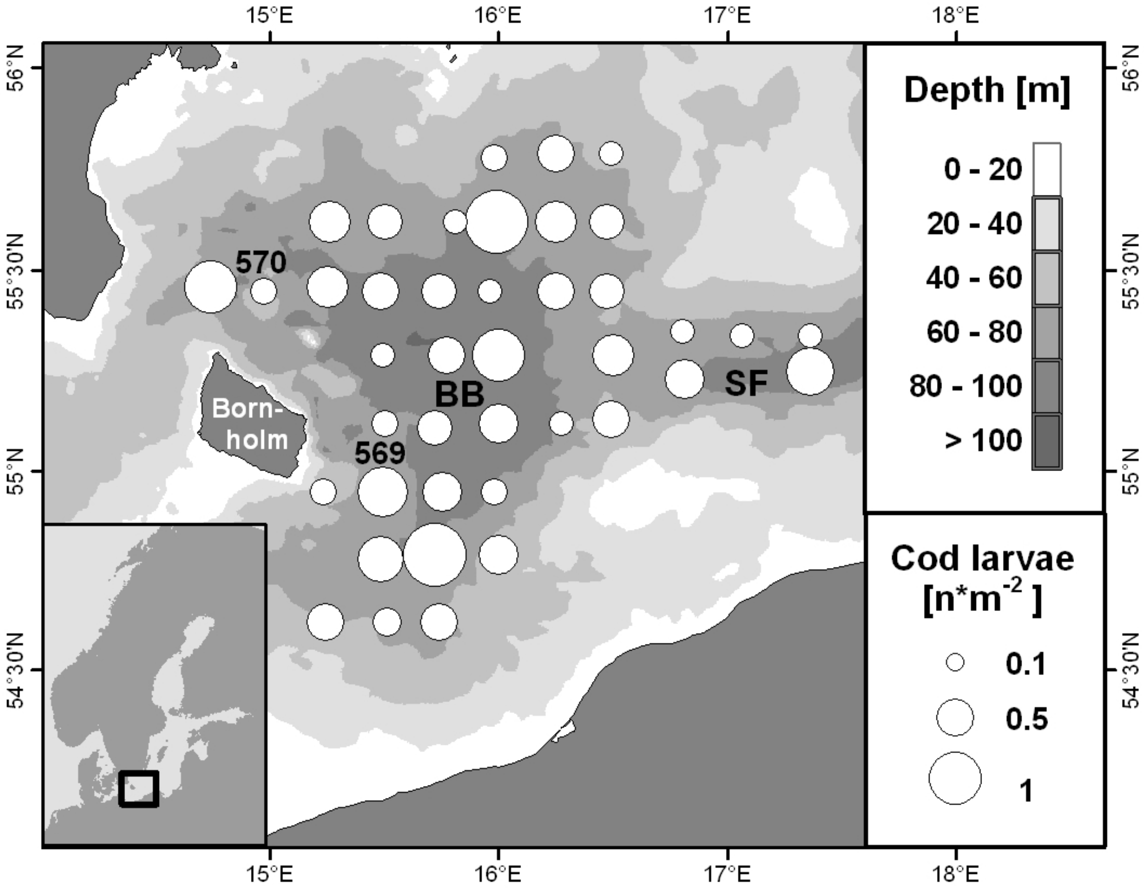


Fig. 1: Study area in the Bornholm Basin, depths (color scale) and abundances of Baltic cod (*Gadus morhua*) larvae determined by double oblique Bongo net hauls (symbols). The insert shows the location of the Bornholm Basin in the Baltic Sea. Numbers above the symbols indicate the positions of the two 24-hour Multinet sampling stations. BB = Bornholm Basin, SF = Slupsk Furrow.

While it has earlier been postulated that zooplankton abundances in the Baltic are generally high enough to exclude starvation as a major source of larval cod mortality (Krajewska-Soltys & Linkowski 1994, Zuzarte et al. 1996), the poor larval condition found by Grønkjær et al. (1997), as well as more recent field (paper 1) and modeling (Hinrichsen et al. 2002) studies, indicate severe starvation, at least for first-feeding larvae. MacKenzie et al. (1996) stated that available prey quantities for larval cod are difficult to assess in the Baltic, due to the strong spatio-temporal patterns in abundance and composition of potential prey. Recently, detailed information on the stage-resolved vertical distribution of the most abundant Baltic copepod species, which may influence the vertical distribution and growth of larval fish, has become available (Fig. 2, Renz & Hirche 2006, Schmidt 2006). In addition to the vertical patterns, the Baltic zooplankton community shows strong spatial, seasonal and long-time dynamics in terms of abundance, distribution and composition of different species and life stages (Fig. 2, Moellmann et al. 2000, Moellmann et al. 2009).

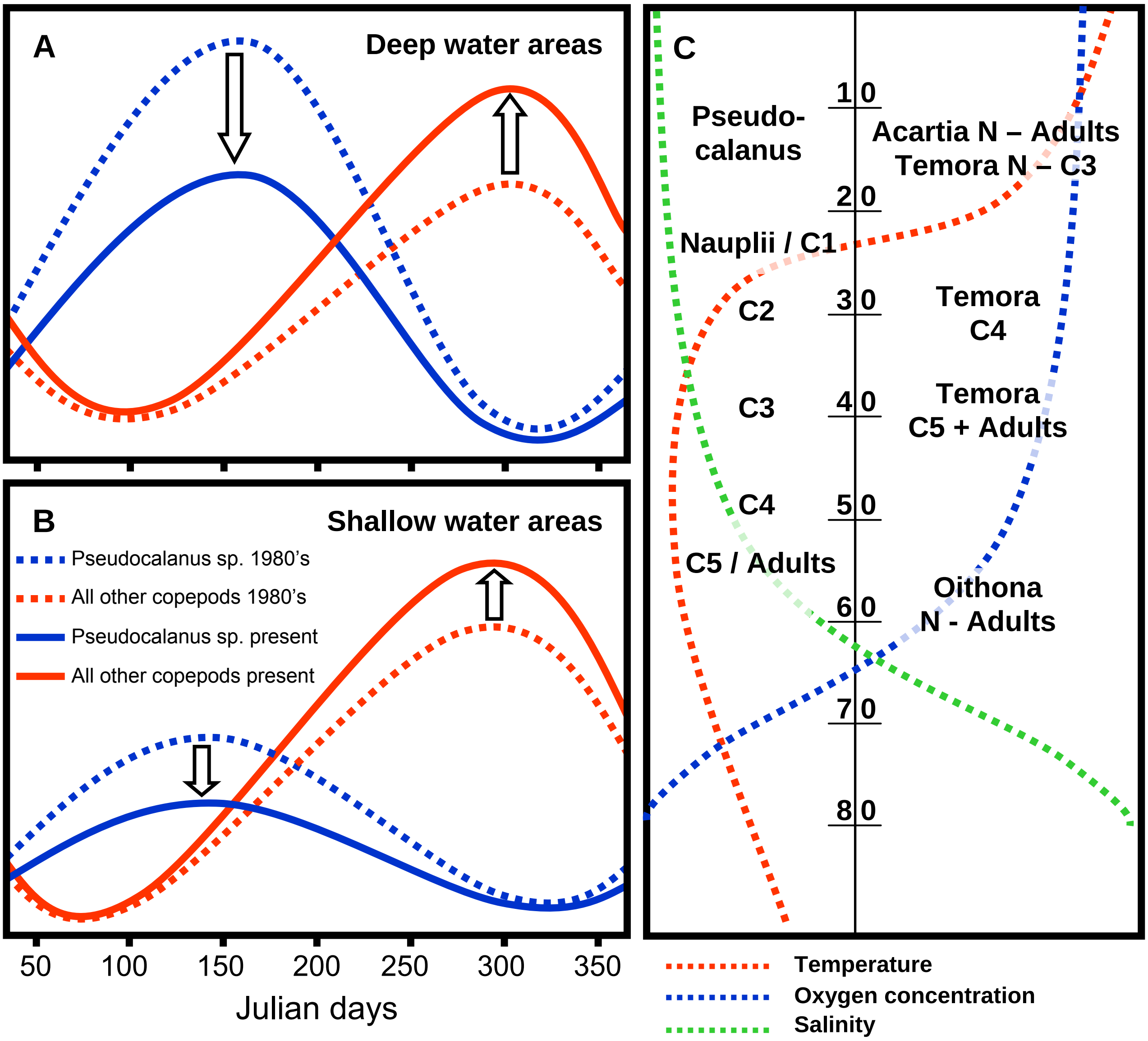


Fig. 2: Scheme of the seasonal and long-time abundance development (1980's vs present, arrows) of the major Baltic copepod species in central Baltic deep water areas (a) and shallow water areas (b), and their schematic vertical distribution (c). The vertical distribution in (c) shows the situation in summer at daytime, as cod larvae are visual feeders, and therefore the vertical distribution of potential prey during daylight hours is relevant for this study. The vertical distribution of the different developmental stages of *Pseudocalanus acuspes* is shown left of the depth scale, while *Acartia sp.*, *Temora longicornis* and *Oithona similis* are shown on the right side. (a + b after Möllmann 2000 and Schmidt 2006, c after Schmidt 2006 and Renz & Hirche 2006).

Consistent with these general patterns, modeling studies (Hinrichsen et al. 2002, Hinrichsen et al. 2003b) have found that the long-term decrease in the abundances of *Pseudocalanus acuspes*, the preferred larval cod prey item (Zuzarte et al. 1996, Voss et al. 2003), has resulted in a shift of first-feeding Baltic cod larvae from a non-limited to a food-limited stage. The models also predicted higher survival probabilities of larvae in the later part of the spawning season, or if larvae were transported into shallower areas, which was supported by a coupled field and drift modeling study (paper 1).

The biophysical modelling and the new knowledge on vertical and horizontal distribution of the larval cod prey items suggest that there should be considerable spatial variation in larval nutritional condition and growth in the Bornholm Basin. This, and the poor knowledge of the role of larval-stage processes in determining Baltic cod recruitment dynamics, prompted us to revisit the vertical distribution and depth-dependent nutritional condition and growth of cod larvae sampled in August 2007. Our results are set in relation to previous studies on the subject that were conducted in 1994 and 1995 (Grønkjær et al. 1997, Grønkjær & Wieland 1997) and are discussed with respect to the recruitment process of Baltic cod.

MATERIAL AND METHODS

Field sampling

Samples of cod larvae were collected in the Bornholm Basin of the Baltic Sea during a cruise with the research vessel 'ALKOR' from August 1-13, 2007. First, double oblique hauls with a Bongo net (60 cm mouth diameter, mesh size 335 and 500 µm) were conducted on a station grid with approximately 10 nautical miles spacing to quickly map the horizontal distribution of larvae in the area (Fig. 1). This was followed by vertically resolving Multinet sampling. Two positions for the Multinet sampling, one in the central and one on the edge of the basin, were chosen on the basis of maximum larval numbers in the Bongo nets (500 µm). Station 569 was located close to the central part of the Bornholm Basin east of Bornholm, while station 570 was located at the basin edge north of Bornholm. At each sampling station vertical profiles of the ambient hydrographic conditions (salinity, temperature, oxygen concentration) were recorded with a CTD.

The Multinet (Hydro-Bios, Kiel, Germany, Type MAXI, aperture 71 X 71 cm = 0.5 m^2) is an opening-closing net system equipped with 9 net bags (mesh size 335 µm), which allowed us to sample one profile of the entire water column in 5 meter depth intervals with a set of two hauls, one haul sampling from the bottom to mid-depths, the other from mid-depth to the surface. On both stations, sampling was conducted over a 24-hour period at intervals of ca. 4 hours, resulting in 6 complete vertical profiles at each station (Station 569: August 9-10, Station 570: August 11-12). In each 5-m depth interval the gear was towed at a speed of 3 knots for approximately 3 minutes and the filtered volume was recorded with electronic flowmeters mounted on the sampling gear.

Upon retrieval of the gear, samples were transferred to plastic jars (Kautex 500 ml) and kept on ice to avoid degradation of nucleic acids. Cod larvae were immediately sorted from the samples under a stereomicroscope and placed into ice-cooled Petri dishes with sea water. Each larva was placed on a glass object slide with engraved scale bar and a picture was taken with a digital camera mounted on a dissecting microscope for subsequent length measurements. Thereafter, larvae were quickly transferred individually into labelled Eppendorf vials filled with sea water and frozen at -80°C. All samples were frozen within 30 min. after capture.

As Baltic cod larvae are scarce, additional hauls in between the standard 4-hour sampling scheme were used to increase the number of larval samples for later growth analyses in the laboratory. These additional nets were deployed at selected depths of larval abundance peaks observed during the standard sampling. A detailed overview of the numbers of larvae caught in the standard and additional sampling per station and depth range, as well as the numbers of larvae used for RNA/DNA analyses, is given in Table 1. At stations 569 and 570, total numbers (+ additional hauls in parentheses) of 83 (151) and 46 (101) Baltic cod larvae were obtained, respectively. For analyses of the vertical distribution, only larvae from the standard sampling scheme were considered. For length frequencies of larvae, both the standard hauls and the standard hauls including the additional samples are presented.

Laboratory analyses

Larval standard length (SL, mm) measurements were conducted on the digital larval images taken immediately after catch onboard the research vessel with the aid of an image analysis system (Image Tool). The vials containing larval samples were allowed to defrost. During the further processing vials were kept on ice as much as possible to avoid measurement bias in the determination of RNA and DNA due to warming. The thawed larvae were photographed again as decribed above to determine their shrinkage due to preservation at -80°C (larval shrinkage results will be presented elsewhere, in the present study, standard lengths from fresh samples are used).

Larvae were refrozen at -74°C and then transferred to a freeze-drier (Christ alpha 1-4) for 16 h at -51°C. Larval freeze-dried mass was then recorded to the nearest µg on a Sartorius Micro SC2 balance. Right and left sagitta and lapillus were quickly removed from freeze dried individual larvae under a dissecting microscope at 60× magnification using a polarised light source and fine insect needles and mounted on glass slides with thermoplastic resin (results of otolith analyses will be presented elsewhere).

Table 1: Overview of Baltic cod larvae sampled in standard and additional hauls in different depth ranges at the two sampling stations, and number of larvae on which RNA/DNA measurements were conducted.

Station	Depth range [m]	standard nets [n]	extra nets [n]	cod larvae standard hauls [n]	cod larvae extra hauls [n]	cod larvae sum [n]	cod larvae RNA/DNA [n]
569	0-5	6	-	0	-	0	0
	5-10	6	-	0	-	0	0
	10-15	6	-	1	-	1	1
	15-20	6	-	2	-	2	2
	20-25	6	-	7	-	7	7
	25-30	6	2	15	35	50	43
	30-35	6	2	9	8	17	16
	35-40	6	-	6	-	6	6
	40-45	6	-	15	-	15	15
	45-50	6	1	8	1	9	9
	50-55	6	2	4	14	18	17
	55-60	6	2	14	10	24	24
	60-65	6	-	1	-	1	1
	65-70	6	-	1	-	1	1
	70-75	6	-	0	-	0	0
	75-80	6	-	0	-	0	0
	80-85	6	-	0	-	0	0
	85-90	6	-	0	-	0	0
	90-95	6	-	0	-	0	0
	SUM	114	9	83	68	151	142
570	0-5	6	-	0	-	0	0
	5-10	6	-	0	-	0	0
	10-15	6	-	0	-	0	0
	15-20	6	-	1	-	1	1
	20-25	6	-	1	-	1	1
	25-30	6	2	9	27	36	36
	30-35	6	2	16	15	31	30
	35-40	6	1	11	13	24	23
	40-45	6	-	0	-	0	0
	45-50	6	-	2	-	2	2
	50-55	6	-	3	-	3	2
	55-60	6	-	2	-	2	2
	60-65	6	-	1	-	1	0
	65-70	6	-	0	-	0	0
	70-75	6	-	0	-	0	0
	75-80	6	-	0	-	0	0
	80-85	6	-	0	-	0	0
	85-90	6	-	0	-	0	0
	90-95	6	-	0	-	0	0
	SUM	114	5	46	55	101	97

Following otolith removal the larvae were rehydrated in Tris-SDS buffer (Tris 0.05 M, NaCl 0.1 M, EDTA 0.01 M, SDS 0.01%) for 30 min. and the concentrations of RNA and DNA of individual larvae were analysed using a modification of the method by Clemmesen (1993) as described in Malzahn et al. (2003) and Belchier et al. (2004). Cells were disrupted by shaking in a cell mill (Mixer Mill MM2 by Retsch) for 15 min with a mixture of two different size glass beads (diameters Ø 2 mm and 0.17-0.46 mm). The homogenate was centrifuged for 8 min at 3829 rzb (6800 rpm) and 0°C (Sigma Laboratories Centrifuges 3-18K). The supernatant was pipetted into a new 1.5 ml cap vial, diluted according to the dry weight of the sample, vortexed, and pipetted into a black 96-well microtitre plate. The fluorometric assay was performed by a Labsystems Fluoroscan Ascent that has integrated dispensers for both ethidium bromide and TE buffer, with an excitation wavelength of 355 nm and measuring at an emission wavelength of 590 nm. Calibration curves for RNA (16S, 23S ribosomal RNA, Boehringer Mannheim) and DNA (Lambda DNA, Roche Diagnostics) were determined. A control homogenate was added in two wells on every measuring day for quality control of the instruments and chemicals used.

Autofluorescence was measured first, before the fluorophore ethidium bromide was added to all of the microplate wells. Then total nucleic acid fluorescence was measured, and RNase was added to the sample wells. After the enzyme treatment (30 min. at 37°C) the remaining DNA was measured. RNA fluorescence was calculated by subtracting DNA fluorescence from the total nucleic acid fluorescence, and by using the calibration curves fitted to the standards. The ratio of DNA and RNA slopes was 2.2. Due to loss or damage during larval handling in the laboratory, 13 out of a total of 252 larvae (9 of 151 and 4 of 101 at stations 569 and 570, respectively, see also table 1) were not available for RNA-DNA analyses.

Determination of larval growth and growth performance

The ratio of RNA to DNA (RD) is one of the most frequently applied methods to analyse nutritional condition and growth of individual field-caught fish larvae. While the mere RNA-DNA ratio provides an indication of the nutritional condition of a larva, it can be converted to an estimate of growth rate by applying laboratory-derived RD-growth models. However, since the rate of protein synthesis per unit RNA is temperature dependent, such growth models need to contain a temperature term (RD-T-G models). As laboratory studies with different temperature and prey levels are time consuming and costly, such models exist only for a few species, but Buckley et al. (2008) have recently presented multi-species growth models based on RD, temperature and growth compiled from several laboratory studies. Even though specific RD-T-G models for cod and a combined cod-haddock data set exist (Caldarone et al. 2003, Buckley et al. 2008), we chose to apply a multi-species model provided by Buckley et al. (2008) including RD and an RD-Temperature interaction term, as this model covers a broader temperature range (3.4-28°C) than the cod-specific models (3-10°C). Thus, the multi-species model better suited the high temperature range (5.5-15.5°C) experienced by the Baltic cod larvae in the present study. In order to be able to apply this model to larval Baltic cod, we converted our RD values to standardized RD (sRD) according to the method outlined in Caldarone et al. (2006), i.e. we standardized to a DNA/RNA slope ratio of 2.4. Weight-specific growth rates (G, d^{-1}) from these sRD data were then derived from the multi-species model (Buckley et al. 2008):

$$(1) \quad G = 0.0145 * sRD + 0.0044 * sRD * T - 0.078$$

with T = mean ambient temperatures in the 5-meter depth intervals where the larvae were caught. G was further converted to specific growth rate (SGR, % * d^{-1}) according to the following equation:

$$(2) \quad SGR = 100 * (e^{G} - 1)$$

Both laboratory and field studies have shown that RNA, DNA, RD, G and SGR are dependent on larval size as well as temperature, at least for larvae growing less than optimally. However, by relating observed growth to the maximal possible growth (Gmax) for a given temperature and larval size combination, one would attain an objective measure of larval condition (Buckley et al. 2006, Buckley et al. 2008). As a reliable measure of Gmax is difficult to obtain, it has been suggested to use a reference growth rate, Gref, of preferably fast growing laboratory fish as a proxy for Gmax (Buckley et al. 2008). We have followed this suggestion in the present study. We calculated Gref of our Baltic cod larvae with an equation provided by Folkvord (2005) from well-fed, fast growing Norwegian coastal cod reared in the laboratory:

$$(3) \quad Gref = 1.20 + 1.80 * T - 0.078 * T * \ln DW - 0.0946 * T * (\ln DW)^{2} + 0.0105 * T * (\ln DW)^{3}$$

with Gref = specific reference growth rate (%*d^{-1}) as proxy for Gmax, T = temperature (°C) and DW = larval dry weight (mg). Finally, through division of our sRD-derived specific growth rates (SGR) by Gref, we obtained growth performance (Gpf).

$$(4) \quad Gpf = SGR/Gref$$

Growth performance is the ratio of actually realized growth in our field samples relative to the fast growth of laboratory-reared larvae (a proxy for maximal possible growth) for a given larval size (dry weight, mg) at a given temperature. Therefore, Gpf provides an objective measure of larval condition that is not dependent on larval size and temperature, and values of Gpf can be directly compared between different temperatures and larval sizes. As Folkvord's (2005) model was not validated for larval dryweights < 0.03 mg, larvae below this threshold level were excluded from further analyses of Gpf.

Data analyses and statistical treatment

The observations of SGR and Gpf were recorded at 12 and 8 different depth levels on stations 569 and 570, respectively. To simplify, these levels were aggregated into 4 depth groups. These depth ranges were chosen on the basis of the vertical profiles of temperature and oxygen concentration and the vertical distribution of potential larval prey items from the literature (Fig. 2) with focus on *Pseudocalanus acuspes*, as this species was found to be positively selected by larval Baltic cod. The first range (“shallow”, < 25 m) represented larvae caught in very warm water in or above the summer thermocline with high abundance of nauplii and C1 copepodites. The second range (“upper-middepths”, 25-35 m) included larvae caught at more moderate temperatures at the lower end of the thermocline with increasing fractions of larger prey (C2 *Pseudocalanus acuspes*, C4 *Temora longicornis*). The third range (“lower-middepth”, 35-50 m at station 569 and 35-45 m at station 570) showed relatively low temperatures below the thermocline and even larger prey items (C3+4 *Pseudocalanus acuspes*, C5-6 *Temora longicornis*). Finally, the fourth depth range (“deep”, >50 m at station 569 and >45 m at station 570) comprised larvae in and below the halocline, that experienced slightly warmer temperatures in concert with lower oxygen concentrations and larger prey items (*Pseudocalanus acuspes* C6), although all life stages of the relatively small species *Oithona similis* are also peaking at these depths (Fig. 2c).

The model reduction to 4 depth levels was tested in a one-way ANOVA model, and found non-significant (Station 569 SGR: $p = 0.68$, Gpf: $p = 0.56$; Station 570 SGR: $p = 0.10$, Gpf: $p = 0.95$). It was also tested if depth had no effect, but that was rejected (Station 569 SGR: $p < 0.001$, Gpf: $p = 0.03$; Station 570 SGR: $p < 0.01$, Gpf: $p < 0.001$). Having reduced the model to 4 depth levels we conducted pairwise comparisons of these levels. At station 569, possible differences in SGR and Gpf between the 4 depth groups were investigated by one-way ANOVAs and post-hoc comparison tests (Student-Newman-Keuls test, $\alpha = 0.05$). At station 570, normality tests for SGR and Gpf failed, and differences between the 4 depth groups were analysed by Kruskal-Wallis ANOVA on ranks and post-hoc comparison tests (Dunn’s test, $\alpha = 0.05$).

No significant correlation between length and growth performance (Gpf) was observed in our data, but specific growth rate (SGR) showed a significant increase with larval length (see results). Even though this relationship was weak and the average increase of SGR with length was relatively small in comparison to the general variability, this may introduce some bias in the results for SGR. Besides, different size classes of larvae may express differences in depth-dependent growth related to the vertical distribution of prey that shows strong differences in abundance, composition and therefore size of potential larval prey items (Fig. 2). Therefore, we divided the larvae into three functional size classes and analysed their growth in relation to depth. Larvae < 4.5 mm were considered pre-feeding yolk-sac larvae, larvae from 4.5-6 mm were considered first-feeding and early feeding larvae, and larvae > 6 mm were regarded as established feeders (Grønkjær & Wieland 1997, CORE 1998).

Possible larval growth differences between depth ranges and stations were analysed by parametric tests (ANOVA, Student's t-test). In cases where the assumptions of normality or homoscedasticity were not fulfilled, non-parametric methods were applied (Kruskal-Wallis ANOVA on ranks, Mann-Whitney U-test). Multiple comparisons between groups were conducted by Student-Newman-Keuls test (α = 0.05) or Dunn's test (α = 0.05).

RESULTS

Larval size and vertical distribution

Standard length frequencies of Baltic cod larvae are presented in Fig. 3. Standard lengths at station 569 ranged from 2-9 mm (median, mean ± sd: 5.6, 5.7 ± 1.4 for standard hauls and 5.4, 5.7 ± 1.3 for all larvae). At station 570, larvae ranged from 3-8 mm in length with the exception of one larva of 12 mm (median, mean ± sd: 5.2, 5.4 ± 1.5 for standard hauls and 5.2, 5.4 ± 1.3 for all larvae). Length distributions at the two stations were similar, however, higher frequencies of larger larvae were found at station 569. The % frequency of larvae in the size classes 4, 5, 6 and > 6 mm were 24, 28, 24 and 14 at station 569 and 33, 26, 22 and 6 at station 570. In comparison, the length frequency distribution of larvae from Grønkjær and Wieland's (1997) study from July 1994 (Fig. 3a) was heavily shifted to smaller sizes (78, 18, 3 and 1 % for the same length classes as above).

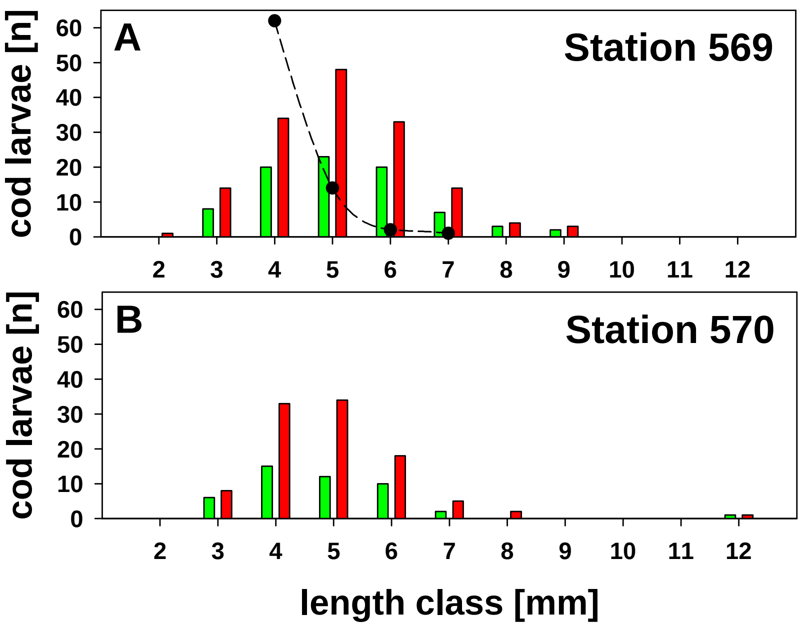


Fig. 3: Baltic cod (*Gadus morhua*) larvae. Length frequency distributions of larvae caught in the standard sampling scheme (green bars) and including larvae caught in additional sampling (red bars) at Station 569 (a) and 570 (b). Black dots and stippled line in (a) represent the length frequency distribution of larvae in July 1994 from the study by Grønkjær et al. (1997).

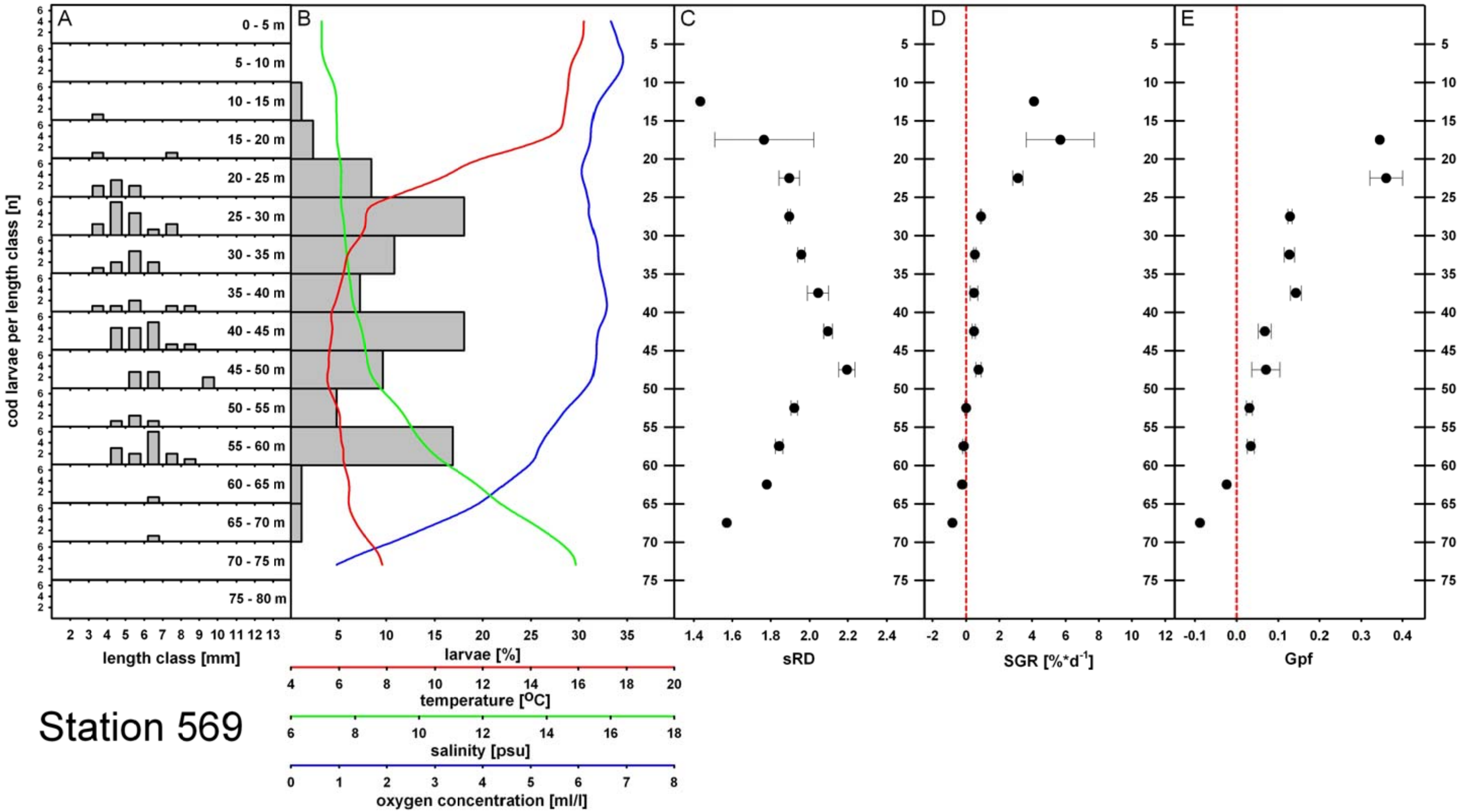


Fig. 4: Baltic cod (*Gadus morhua*) larvae at Station 569. Vertically resolved length frequency distributions (a), vertical distribution and ambient hydrography (b), and vertically resolved average values (+- standard error) of standardized RNA/DNA ratio (c), specific growth rate (d) and growth performance (e). Note: figures a and b are based on larvae obtained during the standard sampling program, while figures c, d and e also include larvae obtained during the additional sampling.

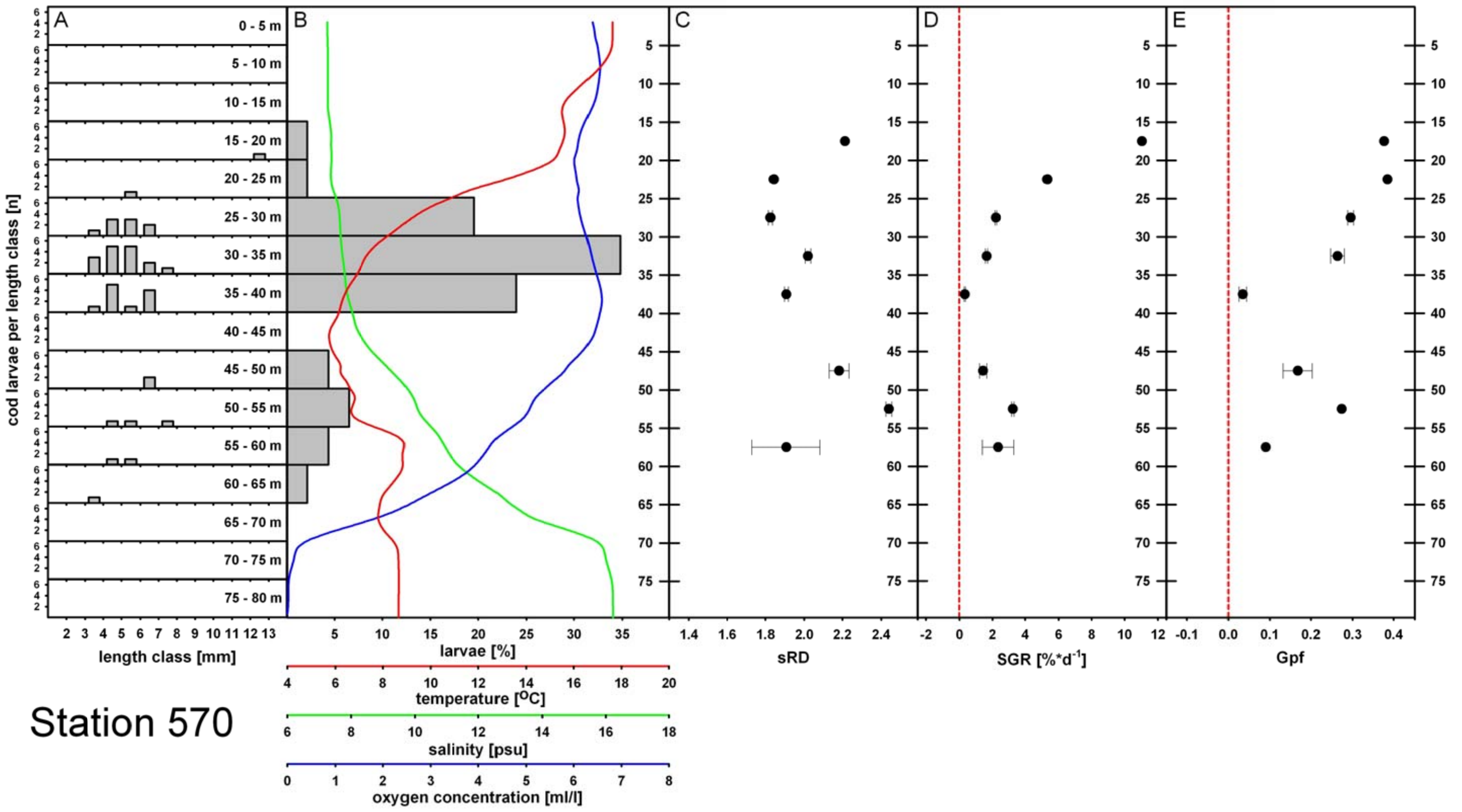


Fig. 5: Baltic cod (*Gadus morhua*) larvae at Station 570. Vertically resolved length frequency distributions (a), vertical distribution and ambient hydrography (b), and vertically resolved average values (+- standard error) of standardized RNA/DNA ratio (c), specific growth rate (d) and growth performance (e). Note: figures a and b are based on larvae obtained during the standard sampling program, while figures c, d and e also include larvae obtained during the additional sampling.

The vertical distribution of larvae at stations 569 and 570 shows different patterns (Fig. 4 and 5, B panels). At station 569 larvae were spread throughout the water column from 10 to 70 m, with three peaks at 25-30, 40-45 and 55-60 m. In contrast, at station 570 a peak at depths between 25 to 40 m and considerably fewer larvae at larger depths were observed.

When regarding the vertically resolved length frequency distributions (A panels), a clear pattern of increasing larval sizes at larger depths was observed at station 569, and linear regression revealed a statistically significant relationship between larval standard length and sampling depth (SL = 0.0409*depth+4.102; r^2=0.145; p=0.0004). However, after a continuous increase of mean lengths from 10 to 45 m, smaller mean lengths where found below 45 m in the region of the halocline (Fig. 6a). At station 570, no such clear pattern and no significant relation between length and depths was found (Fig. 6b). However, this may be related to the generally low number of larvae at larger depths.

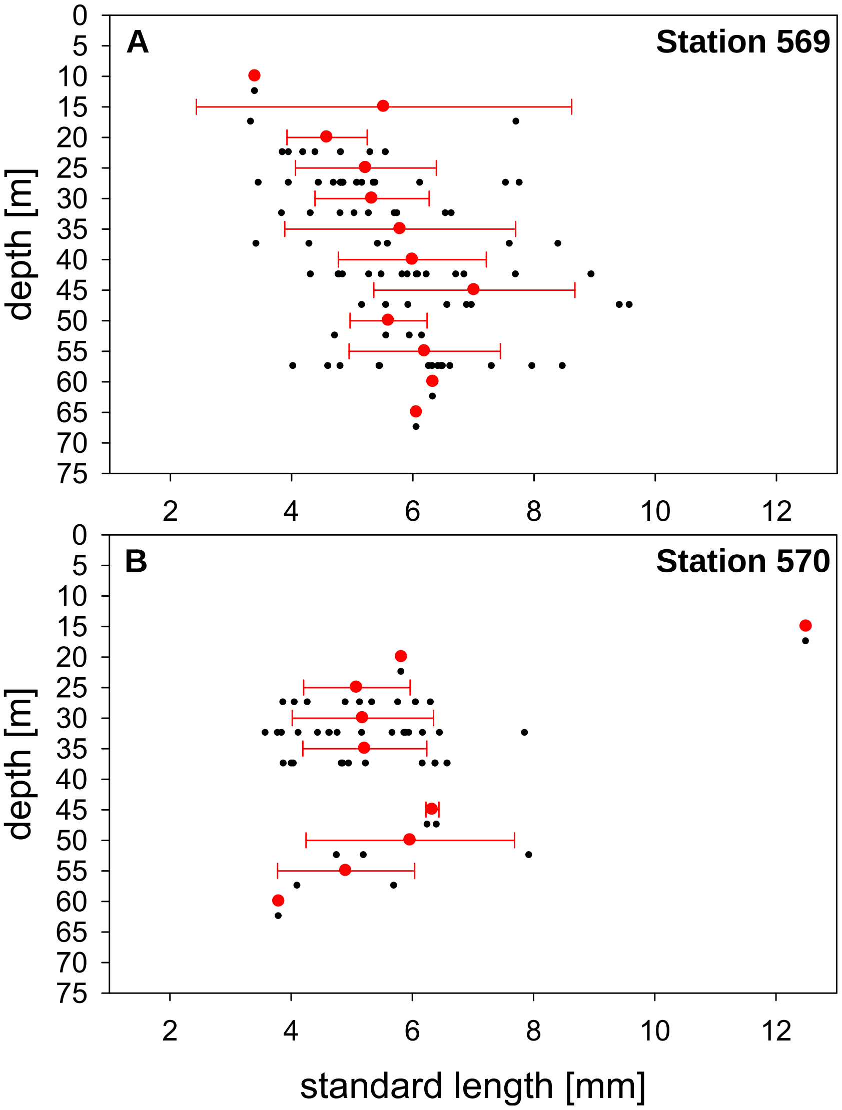


Fig. 6: Baltic cod (*Gadus morhua*) larvae. Standard length vs. mean sampling depth at station 569 (a) and 570 (b). Black symbols show the raw data, red symbols show the average (+- stdev) length per depth stratum (note: for presentation clarity, these symbols were shifted up by 2.5 meters).

Relationships between larval size and RNA, DNA, sRD, SGR and Gpf

The relationship between larval standard length and RNA and DNA content (Fig. 7a) was well-described by power-functions with exponents 2.94 and 2.81, respectively. The relationship between standard length and standardized RNA-DNA ratio was approximately linear with a positive slope of 0.094. (sRD; Fig. 7b).

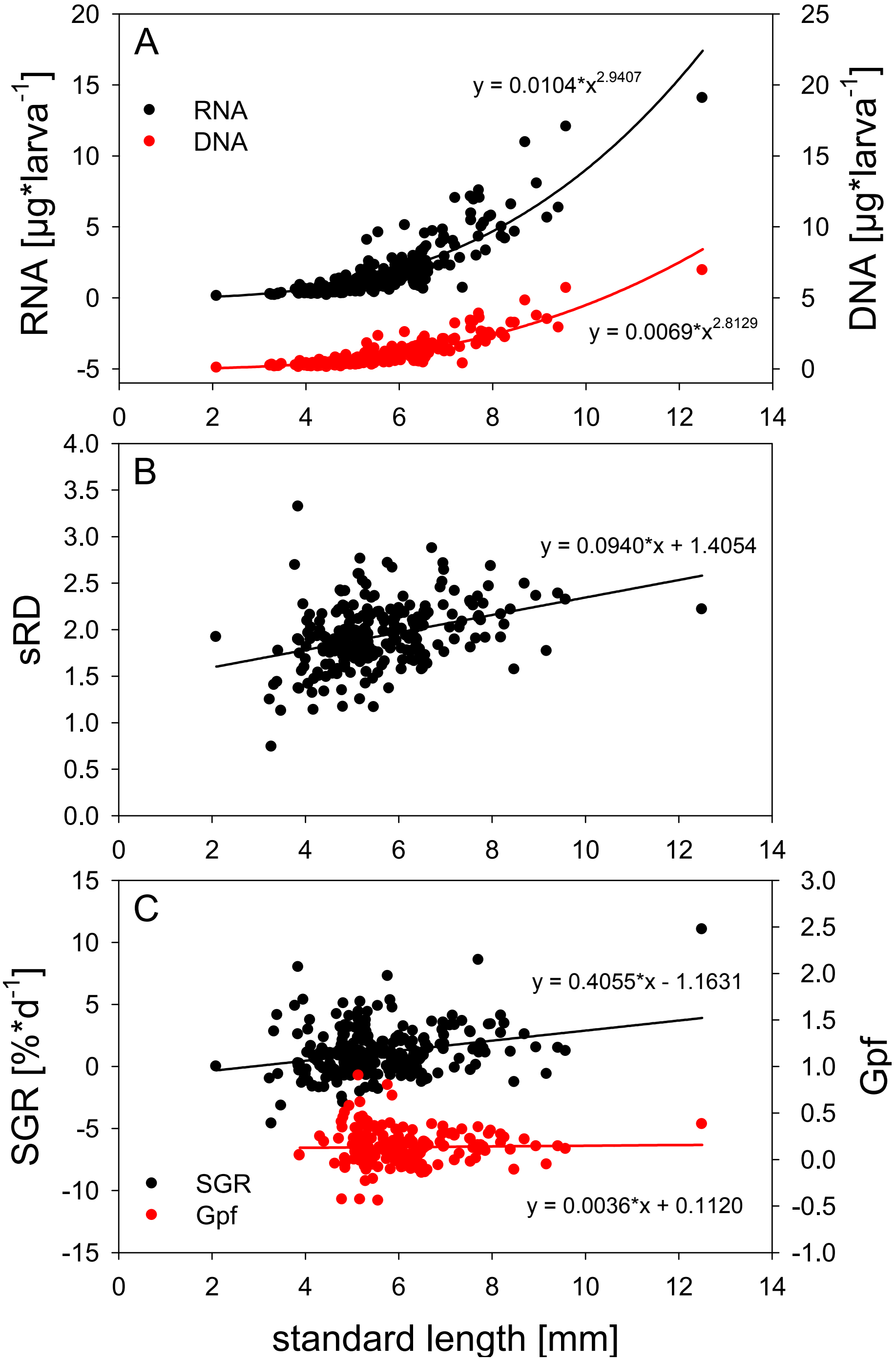


Fig. 7: Baltic cod (*Gadus morhua*) larvae. Relationships between standard length and (a) RNA (r^2 = 0.7549, p < 0.0001) and DNA (r^2 = 0.8853, p < 0.0001) content, (b) standardized RNA/DNA ratio (r^2 = 0.1274, p < 0.0001), and (c) Specific growth rate (r^2 = 0.0744, p < 0.0001) and Growth performance (r^2 = 0.0005, p = 0.7778). (Note: for presentation clarity, the scale for DNA in (a) was shifted by a factor of 5 to avoid overlap between symbols).

For specific growth rate (SGR), a weak but significant linear relationship was found. When the original RNA-DNA ratios were converted to growth performance (Gpf) there was no dependence of larval size on this index and hence this could be used to compare growth performance across size groups (Fig. 7c; for equations, r^2 and p-values, see Fig. 7).

Comparison of specific growth rates of our field-caught Baltic cod larvae with Gref showed that field larvae of all size ranges expressed very poor growth rates, with the majority of values ranging between 0 and 5 %*d^{-1}, while the predicted growth rates of well-fed laboratory larvae showed a rapid increase from about 5 to 10-15 %*d^{-1} and peak values of 25 and 30 %*d^{-1} (Fig. 8).

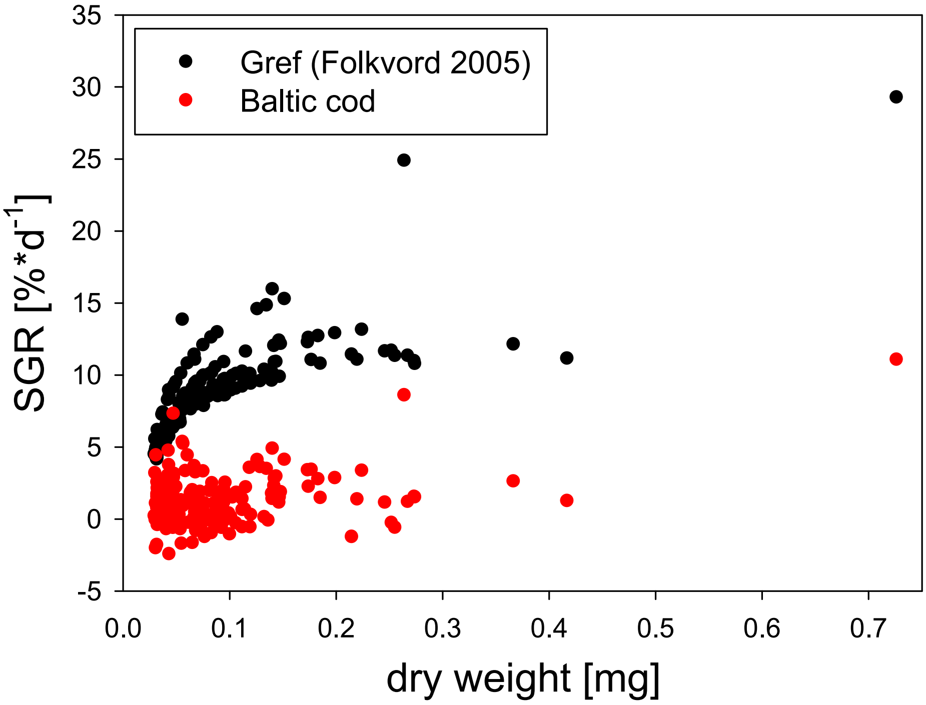


Fig. 8: Larval cod (*Gadus morhua*). Observed specific growth rates (SGR) of individual Baltic cod larvae (red dots, Station 569 and 570 combined) and predicted growth rates for well-fed larvae (black dots) vs. dry weight. Predicted growth rates (i.e. a proxy for Gmax) were estimated using the STDG model by Folkvord (2005) with larval dry weights and ambient temperatures of the Baltic cod larvae from the present study.

Hydrography and depth dependent sRD, SGR and Gpf

A very similar hydrographic situation was observed at both stations, showing the typical summer situation in the Bornholm Basin (Fig. 4 and 5, B panels). An extensive summer thermocline had developed, with temperatures of 16-18°C in the upper 15-20 m. Below this warm surface layer, temperatures rapidly decreased, reaching minimum temperatures slightly below 6°C at 40-45 m. However, while the decrease in temperature was very sharp at station 569, a more continuous temperature decline was observed at station 570. Below 45 m, temperatures increased again at both stations. At station 569, temperature slowly and steadily increased to 8°C at the bottom. In contrast, temperature at station 570 showed a sharp increase to ca. 8.5°C at about 55 m depth. Salinity and oxygen showed the typical picture of permanent stratification, with salinity increasing and oxygen concentration decreasing with larger depth. At station 570, however, the beginning of the salinity increase and oxygen decrease occurred ca. 10 meter higher up in the water column and was slightly steeper than at station 569. Due to the larger station depth (83 m), oxygen concentration reached anoxic levels at station 570, whereas oxygen concentration at the slightly shallower (77 m) station 569 reached a minimum level of about 1 $ml*l^{-1}$ at the bottom.

The development of sRD, SGR and Gpf with depth is depicted in panels C, D and E of Fig. 4 and 5 for stations 569 and 570, respectively. As the amount of protein synthesis taking place in a cell is strongly dependent on ambient temperatures and relatively less RNA is needed to obtain the same growth at higher temperatures (Buckley et al. 1999, Caldarone 2005), the sRD ratio per se has little explanatory value in the highly stratified waters of the Baltic. It is merely presented for the sake of completeness, and we will focus on SGR and Gpf, as they also account for the strong temperature influence on larval growth.

Both growth estimates show similar patterns. At station 569, a continuous decrease with increasing depth can be observed. Relatively high mean SGR values of 3 to 6 found in the thermocline rapidly drop to low (<1) but positive values in the region between thermocline and halocline. Below the halocline, mean growth rates become exclusively negative. With regards to Gpf, the general pattern is similar, but in contrast to SGR larvae in the range 25-40 m seem to show higher values than larvae from 40-50 m, and negative values are not observed until 60 m depth.

At station 570, the vertical pattern in SGR and Gpf development from 15-40 m resembles the one at station 569, although larvae in the upper 35 m generally express higher values than at station 569 for both parameters. However, a pattern very different from the one at station 569 is found below the halocline. Here, growth is apparently increasing again from only slightly positive values at 35-40 m depth to SGR values of 1.5-3.5 and Gpf values of 0.1-0.3 in the depth range 45 to 60 m.

Significant differences in SGR and Gpf between depth groups were found at both stations. At station 569 (Fig. 9a), larvae belonging to the “shallow” group showed significantly better SGR than larvae at all other depths. In addition, the “upper-middepth” range had significantly higher values than the “deep” group, but larval SGR at “lower-middepth” was not significantly different from larvae in either of the two neighboring depth ranges.

At station 570 (Fig. 9b), a different situation occurred. Unfortunately, the “shallow” group had to be excluded from the analysis because it only contained 2 observations, but the mean SGR-value of the two larvae in this depth range was clearly higher than in all other groups. Larvae from the “upper-middepth” and the “deep” group were significantly different from the “lower-middepth” larvae, but not from each other.

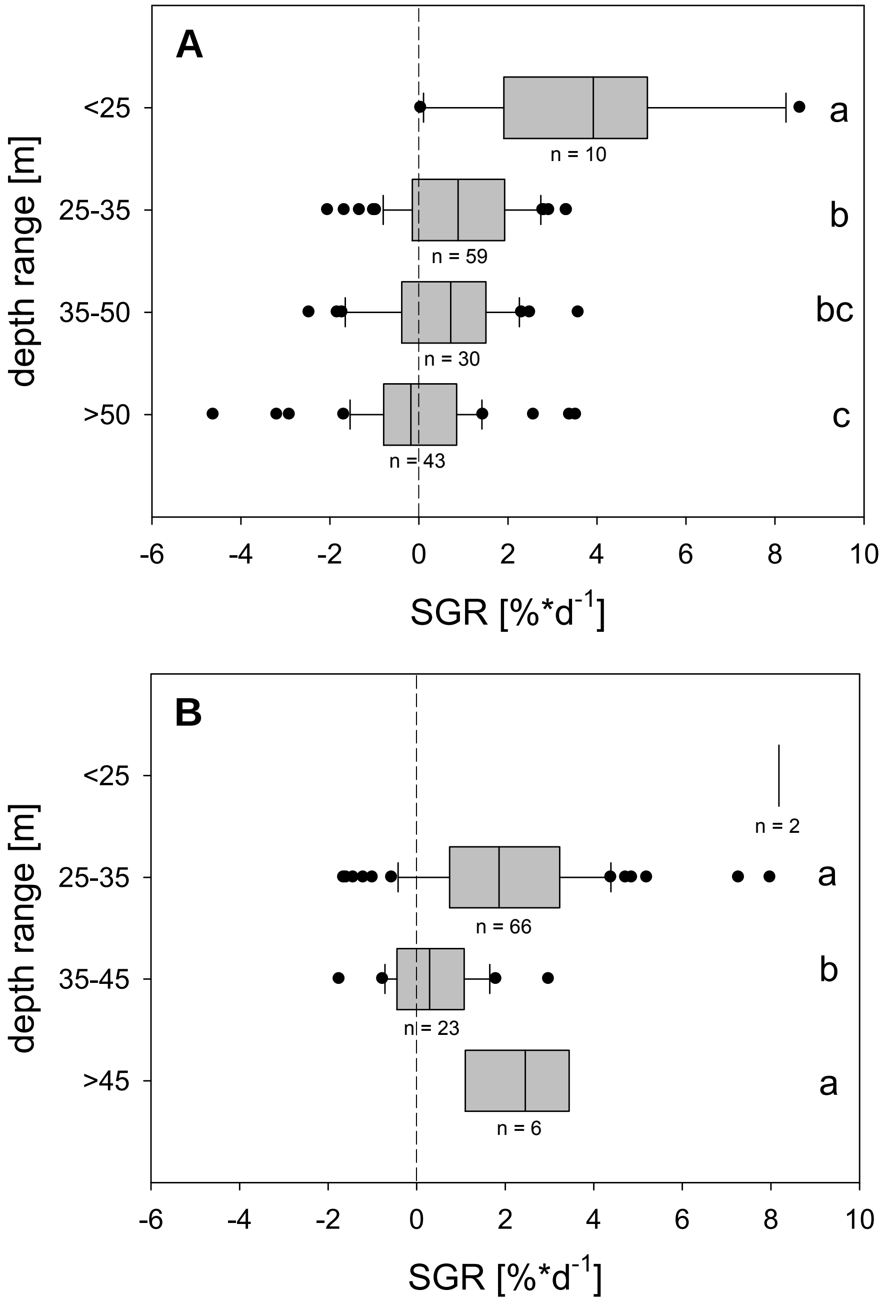


Fig. 9: Baltic cod (*Gadus morhua*) larvae. Specific growth rates (SGR, %*d^{-1}) in relation to sampling depth at station 569 (a) and 570 (b). Significant differences between depth ranges were observed (Station 569: p<0.001, Station 570: p<0.001). SGR of larvae from depth ranges sharing the same letter are not significantly different.

The comparison of Gpf between depth ranges at station 569 showed the same significance levels as for SGR (Fig. 10a). At station 570, the same pattern in mean values as for SGR was observed. However, the difference between “deep” and “lower-middepth” was not significant for Gpf (Fig. 10b).

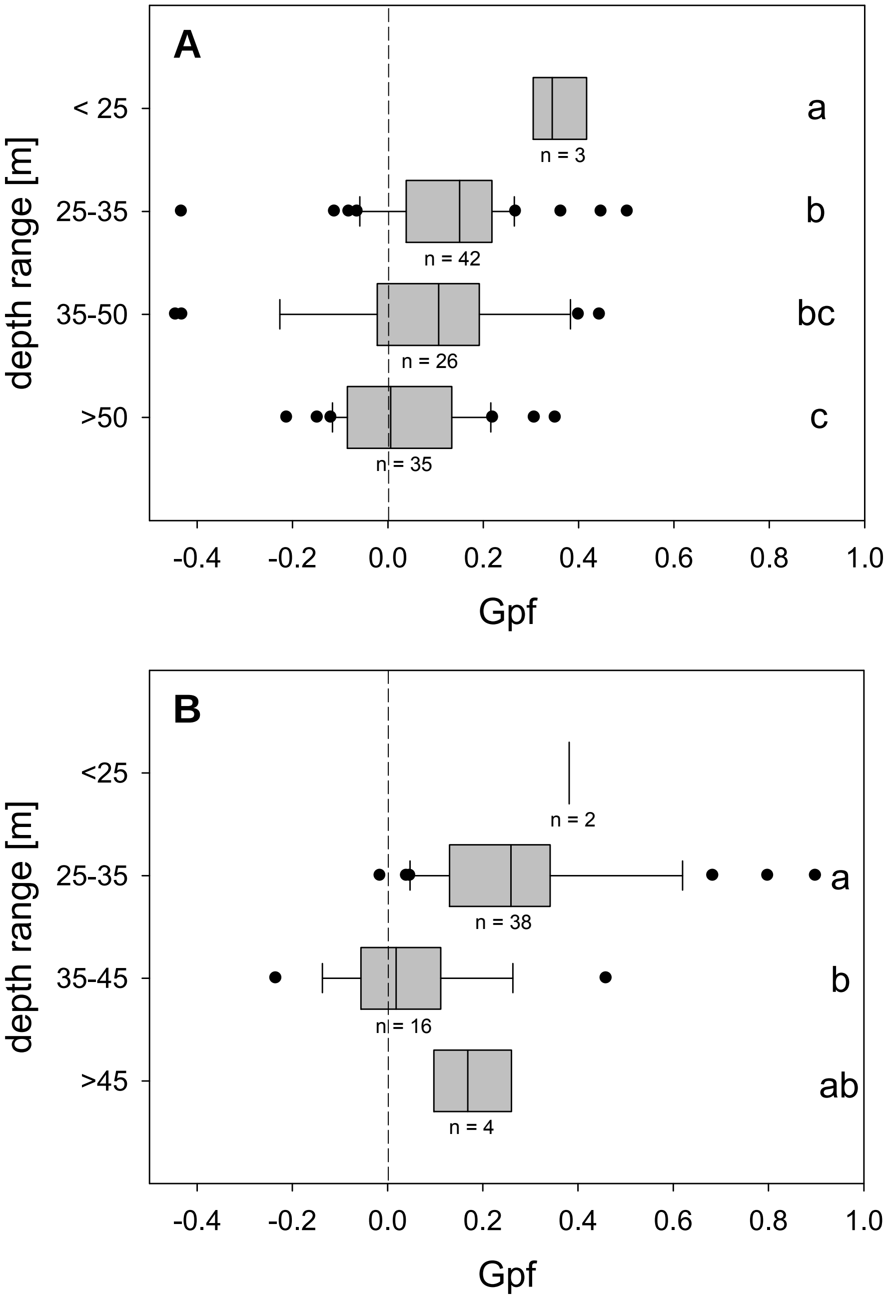


Fig. 10: Baltic cod (*Gadus morhua*) larvae. Growth performance (Gpf) in relation to sampling depth at station 569 (a) and 570 (b). Significant differences between depth ranges were observed (Station 569: p=0.003, Station 570: p<0.001). Gpf of larvae from depth ranges sharing the same letter are not significantly different. Note: as the model for Gref is not confirmed for larvae <0.03 mg dryweight, larvae below this threshold were removed from the analysis of differences in Gpf.

Growth of larvae in dependence of depth and larval size

In the previous section, we have described the depth-dependent growth of larval Baltic cod. However, in those analyses larvae of all sizes were pooled per depths class. As different size classes of larvae may express differences in depth-dependent growth related to the vertical distribution of prey, the larvae were split into three functional size classes and their growth in relation to depth analysed. For all size classes at both stations, the same trends in SGR and Gpf with depth as in the analysis regarding all size classes together were found, showing a general decrease at station 569 and an initial decrease from “shallow” to “lower-middepth” followed by an increase to “deep” waters at station 570 (Tables 2 and 3).

However, differences in the significance levels occurred after splitting the larvae into size classes. While the significance levels of SGR for medium and large and of Gpf for large larvae at station 569 remained the same, in small larvae only the “shallow” group was significantly different from all other depth groups.

Table 2: Baltic cod (*Gadus morhua*) larvae. Specific growth rates (SGR, %*d^{-1}) in relation to sampling depth at station 569 and 570 for different larval size classes. Significant differences between depth ranges were observed ($p < 0.05$). SGR of larvae from depth ranges sharing the same letter are not significantly different (KW = Kruskal-Wallis ANOVA). The column to the right shows results of comparisons between stations.

SGR [%*d^{-1}]		Station 569				Station 570				569 vs. 570
size class	depth range	n	mean ± sd	ANOVA	pos. gr. [%]	n	mean ± sd	ANOVA	pos. gr. [%]	p-value
< 4.5 mm	shallow	6	2.55 ± 2.02	a	100	0	-	-	-	-
	up-mid	9	-0.04 ± 0.10	b	56	14	1.19 ± 2.72	a	57	0.209
	low-mid	3	-0.77 ± 0.89	b	33	5	0.50 ± 0.81	a	80	0.082
	deep	5	-1.89 ± 1.97	b	0	1	3.71 -	-	100	-
4.5 - 6 mm	shallow	3	4.54 ± 0.73	a	100	1	5.32 -		100	-
	up-mid	39	0.65 ± 1.22	b	67	35	2.15 ± 1.85	a	89	< 0.001 * (U-test)
	low-mid	13	0.31 ± 1.40	bc	69	14	0.12 ± 1.11	b	50	0.699
	deep	10	-0.45 ± 1.22	c	30	2	2.08 ± 1.52	-	100	0.026 *
> 6 mm	shallow	1	8.57 -	a	100	1	11.04 -	-	100	-
	up-mid	11	2.02 ± 1.14	b	91	17	2.19 ± 1.28	a	100	0.721
	low-mid	14	1.07 ± 1.23	bc	79	4	0.86 ± 0.86	a	75	0.752
	deep	28	0.35 ± 1.29	c	54	3	2.08 ± 1.15	a	100	0.034 *
all size classes	shallow	10	3.75 ±2.48	a	100	2	8.18 ± 4.04	-	100	0.058
	up-mid	59	0.80 ±1.32	b	69	66	1.96 ± 1.96	a (KW)	85	< 0.001 *
	low-mid	30	0.56 ±1.37	bc	70	23	0.33 ± 1.02	b (KW)	61	0.514
	deep	43	-0.09 ±1.52	c	42	6	2.35 ± 1.20	a (KW)	100	<0.001 *
entire station		142	0.69 ± 1.74	< 0.001 * (KW)	63	97	1.72 ± 2.11	< 0.001 * (KW)	80	< 0.001 * (U-test)

Table 3: Baltic cod (*Gadus morhua*) larvae. Growth performance (Gpf) in relation to sampling depth at station 569 and 570 for different larval size classes. Significant differences between depth ranges were observed (p < 0.05). SGR of larvae from depth ranges sharing the same letter are not significantly different (KW = Kruskal-Wallis ANOVA). The column to the right shows results of comparisons between stations.

Gpf		Station 569				Station 570				569 vs. 570
size class	depth range	n	mean ± sd	ANOVA	pos. gr. [%]	n	mean ± sd	ANOVA	pos. gr. [%]	p-value
< 4.5 mm	shallow	0	-	-	-	0	-	-	-	-
	up-mid	3	0.16 ± 0.10	-	100	0	-	-	-	-
	low-mid	0	-	-	-	1	0.05 -	-	100	-
	deep	0	-	-	-	0	-	-	-	-
4.5 - 6 mm	shallow	2	0.36 ± 0.08	-	100	1	0.39 -	-	100	-
	up-mid	28	0.11 ± 0.18	a	75	22	0.35 ± 0.24	a (KW)	95	< 0.001 *
	low-mid	12	0.05 ± 0.29	a	67	11	0.02 ± 0.18	b (KW)	45	0.732
	deep	7	0.00 ± 0.15	a	43	1	0.09 -	-	100	-
> 6 mm	shallow	1	0.34 -	-	100	1	0.38 -	-	100	-
	up-mid	11	0.17 ± 0.10	a	91	16	0.19 ± 0.10	a	100	0.634
	low-mid	14	0.11 ± 0.13	ab	79	4	0.08 ± 0.09	a	75	0.77
	deep	28	0.03 ± 0.13	b	54	3	0.20 ± 0.08	a	100	0.035 *
all size classes	shallow	3	0.36 ± 0.06	a	100	2	0.38 ± 0.01	-	100	0.583
	up-mid	42	0.13 ± 0.16	b	81	38	0.28 ± 0.21	a (KW)	97	<0.001 * (U-test)
	low-mid	26	0.08 ± 0.22	bc	73	16	0.03 ± 0.15	b (KW)	56	0.464
	deep	35	0.03 ± 0.13	c	51	4	0.18 ± 0.09	ab (KW)	100	0.036 *
entire station		106	0.09 ± 0.18	0.043 * (KW)	70	60	0.21 ± 0.21	0.001 * (KW)	87	< 0.001 *

No significant differences in Gpf were found in the length class 4.5-6 mm. At station 570, only larvae from the early feeding group (4.5-6 mm) showed significantly better SGR and Gpf at “upper-middepth” than at “lower-middepth”, while all other comparisons did not reveal any significant differences. However, it should be noted that the generally lower numbers of larvae at Station 570 and the further reduction in observations due to the exclusion of larvae < 0.03 mg from the Gpf estimations rendered a number of comparisons between depth ranges impossible after splitting the larvae into length groups.

Both SGR and Gpf show a high variability as evidenced from the high standard deviations (Tables 2 and 3). However, for the individual larva, it may not only be important how fast it is growing, but also if it is growing at all or if it is soon to face starvation mortality. Therefore, we also analysed the frequency of larvae expressing positive growth per length and depths group (Tables 2 and 3). Not surprisingly, the same trends as for SGR and Gpf were observed. At station 569, a continuous decrease of positively growing larvae with depth was observed. While all larvae of all size classes in the “shallow” group showed positive growth, the fraction of growing larvae continuously declined with depth. Interestingly, for all other depth groups the fraction of larvae with positive growth increased with larval size. For example, at “upper-middepth”, fractions of growing larvae were 56, 67 and 91% for small, medium and large larvae, and in the “deep” depth range, fractions of growing larvae increased from 0 to 30 and 54 % with larval size. At station 570, again, a different situation was found. Here, fractions of growing larvae were generally high, ranging mainly between 85 and 100 %. Only at “lower-middepth”, and at “upper-middepth” for the smallest larvae, were considerably lower fractions of growing larvae found.

Regarding growth performance, the same trends in the fractions of growing and starving larvae were found at both stations.

Growth differences between stations

To elucidate possible growth differences of larvae in dependence of their horizontal catch location in the Bornholm Basin, we compared SGR and Gpf between the two sampling stations (Tables 2 and 3). When considering all larvae from the entire station, SGR and Gpf were generally significantly higher at station 570. As could be expected from the general differences in the development of growth at depth between stations, analysis of SGR and Gpf by depth range showed significantly better growth at station 570 in the “deep” range. While both growth estimates were not significantly different in the “shallow” and “lower-middepth” ranges, larvae at “upper-middepth” grew significantly better at station 570 than at 569. Splitting the larvae into size groups revealed that this was due to significantly better growth at station 570 in the early feeding group. In contrast, both SGR and Gpf of the larger larvae were surprisingly similar between stations, with the exception of the “deep” larvae.

DISCUSSION

We found significant differences in the vertical distribution and growth of cod larvae in relation to their size and their vertical and horizontal catch locations in the Bornholm Basin of the Baltic Sea, which may be caused by strong vertical and horizontal gradients in the ambient biotic and abiotic environment. Generally, larval Baltic cod grew poorly, indicating food-limitation, especially for early larvae in the deeper parts of the basin. This study provides support for the suggestion that larval-stage processes are crucial in shaping the recruitment dynamics of the Eastern Baltic cod stock.

Vertical distribution

The larval abundance peaked at depths between 25-40 m on station 570 in the northwestern Bornholm Basin which agrees well with earlier studies conducted in 1994 and 1995 (Grønkjær et al. 1997, Grønkjær & Wieland 1997), while the vertical distribution at station 569 southeast of Bornholm does not. Also increasing larval lengths with depth seem to be in contrast to previous findings (Grønkjær & Wieland 1997), who reported significantly larger larval mean lengths above the halocline, which was interpreted as an ontogenetic vertical first-feeding migration. However, when comparing larval length frequency distributions between the two studies (cf. Fig. 3) it becomes apparent that few larvae larger than 5 mm were found in 1994/1995, while our samples contained a relatively large fraction of larger larvae. Thus, our study actually supports the suggested necessity of an initial ontogenetic vertical migration, as smaller larvae, mainly in the first and early feeding size class, were caught at shallower depths. Furthermore, we suggest that the ontogenetic vertical migration may continue as the larvae become larger.

Larger Baltic cod larvae include increasing amounts of larger prey items in their diet, showing a preference for all developmental stages of *Pseudocalanus acuspes* (Zuzarte et al. 1996, Voss et al. 2003), which agrees well with larval cod food preferences in other areas (Kane 1984, McLaren & Avendano 1995, Lough et al. 1996, Munk 1997). The vertical distribution of this copepod shows marked stage-specific differences, with increasingly larger stages at larger depths (Fig. 2, Renz & Hirche 2006, Schmidt 2006). Based on these observations, we suggest the following ontogenetic migration route: newly hatched larvae conduct an initial vertical migration from hatching depths to sub-surface layers in order to initiate feeding on nauplii, but as soon as the larvae are capable of coping with larger prey, they continue their ontogenetic vertical migration in the opposite direction, thereby following the increasingly larger copepodite stages of *Pseudocalanus acuspes* at larger depths. The fact that no significant differences in larval size between depths were found at station 570 is probably due to the higher frequency of small larvae that still mainly rely on nauplii in the upper layers and to the generally low number of observations at larger depths.

Even though low sample sizes prevented a detailed analysis, our data show no signs of extended diel vertical migrations that could bias the observed length-dependent vertical distribution. This is also in concordance with observations on cod larvae on Georges Bank that did not conduct extended diel vertical migrations until sizes of > 9 - 13 mm (Lough & Potter 1993). Other studies have reported various depth ranges of peak abundances of Baltic cod larvae, ranging from 20-30 (Wieland & Zuzarte 1991) over 30-60 (Poulsen 1931) and 40-65 (Mueller 1988) to 70-80 m (Wieland & Zuzarte 1991). Unfortunately, these studies give no or insufficient information on larval lengths, which precludes a comparison with our findings. We conclude that larval abundance and distribution per se, i.e. without any information on larval size, have little value in furthering our understanding of diel or ontogenetic vertical migration behaviour of larval Baltic cod. However, larval behaviour in relation to the ambient environment may have an important influence on larval growth, survival and eventually recruitment. Future studies should therefore aim to resolve and to substantiate the diel and the suggested ontogenetic vertical migration behaviour.

Larval Baltic cod growth

Suitability of using reference growth rates to estimate growth performance in field caught larvae and general growth performance of larval Baltic cod

The observed relationships between larval size (SL) and standardized RNA-DNA ratio (sRD) as well as specific growth rate (SGR), and the possible dependence of sRD on temperature (Buckley et al. 2006), make the interpretation and comparison of RNA-DNA derived specific growth rates (SGR) between different habitats difficult, especially in environments with pronounced vertical temperature gradients as observed in the Baltic.

Therefore, in addition to SGR and to obtain an objective measure of larval condition, the present study attempted for the first time to estimate growth performance (Gpf) for larval Baltic cod. Gpf was estimated by relating SGR to modeled reference growth rates (Gref) for fast-growing, laboratory reared cod larvae (Folkvord 2005), as suggested by Buckley et al. (2008). As both a temperature and a larval dry weight term are included in Folkvord's (2005) model for Gref, Gpf should provide an objective measure of larval condition due to food intake regardless of ambient temperature and larval size.

We consider the standardization to a reference growth rate (Gref) as a valuable tool for improving investigations of larval fish growth, as it theoretically provides an objective measure of larval condition, even though the applicability of Gpf to a field setting may require further investigation and validation (Buckley et al. 2008). Especially the inclusion of a photoperiod term may be expected to improve the utility of this approach, as Buckley et al. (2006) achieved a remarkable improvement in the correspondence of growth estimates from Folkvord's (2005) model and from Georges Bank field larvae when correcting for differences in photoperiod. However, the photoperiods in our field study in the Baltic were very similar to those in the laboratory study that provided the basis for Folkvord's model. Thus, we conclude that Gpf estimated from this model is likely providing an objective measure for the condition of Baltic cod larvae in the present study.

Comparisons of Gref with otolith-based growth estimates of field caught cod larvae led Folkvord (2005) to conclude that larvae in the field are growing close to their maximum size- and temperature-dependent capacity. It was previously suggested that abundances of nauplii and copepodites in the Central Baltic should be sufficient to ensure that starvation is not a major source of larval Baltic cod mortality (Krajewska-Soltys & Linkowski 1994, Zuzarte et al. 1996). Contrasting to these assumptions, setting our RNA-DNA derived growth rates of Baltic cod in relation to Gref (cf. Fig. 8) showed that Baltic cod larvae in August 2007 were growing poorly. This probably reflects food limitation, which is in line with the finding of a significant relationship between food abundance and survival from the egg to the larval stage in Baltic cod (Koester et al. 2003).

Depth-dependent growth, growth performance and potential prey availability

The two dominating factors influencing growth are temperature and food intake (Blaxter 1992). The observed growth differences between depths are likely due to vertical differences in ambient temperatures and prey availabilities. In the 1994 and 1995 spawning seasons, Baltic cod larvae grew better above the halocline than below, which was hypothesized to be related to increased prey encounter rates at favourable light and oxygen conditions (Grønkjær et al. 1997, Grønkjær & Wieland 1997). Our study largely corroborates the finding of decreasing growth with increasing depth, although relatively high growth in the deeper waters of station 570 was unexpected. However, the number of observations in these depths was very low, which may indicate that weaker larvae had already been removed from the system, leaving only few larvae with relatively high growth.

Due to the high spatial and temporal variability in composition and abundance of Baltic copepod species and their developmental stages (Fig. 2, Moellmann et al. 2000, Renz & Hirche 2006, Schmidt 2006), Baltic cod larvae are, depending on their vertical position, exposed to very variable temperatures and prey fields, both in terms of abundance and composition. Contrasting to laboratory studies which suggested temperature optima for larval cod growth to be at or above 14°C (Otterlei et al. 1999), optimum temperatures for growth in the field may be considerably lower if food is limited, as higher temperatures result in increased metabolic costs and require higher feeding rates (Brett 1979). For cod larvae on Georges Bank, e.g., Buckley et al. (2004) reported a dome-shaped relationship between growth and water temperature, with a maximum at ca. 7°C.

In our study in the Baltic, highest growth rates were found in the shallowest and warmest layers. However, the vertical distribution showed that only very few larvae were dwelling at high temperatures, despite the fact that prey availability, especially for first-feeding larvae, is certainly high in this depth range, as nauplii of *Pseudocalanus acuspes*, *Temora longicornis* and *Acartia sp.* are aggregating here (Renz & Hirche 2006, Schmidt 2006). This may indicate that first feeding larvae, after their ontogenetic vertical migration, may be forced to reside in relatively warm waters, as they only here can find sufficient abundances of suitable prey, but the high temperatures will lead to high energy demands and high starvation mortalities. Alternatively, first-feeding larvae may avoid these high temperature waters, but the lower prey abundances at the sub-thermocline layer may also result in relatively high starvation.

Such a possible food-temperature trade-off has certainly the largest consequences for early feeding larvae. Although larger larvae in the established feeder group also showed slower growth and increasing numbers of starving larvae with depth, the frequencies of starving larvae were decreasing with larval size in all depth ranges. This indicates that larger larvae were better in coping with the environmental situation at larger depths. Larger larvae may be able to actively choose between the above mentioned trade-off situation. As soon as they are capable of feeding on larger prey items, they may choose to migrate to deeper, cooler layers. This may be an additional explanation for the observation of larger larvae at larger depths, as the proposed continuation of the ontogenetic vertical migration by larger larvae to greater depths may provide them a twofold advantage: they may (i) find larger, more suitable prey and (ii) may save energy in deeper, colder water.

As larval fish mortality rates are generally very high, it has been supposed that individuals expressing fast growth are at an advantage by faster out-growing the smallest size classes most vulnerable to predators (Houde 1987). However, fast growth also requires more food, and one might ask what would be the best growth strategy in the absence of predation? In this case, fast growth may not be the optimal strategy, as larvae with slower growth require less food and may therefore have a higher starvation resistance. In fact, it has been suggested that environments with limiting food supply are favouring larvae with low standard metabolic rates (Kieser 1995, Djawdan et al. 1997, Bochdansky et al. 2005).

Such a situation may exist for Baltic cod in the present environmental situation. While predation on Baltic cod eggs can reach substantial levels, predation on larvae is low due to a limited vertical overlap of cod larvae and the only identified ichthyoplankton predators, i.e. Baltic sprat and herring (Koester & Schnack 1994, Koester & Moellmann 2000). Furthermore, the marked decline in abundances of *Pseudocalanus acuspes* during the past decades (Moellmann et al. 2000) resulted in lower prey availability for larval cod. Thus, in this environmental setting, a slow-growth strategy may actually ensure higher survival than faster growth.

When comparing growth of cod larvae from (i) the present study in the Baltic, (ii) Georges Bank (Caldarone, unpubl. data) and (iii) a mesocosm study (Clemmesen, unpubl. data), it becomes evident that there is an overlap between slow-growing larvae from the mesocosm and the Baltic, while Georges Bank larvae express considerably higher growth rates (Fig. 11).

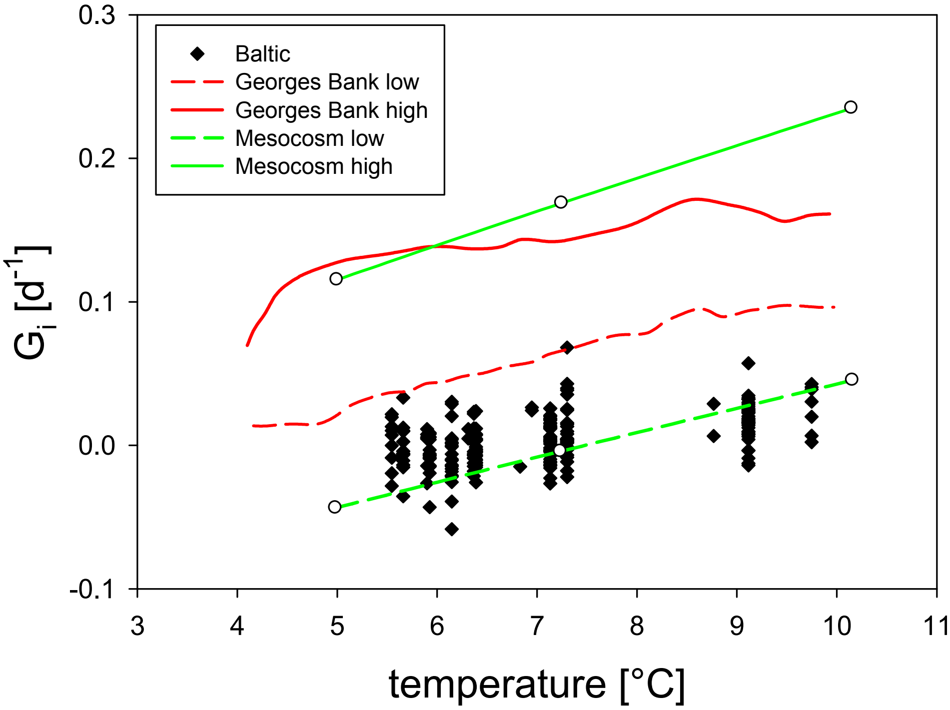


Fig. 11: Growth comparison of larval Baltic cod from this study (black diamonds) with cod larvae at the upper and lower growth limits on Georges Bank (high: solid red line; low: dashed red line) and from Mesocosms (high: solid green line; low: dashed green line). (Note: The data for Georges Bank (Caldarone, unpubl.) and the Mesocosm study (Clemmesen, unpubl.) were given as recent growth (G_i) expressed as the instantaneous protein-specific growth rate (d^{-1}), based on the following equation given by Caldarone (2005): $G_i = 0.045*RD + 0.009*T - 0.147$, with T = temperature and RD = RNA/DNA ratio. Therefore, for this comparison RNA/DNA ratios of Baltic cod were converted to G_i according to this equation).

The reason for this may be differences in predation pressure between the three systems. Predation on larval cod on Georges Bank is believed to be an important source of pre-recruit mortality, even though direct empirical evidence is limited (Garrison et al. 2002, ICES 2005). The Georges Bank ecosystem is, contrasting to the Baltic, highly diverse (Link et al. 2009), which results in a whole suite of potential vertebrate (Garrison et al. 2000, Garrison et al. 2002) and invertebrate (ICES 2005) larval fish predators that may immediately remove weak larvae in starving condition. In contrast, food may be severely limited for larval cod in the Baltic but predation is low. Even if slow growth may not be an active strategy of larval Baltic cod, our data show at least that the ecosystem in the Bornholm Basin, just as the predator-free mesocosm, is tolerating slow growing larvae and that they are apparently not immediately removed from the system.

Both field (Buckley & Lough 1987) and modeling (Werner et al. 1996) studies have shown that cod larvae grow and survive better at low prey densities than larval haddock. Although slow growth close to starvation threshold levels will probably still result in high starvation mortalities, this indicates that Baltic cod larvae may be able to survive relatively long at relatively low prey densities and growth rates, and the low predation pressure may allow a number of larvae to survive to more advanced stages and eventually to recruit to the fishable stock.

Growth differences between stations

While growth at the two stations was not significantly different in the “shallow” and “lower-middepth” ranges, larvae at “upper-middepth” grew significantly better at station 570 than at 569, and splitting into size classes revealed that this was due to significantly better growth in the early feeding group. In contrast, growth of the larger larvae was surprisingly similar between stations. This provides further evidence that first feeding larvae were food-limited in the basin centre, due to low *Pseudocalanus acuspes* abundance, while they may have found a relatively favourable prey field with high nauplii abundances of other copepod species at the edges of the Bornholm Basin. This agrees well with results from an earlier modeling (Hinrichsen et al. 2002) and a recent field (paper 1) study, and suggests that a major bottleneck in Baltic cod recruitment can be further isolated as the stage of first and early feeding larvae.

Implications for recruitment

Larval growth, survival and eventually recruitment are without doubt depending on the ambient environmental conditions during the recruitment processes. Larval abundance and distribution per se probably have little value in furthering our understanding of the processes determining recruitment success. However, the individual behaviour of larval Baltic cod, in response to the suggested temperature and food related trade-off situation, has the potential to mediate between environmental fluctuations and recruitment variability. Modelling studies on larval Atlantic cod investigating a similar trade-off based on different feeding-predation scenarios showed that active vertical migration behaviour significantly increased survival (Vikebø et al. 2007, Kristiansen et al. 2009).

By conducting vertical migrations, larvae may actually be able to switch between different temperature-prey scenarios, and different larval stages may choose different strategies. For Atlantic cod larvae on Georges Bank, which like Baltic cod also aggregate in the summer thermocline (Lough & Potter 1993), Buckley et al. (2004) estimated that a 1.5°C deviation from the optimum temperature for growth would result in a five-fold decrease in survival to the pelagic juvenile stage. In the highly stratified Baltic, a temperature difference of 1.5°C may be achieved by moving as little as 2-3 meters in vertical direction (cf. Fig. 2), a distance that even small larvae should be able to complete within few hours (MacKenzie & Kiørboe 1995, Peck et al. 2006).

Clearly, the impact of such a trade-off would be strongest during summer, when the summer thermocline and the associated temperature differences in the usual larval dwelling depths are most pronounced, and abundances of potential larval prey items are low (Moellmann et al. 2000). Food shortage related to the Baltic zooplankton dynamics was hypothesized to be the reason for observed lower larval survival during summer (Hinrichsen et al. 2003a), paper 1). The interplay of prey abundance, temperature and starvation could be a further reason for these observations. This may also give an additional explanation for the pronounced decline in overall recruitment levels (Koester et al. 2001, Koester et al. 2005) after a shift in peak spawning time of Baltic cod from spring to summer (Wieland et al. 2000).

For Georges Bank cod, Buckley et al. (2006) found on average 4.9% of first-feeding larvae to be in starving condition, even though inter-annual differences were large (19.5, 1.4 and 0.5% in April 1995, 1997 and 1999, respectively), while only <= 1% of larger, older larvae in the established feeder stage showed negative growth. In combination with their results on larval haddock and a study on walleye Pollock (Theilacker et al. 1996), they suggested that these gadoid species appear to be vulnerable to starvation for a 2 week period following first feeding, while starvation is not an important source of mortality for established feeders.

In contrast, even though frequencies of starving larvae decreased with size, nutritional condition and growth rates in our study on Baltic cod was considerably lower for all larval size classes (cf. Fig. 11). This indicates that although the first feeding stage is probably a major bottleneck in the recruitment process of Baltic cod, additional recruitment regulation at older stages is as well possible through food-limited growth (cf. paper 2) and the resulting prolongation of the vulnerable larval phase (Houde 1987).

To compare our results with earlier findings by Grønkjær et al. (1997), we must regard them in relation to the spawning stock and another major recruitment determinator, the egg mortality due to low oxygen concentration and predation by clupeids (Koester et al. 2005). After being on historically high levels during the early 1980's (Eero et al. 2008), the spawning stock biomass (SSB) began to rapidly and continuously decline from the mid 1980's, falling from almost 700.000 t in 1980 to 93.000 t in 1992. In 1991, high oxygen-related egg survival and low predation pressure were observed in the Bornholm Basin (Koester et al. 2005). However, this favourable egg environment could not be fully utilized by the stock, as SSB was on a very low level, resulting in low egg abundance. Surprisingly, larval abundance and recruitment (age 2) was relatively high when compared to the other years after the major stock decline. This relatively strong 1991 year-class resulted in an increase in SSB, especially in 1994 and 1995. After the major Baltic inflow in 1993, the scene was set for high recruitment success: a decent SSB, favorable oxygen environment for egg survival and low predation pressure. Indeed, the following years (1994-1997) showed very high egg abundances in the Bornholm Basin, with a record high abundance in 1994. However, this was not reflected in high recruitment, with especially the 1994 and 1995 year-classes being very weak.

Thus, a major mortality source must have operated between the egg stage and the recruits. Predation on Baltic cod larvae does not play a major role (Koester & Schnack 1994, Koester & Moellmann 2000). Cannibalism on juveniles has been observed in Baltic cod, however, this process is negligible at low stock sizes (Neuenfeldt & Koester 2000, Uzars & Plikshs 2000). This leaves larval starvation as the most likely source of mortality. Indeed, virtually no larvae were observed in ichthyoplankton surveys in 1995. In 1994, higher numbers of larvae were observed, especially late in the season (Grønkjær et al. 1995). However, in relation to the record high egg abundance in 1994, larval abundance must still be regarded as low. Besides, the vast majority of the sampled larvae belonged to the size class of first feeding larvae, and hardly any larger larvae were observed (cf. Fig. 3, Grønkjær & Wieland 1997). In this respect, it is also striking that no increase in mean larval length from May over June to July was observed in 1994 (Grønkjær & Wieland 1997), suggesting very low survival beyond the first-feeding stage throughout the spawning season. In fact, the occurrence of small (and only small) larvae throughout the season is an additional indication for the influence of larval starvation mortality, as it largely rules out the possibility of heavy mortality during the late egg stage.

In contrast, comparison of larval length frequency distributions from 1994 and 1995 with the present study in 2007 (cf. Fig. 3, Grønkjær & Wieland 1997) shows a clear trend to higher numbers of larger larvae in the latter year, indicating better larval survival beyond the first feeding stage.

This is further corroborated by lower frequencies of larvae in starving condition observed in our investigation. Figure 12 summarizes the development from SSB to recruitment for the year-classes 1994, 1995 and 2007, including estimates of SSB and age 2 recruits (from ICES 2009), abundances of early and late egg stages as well as larvae (from an ichthyoplankton database held at IFM-GEOMAR) and frequencies of larvae expressing positive growth (from the present study and from Grønkjær et al. 1997).

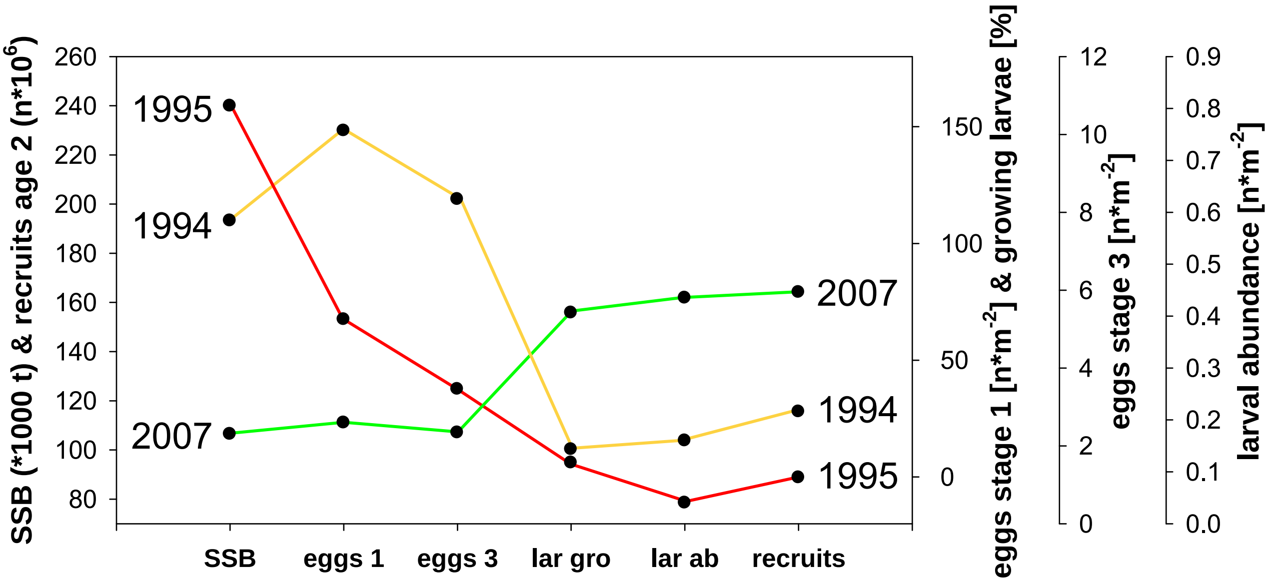


Fig. 12: Development from spawning stock to recruits in 1994, 1995 and 2007. The shift from high SSB to low recruitment and vice versa is occurring between the late egg stage and the ratio of larvae in growing condition. Values are for July 1994, July 1995 and August 2007 (due to the lack of RNA/DNA data for July 1995, % growing larvae for 1995 is from May, assuming a similar percentage of growing larvae throughout the season). SSB = spawning stock biomass, eggs 1 = stage 1 eggs, eggs 3 = stage 3 eggs, lar gro = ratio of larvae showing positive growth, lar ab = average larval abundance, recruits = recruits at age 2 (note that the 2007 recruits are a prediction from XSA, as no assessment was done yet to determine the recruitment of the 2007 year-class (ICES 2009).

The two earlier years started out with a relatively high SSB, resulting in high abundances of eggs in stage 1, and due to the favorable oxygen conditions, abundances of late stage eggs were still on high levels. However, the frequencies of larvae with positive growth rates and larval abundance data indicate that the switch from high SSB to low recruitment, and vice versa, occurred during the larval stage. Even though larval growth estimates are so far only available for these 3 years and the inclusion of data from additional years is needed to draw further conclusions on the relative importance of larval survival in relation to other recruitment processes, the development from SSB to recruits in several other years concurs with our observations. For example, in 1991 a relatively strong year-class emerged from a low SSB and low egg abundances. Furthermore, larval abundances in recent years were relatively high (Huwer, pers. obs.) and recruitment of the 2005 and 2006 year-classes has been the highest since 1987, despite apparently unchanged environmental conditions for egg survival. We conclude that larval-stage processes have the potential to introduce major variability in the recruitment levels of Baltic cod, but further studies are needed to assess their relative importance in relation to other processes.

References

Bagge O., Thurow F., Steffensen E., Bay J. (1994) The Baltic cod. Dana 10:1-28

Belchier M., Clemmesen C., Cortes D., Doan T., Folkvord A., Garcia A., Geffen A. J., Hoie H., Johannessen A., Moksenss E., de Pontual H., Ramirez T., Schnack D, Sveinsbo B. (2004) Recruitment studies: manual on precision and accuracy of tools. ICES Techniques in Marine Environmental Science 33, 35 pp.

Blaxter J.H.S. (1992) The effect of temperature on larval fishes. Netherlands Journal of Zoology 42:336-357

Bochdansky A.B., Gronkjaer P., Herra T.P., Leggett W.C. (2005) Experimental evidence for selection against fish larvae with high metabolic rates in a food limited environment. Marine Biology 147:1413-1417

Brett J.R. (1979) Environmental factors and growth. In: W.S.Hoar, D.J.Randall, and J.R.e.Brett (eds) Fish physiology. Volume 8. Bioenergetics and growth. Academic Press, New York, p 599-675

Buckley L.J., Lough R.G. (1987) Recent growth, biochemical composition, and prey field of larval haddock (*Melanogrammus aeglefinus*) and Atlantic cod (*Gadus morhua*) on Georges Bank. Canadian Journal of Fisheries and Aquatic Sciences 44:14-25

Buckley L., Caldarone E.M., Ong T.L. (1999) RNA-DNA ratio and other nucleic acid-based indicators for growth and condition of marine fishes. Hydrobiologia 401:265-277

Buckley L.J., Caldarone E.M., Lough R.G. (2004) Optimum temperature and food-limited growth of larval Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) on Georges Bank. Fisheries Oceanography 13:134-140

Buckley L.J., Caldarone E.M., Lough R.G., Onge-Burns J.M. (2006) Ontogenetic and seasonal trends in recent growth rates of Atlantic cod and haddock larvae on Georges Bank: effects of photoperiod and temperature. Marine Ecology Progress Series 325:205-226

Buckley L.J., Caldarone E.M., Clemmesen C. (2008) Multi-species larval fish growth model based on temperature and fluorometrically derived RNA/DNA ratios: results from a meta-analysis. Marine Ecology Progress Series 371:221-232

Caldarone E.M. (2005) Estimating growth in haddock larvae *Melanogrammus aeglefinus* from RNA:DNA ratios and water temperature. Marine Ecology Progress Series 293:241-252

Caldarone E.M., St.Onge-Burns J.M., Buckley L.J. (2003) Relationship of RNA/DNA ratio and temperature to growth in larvae of Atlantic cod *Gadus morhua*. Marine Ecology Progress Series 262:229-240

Caldarone E.M., Clemmesen C.M., Berdalet E., Miller T.J., Folkvord A., Holt G.J., Olivar M.P., Suthers I.M. (2006) Intercalibration of four spectrofluorometric protocols for measuring RNA/DNA ratios in larval and juvenile fish. Limnology and Oceanography: Methods 4:153-163

Chicharo M.A., Chicharo L. (2008) RNA : DNA ratio and other nucleic acid derived indices in marine ecology. International Journal of Molecular Sciences 9:1453-1471

Clemmesen C. (1993) Improvements in the fluorimetric determination of the RNA and DNA content of individual marine fish larvae. Marine Ecology Progress Series 100:177-183

Clemmesen C. (1996) Importance and limits of RNA/DNA ratios as a measure of nutritional condition in fish larvae. In: Y.Watanabe, Y.Yamashita, and Y.Oozeki (eds) Survival Strategies in Early Life Stages of Marine Resources. A.A. Balkema, Rotterdam, p 67-82

CORE 1998. Mechanisms influencing long time trends in reproductive success and recruitment of Baltic Cod: Implications for fisheries management. EU-Project AIR CT94 1226, Final Report.

Djawdan M., Rose M.R., Bradley T.J. (1997) Does selection for stress resistance lower metabolic rate? Ecology 78:828-837

Eero M., Koster F.W., MacKenzie B.R. (2008) Reconstructing historical stock development of Atlantic cod (*Gadus morhua*) in the eastern Baltic Sea before the beginning of intensive exploitation. Canadian Journal of Fisheries and Aquatic Sciences 65:2728-2741

Folkvord A. (2005) Comparison of size-at-age of larval Atlantic cod (*Gadus morhua*) from different populations based on size- and temperature-dependent growth models. Canadian Journal of Fisheries and Aquatic Sciences 62:1037-1052

Garrison L.P., Michaels W., Link J.S., Fogarty M.J. (2000) Predation risk on larval gadids by pelagic fish in the Georges Bank ecosystem. I. Spatial overlap associated with hydrographic features. Canadian Journal of Fisheries and Aquatic Sciences 57:2455-2469

Garrison L.P., Michaels W., Link J.S., Fogarty M.J. (2002) Spatial distribution and overlap between ichthyoplankton and pelagic fish and squids on the southern flank of Georges Bank. Fisheries Oceanography 11:267-285

Grønkjær P., Moellmann C., Voss R. (1995) Abundance and distribution of larval cod (*Gadus morhua*) in the Bornholm Basin. ICES CM1995/J:24

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

Grønkjær P., Clemmesen C., St.John M.A. (1997) Nutritional condition and vertical distribution of Baltic cod larvae. Journal of Fish Biology 51:352-369

Hinrichsen H.H., St John M.A., Aro E., Grønkjær P., Voss R. (2001) Testing the larval drift hypothesis in the Baltic Sea: retention versus dispersion caused by wind-driven circulation. ICES Journal of Marine Science 58:973-984

Hinrichsen H.H., Moellmann C., Voss R., Koester F.W., Kornilovs G. (2002) Biophysical modeling of larval Baltic cod (*Gadus morhua*) growth and survival. Canadian Journal of Fisheries and Aquatic Sciences 59:1858-1873

Hinrichsen H.H., Boettcher U.Y., Koester F.W., Lehmann A., St.John M. (2003a) Modelling the influences of atmospheric forcing conditions on Baltic cod early life stages: distribution and drift. Journal of Sea Research 49:187-201

Hinrichsen H.H., Lehmann A., Moellmann C., Schmidt J. (2003b) Dependency of larval fish survival on retention/dispersion in food limited environments: the Baltic Sea as a case study. Fisheries Oceanography 12:425-433

Hinrichsen H.H., Schmidt J.O., Petereit C., Moellmann C. (2005) Survival probability of Baltic larval cod in relation to spatial overlap patterns with their prey obtained from drift model studies. ICES Journal of Marine Science 62:878-885

Houde E.D. (1987) Fish early life dynamics and recruitment variability. American Fisheries Society Symposium Series 2:17-29

ICES 2005. Spawning and life history information for North Atlantic cod stocks. ICES Cooperative Research Report, No. 274. 152 pp.

ICES 2009. Report of the Baltic Fisheries Assessment Working Group. Copenhagen, 22-28 April 2009. ICES CM 2009/ACOM:07

Kane J. (1984) The feeding habits of co-occurring cod and haddock larvae from Georges Bank. Marine Ecology Progress Series 16:9-22

Kieser J. (1995) Stress and economical constraints to phenotypic evolution. Evolutionary Theory 10:305-316

Koester F.W., Schnack D. (1994) The role of predation on early life stages of cod in the Baltic. Dana 10:179-201

Koester F.W., Moellmann C. (2000) Trophodynamic control by clupeid predators on recruitment success in Baltic cod? ICES Journal of Marine Science 57:310-323

Koester F.W., Hinrichsen H.H., St.John M.A., Schnack D., MacKenzie B., 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

Koester F.W., Hinrichsen H.H., Schnack D., St John M.A., MacKenzie B.R., Tomkiewicz J., Moellmann C., Kraus G., Plikshs M., Makarchouk A., Aro E. (2003) Recruitment of Baltic cod and sprat stocks: identification of critical life stages and incorporation of environmental variability into stock-recruitment relationships. Scientia Marina 67:129-154

Koester F.W., Moellmann C., Hinrichsen H.H., Wieland K., Tomkiewicz J., Kraus G., Voss R., Makarchouk A., MacKenzie B.R., St.John M.A., Schnack D., Rohlf N., Linkowski T., Beyer J.E. (2005) Baltic cod recruitment - the impact of climate variability on key processes. ICES Journal of Marine Science 62:1408-1425

Krajewska-Soltys A., Linkowski T.B. (1994) Densities of potential prey for cod larvae in deep-water basins of the southern baltic. ICES CM1994/J:17

Kristiansen T., Jorgensen C., Lough R.G., Vikebo F., Fiksen O. (2009) Modeling rule-based behavior: habitat selection and the growth-survival trade-off in larval cod. Behavioral Ecology 20:490-500

Link J.S., Bogstad B., Sparholt H., Lilly G.R. (2009) Trophic role of Atlantic cod in the ecosystem. Fish and Fisheries 10:58-87

Lough R.G., Potter D.C. (1993) Vertical distribution patterns and diel migrations of larval and juvenile haddock *Melanogrammus aeglefinus* and Atlantic cod *Gadus morhua* on Georges Bank. Fishery Bulletin U.S. 91:281-303

Lough R.G., Caldarone E.M., Rotunno T.K., Broughton E.A., Burns B.R., Buckley L.J. (1996) Vertical distribution of cod and haddock eggs and larvae, feeding and condition in stratified and mixed waters on southern Georges Bank, May 1992. Deep-Sea Research II 43:1875-1904

MacKenzie B.R., Kiørboe T. (1995) Encounter rates and swimming behaviour of pause-travel and cruise larval fish predators in calm and turbulent laboratory environments. Limnology and Oceanography 40:1278-1289

MacKenzie B., St.John M.A., Wieland K. (1996) Eastern Baltic cod: Perspectives from existing data on processes affecting growth and survival of eggs and larvae. Marine Ecology Progress Series 134:265-281

Malzahn A.M., Clemmesen C., Rosenthal H. (2003) Temperature effects on growth and nucleic acids in laboratory-reared larval coregonid fish. Marine Ecology Progress Series 259:285-293

Malzahn A.M., Clemmesen C., Wiltshire K.H., Laakmann S., Boersma M. (2007) Comparative nutritional condition of larval dab *Limanda limanda* and lesser sandeel *Ammodytes marinus* in a highly variable environment. Marine Ecology Progress Series 334:205-212

McLaren I.A., Avendano P. (1995) Prey field and diet of larval cod on Western Bank, Scotian Shelf. Canadian Journal of Fisheries and Aquatic Sciences 52:448-463

Moellmann C., Kornilovs G., Sidrevics L. (2000) Long-term dynamics of main mesozooplankton species in the central Baltic Sea. Journal of Plankton Research 22:2015-2038

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

Mueller A. (1988) Vertical distribution of ichthyoplankton in the Bornholm Basin. Kieler Meeresforschungen., Sonderheft 6:341-347

Munk P. (1997) Prey size spectra and prey availability of larval and small juvenile cod. Journal of Fish Biology 51:340-351

Neuenfeldt S., Koester F.W. (2000) Trophodynamic control on recruitment success in Baltic cod: the influence of cannibalism. ICES Journal of Marine Science 57:300-309

Otterlei E., Nyhammer G., Folkvord A., Stefansson S.O. (1999) Temperature- and size-dependent growth of larval and early juvenile Atlantic cod (*Gadus morhua*): a comparative study of Norwegian coastal cod and northeast Arctic cod. Canadian Journal of Fisheries and Aquatic Sciences 56:2099-2111

Peck M.A., Buckley L.J., Bengtson D.A. (2006) Effects of temperature and body size on the swimming speed of larval and juvenile Atlantic cod (*Gadus morhua*): implications for individual-based modelling. Environmental Biology of Fishes 75:419-429

Poulsen E.M. (1931) Biological investigations upon the cod in Danish waters. Meddelelser fra kommissionen for Danmarks Fiskeri- og Havundersøgelser, Serie Fiskeri, Bind IX, Nr. 1:1-148

Renz J., Hirche H.J. (2006) Life cycle of *Pseudocalanus acuspes* Giesbrecht (Copepoda, Calanoida) in the Central Baltic Sea: I. Seasonal and spatial distribution. Marine Biology 148:567-580

Schmidt J.O. (2006) Small and meso-scale distribution patterns of key copepod species in the Central Baltic Sea and their relevance for larval fish survival. PhD thesis, Christian-Albrechts-University, Kiel, Germany

Schmidt J.O., Hinrichsen H.H. (2008) Impact of prey field variability on early cod *Gadus morhua* larval survival: a sensitivity study of a Baltic cod Individual-based Model. Oceanologia 50:205-220

Theilacker G.H., Bailey K.M., Canino M.F., Porter S.M. (1996) Variations in larval walleye pollock feeding and condition: a synthesis. Fisheries Oceanography 5:112-123

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

Vikebø F., Jørgensen C., Kristiansen T., Fiksen Ø. (2007) Drift, growth, and survival of larval Northeast Arctic cod with simple rules of behaviour. Marine Ecology Progress Series 347:207-219

Voss R., Hinrichsen H.H., St.john M. (1999) Variations in the drift of larval cod (*Gadus morhua* L.) in the Baltic Sea: combining field observations and modelling. Fisheries Oceanography 8:199-211

Voss R., Koester F.W., Dickmann M. (2003) Comparing the feeding habits of co-occurring sprat (*Sprattus sprattus*) and cod (*Gadus morhua*) larvae in the Bornholm Basin, Baltic Sea. Fisheries Research 63:97-111

Werner F.E., Perry R.I., Lough R.G., Naimie C.E. (1996) Trophodynamic and advective influences on Georges Bank larval cod and haddock. Deep-Sea Research Part II-Topical Studies in Oceanography 43:1793-1822

Wieland K., Zuzarte F. (1991) Vertical distribution of cod and sprat eggs and larvae in the Bornholm Basin (Baltic Sea) 1987-1990. ICES CM1991/J:37

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 the timing of spawning of Baltic cod: possible causes and implications for recruitment. ICES Journal of Marine Science 57:452-464

Zuzarte F., Koester F.W., Moellmann C., Voss R., Grønkjær P. (1996) Diet composition of cod larvae in the Bornholm Basin. ICES CM 1996/J:19

PAPER 4

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Research article

Abundance, horizontal and vertical distribution of the invasive ctenophore *Mnemiopsis leidyi* in the central Baltic Sea, November 2007

Bastian Huwer[1]*, Marie Storr-Paulsen[1], Hans Ulrik Riisgård[2] and Holger Haslob[3]
[1]National Institute of Aquatic Resources, Technical University of Denmark, Charlottenlund Castle, DK-2920 Charlottenlund, Denmark
[2]Marine Biological Research Centre, University of Southern Denmark, Hindsholmvej 11, DK-5300 Kerteminde, Denmark
[3]Leibniz-Institute of Marine Sciences, IFM-GEOMAR, Düsternbrooker Weg 20, 24105 Kiel, Germany
**Corresponding author*
E-mail: bhu@difres.dk

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Abstract

The distribution and abundance of the invasive ctenophore *Mnemiopsis leidyi* in the Bornholm Basin, an important spawning ground of several fish stocks, and in adjacent areas in the central Baltic Sea was studied in November 2007. The study showed that *M. leidyi* were relatively small (body length 18.6 ± 7.6 mm) and they were patchily distributed over a large part of the investigated area. Specimens were found on 68 and 59% of stations sampled with a Bongo net (n=39) and an Isaac-Kidd midwater trawl (n=51), respectively. Vertically, the highest densities of *M. leidyi* occurred at 40 to 60 m around the halocline. Horizontally, the highest abundances were found north and west of Bornholm, but relatively high densities were also observed in the Slupsk Furrow. The mean abundance was 1.58 ± 2.12 ind. m^{-2}, the peak abundance was 8.92 ind. m^{-2}, and the average and peak population density were 0.03 ± 0.05 and 0.28 ind. m^{-3}, respectively. The abundances are low compared to densities recently observed in other areas of the Baltic region (e. g. Limfjorden, Åland Sea) and the estimated predation impact on zooplankton by *M. leidyi* was negligible in November 2007. However, because of the ctenophore's wide distribution in the central Baltic Sea, its ability for rapid population growth, and its potential influence on fish stocks by competing for food and by preying on fish eggs and newly hatched larvae, close monitoring of the future development of *M. leidyi* in the Baltic Sea is strongly recommended.

Key words: *Mnemiopsis leidyi*, comb jelly, ctenophora, invasive species, Baltic fish stocks, Bornholm Basin

Introduction

Several studies have recently described occurrences of the invasive lobate ctenophore *Mnemiopsis leidyi* A. Agassiz, 1865 in the Baltic Sea (Javidpour et al. 2006; Haslob et al. 2007; Janas and Zgrundo 2007; Kube et al. 2007; Lehtiniemi et al. 2007; Tendal et al. 2007). The ctenophore was accidentally introduced with cargo ballast water into the Black Sea in the early 1980s, where its explosive population growth coincided with a breakdown of, in particular, the anchovy fishery (Vinogradov et al. 1989; Mutlu 1999; Kideys 2002). Subsequently, it spread into adjacent waters of the Mediterranean and to the Caspian Sea (Kideys and Niermann 1993; Shiganova 1993; Shiganova et al. 2001). In autumn 2006 *M. leidyi* was observed, nearly simultaneously, at several locations in northern Europe, including the western Baltic Sea (Faasse and Bayha 2006; Javidpour et al. 2006; Boersma et al. 2007; Oliveira 2007; Tendal et al. 2007). Early in 2007, observations of *M. leidyi* in Danish waters and the Baltic Sea commenced to become numerous, and in many cases there were indications of mass occurrences (Tendal et al. 2007; Lehtiniemi et al. 2007). *M. leidyi* has been documented to overwinter in low abundances (1-4 ind. m^{-3}) in the southern Baltic Sea at temperatures below 10 ºC (Kube et al. 2007). This has given the ctenophore an opportunity to extend its distribution range from the south-western to the central Baltic Sea between autumn 2006 and spring 2007 (Kube et al. 2007). In August 2007, very high densities were registered in the central parts of a shallow Danish fjord system (Limfjorden) where some localities reached values above 200 ind. m^{-3}, and in one case (Skive Fjord) the density was measured to be 867 ± 121 ind. m^{-3} (Riisgård et al. 2007). These values considerably exceeded abundances reported from the northern Baltic Sea during spring and summer 2007 (Lehtiniemi et al. 2007) and even most values reported from the Black Sea during the period when the zooplankton and fish stocks collapsed in this area (Purcell et al. 2001b; Shiganova et al. 2001).

The strong focus on the mainly carnivorous *M. leidyi* is due to its predation impact on zooplankton and ichthyoplankton which may be detrimental to fish populations (Purcell et al. 2001b; Kideys 2002). Furthermore, *M. leidyi* has a great invasive potential due to its ability of rapid growth and reproduction, and its high tolerance of broad ranges of temperatures and salinities (Kremer 1994; Shiganova 1998; Purcell et al. 2001b). Individual growth rates and egg production in *M. leidyi* varies with size, food availability and temperature (Kremer 1994; Purcell et al. 2001b) and Kremer (1994) concluded that three factors act in a hierarchy to determine the abundance of *M. leidyi*: temperature, food availability and mortality (predation), in decreasing order of importance.

Most of the recent studies on *M. leidyi* in the Baltic Sea are restricted to coastal areas and report on independent, purely qualitative catches or sightings obtained by various methods on different dates over a broad time scale. Exceptions are the studies by Lehtiniemi et al. (2007) who described abundances of *M. leidyi* in the Gulf of Finland, the Åland Sea and the Gulf of Bothnia, and by Haslob et al (2007) who investigated *M. leidyi* abundances on a station grid in the Bornholm Basin. The Bornholm Basin is of great importance for several fish species in the Baltic Sea, especially for the eastern Baltic cod *Gadus morhua* Linnaeus, 1758, as this area presently represents the only spawning ground that supports successful reproduction of this stock (Hinrichsen et al. 2007; Köster et al. 2005). Haslob et al. (2007) observed that the vertical distribution of *M. leidyi* showed an overlap with the water layers where cod eggs and, to a lesser degree, sprat eggs are neutrally buoyant. They hypothesized that this overlap may result in reduced recruitment success of these fish stocks due to predation by *M. leidyi* on fish eggs, as well as by competition for zooplankton food, influencing the survival success of fish larvae.

The present study investigated the horizontal and vertical distribution as well as abundances of *M. leidyi* in the Bornholm Basin and surrounding areas in November 2007. To our knowledge, this study represents the first extensive and systematic investigation on the distribution of *M. leidyi* in the central Baltic Sea on such a broad scale.

Materials and Methods

Samples of *M. leidyi* were collected during a cruise with the Danish research vessel 'DANA' from November 1st to 18th, 2007. The investigation covered an area from approximately 14.15° E to 18.15° E and 54.30° N to 56.15° N. The sampling was conducted with three different gears to obtain a coverage of the horizontal and vertical distribution of *M. leidyi*: an Isaac-Kidd midwater trawl (IKMT), a Multinet (5 nets), and a Bongo net. Corresponding ambient hydrographic conditions (salinity, temperature, oxygen concentration) were recorded at the sampling stations with a CTD (Sea-Bird plus).

Sampling with the Isaac-Kidd midwater trawl (mesh size 4 mm in the cod end) was conducted to investigate the horizontal and vertical distribution of *M. leidyi*. Hauls were taken on a regularly-spaced station grid with a distance of approximately 13.5 nautical miles between sampling stations. The duration of a haul was 30 min, and the gear was equipped with a flowmeter to measure the volume of filtered water. On stations with a bottom depth shallower than 35 m, one haul was made with the gear undulating between the surface and 5 m above the sea floor.

On stations deeper than 35 m, a two-layer sampling strategy was adopted to investigate the vertical distribution of *M. leidyi*. Thus, two hauls were taken; during the first haul, the gear was undulating between 5 and 25 m above the sea floor, while the second haul covered the remaining part of the water column, undulating between 25 m above the bottom and the surface. The decision of conducting two hauls at stations deeper than 35 m was based on the depth range at which the halocline was found in the study area (35-50 m), as previous studies by Haslob et al. (2007) and Kube et al. (2007) found *M. leidyi* exclusively below the halocline. Altogether, 91 IKMT hauls were taken on 51 stations.

To get a finer resolution of the vertical distribution of *M. leidyi* than obtained with the two-layer sampling strategy using the IKMT, hauls with an opening/closing Multinet (mesh size 335 µm, aperture 0.25 m^2) were taken on three stations. The vertical distribution of *M. leidyi* was resolved in steps of 5 or 10 m. The gear was towed, undulating in each depth range for approximately 5 to 6 min.

To assess abundances of *M. leidyi*, hauls with a Bongo net were taken on a total of 39 stations. The Bongo net (60 cm mouth diameter) was equipped with 500 µm mesh size nets, cod ends with 335 µm mesh size, and a flowmeter. This gear was towed in a double oblique haul integrating the entire water column, from 5 m above the bottom to the surface. The numbers of specimens from the two nets were combined. Counts of *M. leidyi* were standardised to individuals per m^2 by accounting for the filtered water volume and the maximum depth of the tow.

Specimens of *M. leidyi* were sorted from the samples, counted and the body oral-aboral length of each individual was measured to the nearest 1.0 mm with the aid of a sliding caliper. All samples were analysed within 30 min after capture. Individuals caught with Bongo and Multinet were generally less damaged than individuals captured with the IKMT, probably due to the different mesh sizes and haul durations.

A comparison of *M. leidyi* length distributions caught with the IKMT and with the Bongo net reflected that the catchability for smaller individuals (<10 mm) was lower with the IKMT (Figure 1), due to the relatively large mesh size of this gear. Generally, the catchability of the IKMT gear was smaller than the catchability of the Bongo net.

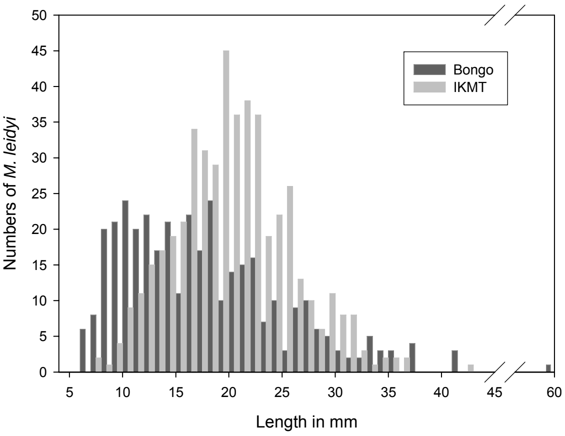

Figure 1. Mnemiopsis leidyi. Size distribution of ctenophores sampled with Isaac-Kidd midwater trawl (IKMT) and Bongo net.

However, we assume that the catchability of the IKMT is equal amongst hauls, and that IKMT stations are comparable with each other. A direct calculation of abundances per filtered volume from IKMT catches would largely underestimate true abundances of ctenophores. Assuming that the Bongo net has a catchability of 1, we compared Bongo catches to IKMT catches at those stations that were sampled with both gears. Only individuals >10 mm were considered in this analysis. One outlier was excluded (Bongo n=61, IKMT n=3), which may be due to a small scale patchiness in the distribution of *M. leidyi*. The analysis resulted in a significant linear relation between IKMT and Bongo catches ($P<0.001$, $r^2=0.72$), and we used this relationship to convert IKMT data to abundance estimates (ind. m^{-2}).

Results

While the size distributions of *M. leidyi* in the catches using the Multinet and the Bongo net were similar (cod end mesh size was 335 µm in both gears), the size distribution of *M. leidyi* retained in the IKMT and Bongo nets differed due to the different mesh sizes. *M. leidyi* between 6-59 mm (average 18.6 mm ± 7.6 SD) and 8-43 mm (average 21 mm ± 5.7 SD) were retained in the Bongo net and the IKMT, respectively (Figure 1). Although the IKMT was able to catch some *M. leidyi* <10 mm, the catchability of this gear for smaller specimens was lower in comparison to the Bongo net. Thus, for the comparison of IKMT catches to Bongo net catches, only specimens >10 mm were considered.

The IKMT catches showed highest numbers of *M. leidyi* to occur in the deep hauls (Figure 2) where 70% of specimens were caught, whereas 30% were caught in the shallow hauls. A peak in the deep-haul density of *M. leidyi* was observed in the area north of Bornholm (Figure 2b), although a relatively large number of specimens were also caught by shallow hauls taken close to the coasts of Sweden, Bornholm and Poland (Figure 2a).

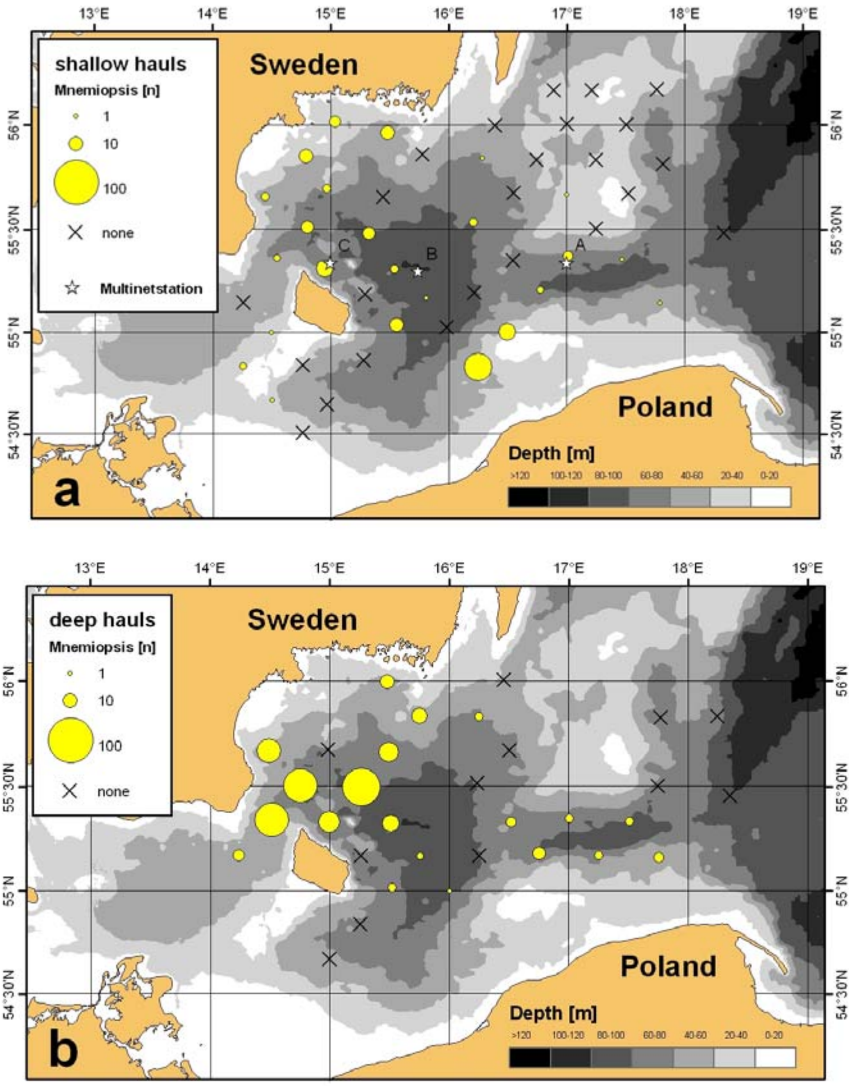

Figure 2. Mnemiopsis leidyi. Horizontal distribution of numbers of ctenophores per haul sampled with Isaac-Kidd midwater trawl (circles) and stations without ctenophores (crosses) in (a) shallow, and (b) deep hauls. Figure 2a also depicts the positions of Multinet stations A, B and C (white stars).

The results from the three Multinet stations support the observation from the IKMT catches that highest densities of *M. leidyi* mainly occurred at larger depths (Figure 3). In comparison with the CTD data, the vertical distribution of Multinet catches shows that the highest *M. leidyi* densities were found close to the halocline, and at two stations (A and C) *M. leidyi* was not observed above 35 m, but it was found at low oxygen levels down to 0.29 ml l^{-1}.

Generally, *M. leidyi* was widely distributed in the study area being present in 68% of the Bongo net stations and 59% of the IKMT stations (Figures 2 and 4). The horizontal distribution of *M. leidyi* sampled with the Bongo net revealed highest abundances north and west of Bornholm, and relatively high densities were observed in the Slupsk Furrow which connects the Bornholm Basin to the Gdansk Deep further to the east (Figure 4). However, no *M. leidyi* were observed in the southwestern part of the investigation area and in the northeastern part, in the region around the Middelbanke with very shallow water. The maximum abundance of *M. leidyi* caught at the Bongo net stations was 8.92 ind. m^{-2} (0.28 ind. m^{-3}), with mean densities of 1.58 ± 2.12 ind. m^{-2} (0.03 ± 0.05 ind. m^{-3}).

The horizontal distribution and abundance estimates obtained from the IKMT catches (Figure 5) are largely in concordance with the results from the Bongo net samplings. Again, highest abundances were observed in the area north of Bornholm. However, abundances in the Slupsk Furrow were somewhat lower than observed by the Bongo net sampling, while the IKMT sampling suggested a second, smaller abundance peak at the southeastern edge of the Bornholm Basin, an area that was not covered by the Bongo net sampling. The observation that no *M. leidyi* occurred in the southwestern and northeastern parts of the investigated area was also confirmed by the IKMT sampling. However, the maximum values of abundance estimates from the IKMT sampling were lower compared to the Bongo net sampling (maximum 4.42 ind. m^{-2} for the IKMT and 8.92 ind. m^{-2} for the Bongo net sampling). It should be kept in mind, though, that the abundances obtained by means of the IKMT samplings only included ctenophores >10 mm body length.

Using equations given by Riisgård et al. (2007), the population filtration rate of *M. leidyi* with mean body length (18.8 mm) and peak density (0.28 ind. m^{-3}) found in the present study was estimated to be $F_{pop} = 2.3\times10^{-3}$ m^3 d^{-1}, and subsequently the half-time of zooplankton (copepods) was found to be $t_{1/2} = 300$ d.

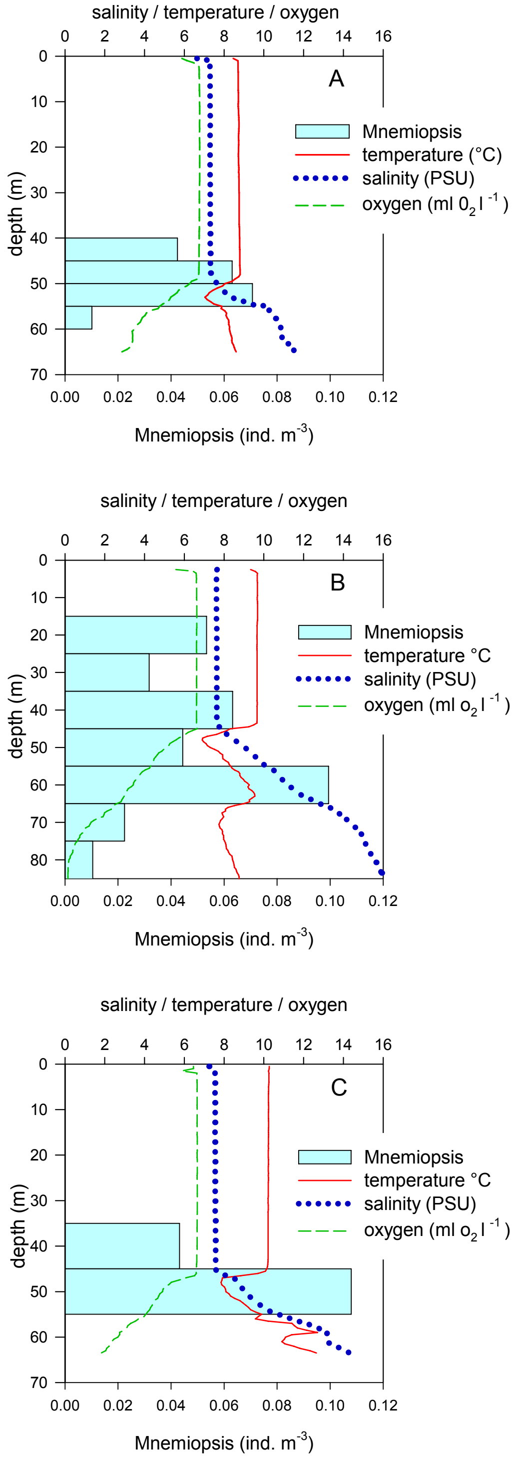

Figure 3. Mnemiopsis leidyi. Vertical distribution of ctenophores sampled with Multinet on three stations (A, B, C, see Figure 2a) in relation to temperature, salinity and oxygen concentration as determined by CTD measurements.

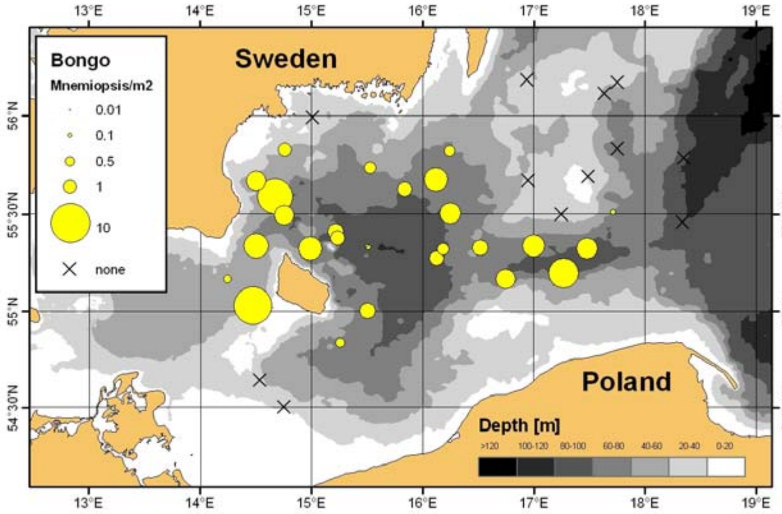

Figure 4. Mnemiopsis leidyi. Abundance of ctenophores (ind. m^{-2}) sampled with Bongo net

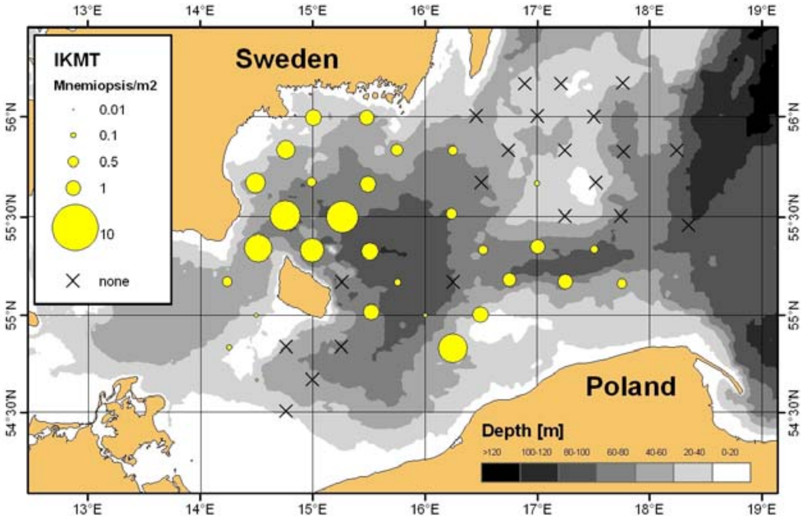

Figure 5. Mnemiopsis leidyi. Abundance of ctenophores (> 10 mm; ind. m^{-2}) sampled with Isaac-Kidd midwater trawl (IKMT).

Discussion

Hydrographic influence on distribution

Temperature appears to be of overriding importance in determining conditions suitable for population increase and expansion of *M. leidyi* (Kremer 1994; Mutlu 1999; Purcell et al. 2001b; Shiganova et al. 2001; Purcell and Decker 2005). In its native environment, reproduction occurs from spring through autumn at temperatures ≥12 °C, reproduction peaks at temperatures of 24–28 °C (Purcell et al. 2001b), and in the Sea of Azov Shiganova et al. (1998, 2001) did not find any specimens when the temperature dropped below 4 °C.

Lehtiniemi et al. (2007) found the highest densities of *M. leidyi* eggs (90 eggs m^{-3}) around the halocline at 80-60 m depth where the temperature ranged between 4.5-5 ºC. This indicates that although the optimal spawning temperature for *M. leidyi* in the Black Sea or in its native environment is high, *M. leidyi* may have adopted to the Baltic Sea environment and spawn now at lower temperatures. Besides, higher abundances of *M. leidyi* than previously recorded in the Black Sea and the Caspian Sea have been registered in a shallow Danish fjord system, at relatively low temperatures (11-19 °C) (Riisgård et al. 2007).

M. leidyi does not seem to be limited by salinities >2 PSU, but low winter temperatures, particularly in combination with low salinities, may prevent survival throughout the winter in some locations, e.g. the Sea of Azov (Purcell et al. 2001b). Data by Kube et al. (2007) show that *M. leidyi* occurred in the central Baltic Sea during the winter months below the halocline where temperatures do not drop below 4°C. Therefore, it seems reasonable to suggest that *M. leidyi* may use the Bornholm Basin as a refuge during winter, and to expand its distributional range in spring when temperature and food availability are increasing. It has been shown that *M. leidyi* also overwinters in the Gulf of Finland (Lehtiniemi et al. 2007), and it is therefore possible that other areas in addition to the Bornholm Basin act as winter refuges.

Lehtiniemi et al. (2007) suggested that the distribution and further expansion of *M. leidyi* in the northern Baltic Sea may be restricted by low salinity or low oxygen concentrations as they did not find the ctenophore at salinities <5 PSU, or on localities where oxygen was depleted at water depths below 60-70 m. In the present study, we found individuals of *M. leidyi* at oxygen levels down to 0.29 ml l^{-1} which is in accordance with laboratory experiments showing 100% survival in a 96 h incubation at an oxygen concentration of 0.5 ml l^{-1} (Purcell et al. 2001a). This suggests that in the Baltic Sea, salinity may exert a stronger influence than oxygen on the expansion and distribution of the ctenophore.

In its native environment, *M. leidyi* encounters wide ranges of temperatures (2-32 °C) and salinities (2-38 PSU) (Purcell et al. 2001b). Nevertheless, both ctenophore size and size-specific egg production were less at low temperature (9 °C) and salinity (7 PSU) than at warmer temperatures and higher salinities tested in the laboratory (Purcell and Decker 2005). Thus, even though *M. leidyi* has been reported to tolerate low salinities, it probably has a preference for higher salinities. Accordingly, it can not be precluded that in the Baltic Sea, *M. leidyi* is actively or passively (via drift) distributing to areas or depths with higher salinities and/or temperatures where growth and reproduction are optimal. This possibility receives some support from the depth-stratified IKMT and Multinet samplings which showed a clear peak in abundances of *M. leidyi* in the deeper water layers of the Bornholm Basin where higher salinities are found. However, in contrast to the studies by Haslob et al. (2007) and Kube et al. (2007) who found *M. leidyi* exclusively below the halocline, the stratified samplings in the present study showed that in November 2007, the ctenophore was also distributed above the halocline, and in shallower, less saline coastal areas. The preference of the ctenophore for high saline water may possibly reflect an active search, and if this is true, an outbreak of *M. leidyi* in the central Baltic Sea may hitherto have been restricted by low salinities. This hypothesis receives further support by findings of Riisgård et al. (2007), who observed high densities of *M. leidyi* at salinities of 27-28 PSU.

Densities in the Bornholm Basin

In May 2007, Haslob et al. (2007) investigated the abundance of *M. leidyi* in the Bornholm Basin. They found abundances of up to 7.74 ind. m^{-2} in the central Basin. The *M. leidyi* abundances observed during the present study in November 2007 showed a similar range, with maximum abundances of 8.92 ind. m^{-2}. However, the horizontal distribution of *M. leidyi* exhibited differences between the two studies. While Haslob et al. (2007) found the abundance peak to be in the central Bornholm Basin in May 2007, we observed the highest abundances at the northwestern and southeastern edges of the Bornholm Basin.

In the late summer of 2007, Riisgård et al. (2007) found densities of mainly small (5 to 15 mm) *M. leidyi* to be between 18 and 867 ind. m^{-3} in Limfjorden, a shallow Danish fjord system. These densities even exceeded those observed in the Black Sea in 1989 when the zooplankton and fish stocks collapsed, and where the mean and maximum density was 12.4 and 304 ind. m^{-3}, respectively (Shiganova et al. 2001).

Lehtiniemi et al. (2007) reported abundances of 694 ind. m^{-2} and densities of 24 ind. m^{-3} for the northern Baltic Sea in September 2007. Compared to these high figures, the levels registered in the Bornholm Basin in November 2007 seem modest. However, as shown by Lehtiniemi et al. (2007), abundances may increase remarkably within a few weeks in some areas, which confirms the great potential of *M.*

leidyi to reproduce and reach outbreak levels within a short time.

Potential influence of the Baltic sprat stock on M. leidyi population dynamics

It is striking that high abundances of *M. leidyi* have been observed in areas west and north of the central Baltic (Riisgård et al. 2007; Lehtiniemi et al. 2007), while the abundance in the Bornholm Basin and the surrounding areas is low. An explanation for this could be competition for food (zooplankton) caused by the currently very large stock of sprat *Sprattus sprattus* (Linnaeus, 1758). Among other possible factors, Purcell et al. (2001b) identified low competition for food by heavily overfished zooplanktivorous fish stocks to be one of the main reasons for the population explosion of *M. leidyi* in the Black Sea. In the Baltic, however, the sprat stock has increased considerably since the late 1980s and has been on a high level in recent years (Figure 6, Möllmann and Köster 2002). Möllmann et al. (2005) have shown a decrease in Baltic sprat condition due to strong intra-specific competition for zooplankton at large stock size.

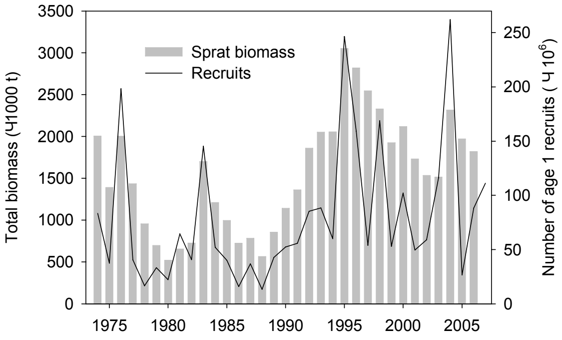

Figure 6. Time series of total sprat biomass and recruits at age 1 in the Baltic Sea (ICES subdivisions 22-32). Data from ICES (2007).

Accordingly, sprat may act as an important competitor for zooplankton in the central Baltic Sea, especially as sprat are migrating into the Bornholm Basin during spring and early summer for spawning (Aro 1989), i.e. periods likely to provide the best conditions for *M. leidyi* development. In addition to that, feeding sprat concentrate at depths between 50 m and the oxygen depleted deep water (Köster and Schnack 1994), i.e. the same depth range where the highest abundances of ctenophores have been found (Figure 3, Haslob et al. 2007).

Thus, the competition for food exerted by the presently large Baltic sprat stock may so far have prevented the population of *M. leidyi* to reach outbreak levels in the central Baltic Sea.

Predation impact of M. leidyi on zooplankton and cod eggs in the central Baltic Sea

Based on the calculations of population filtration rate and the half-time of zooplankton ($t_{1/2}$ = 300 d), the predation impact of *M. leidyi* on zooplankton in the central Baltic Sea in November 2007 is regarded negligible. Nevertheless, it may become significant ($t_{1/2}$ = 20-30 d) if the *M. leidyi* population density increases 10 to 15 times which may be realistic during the productive period. In this regard, the fact that *M. leidyi* was found around the entire Bornholm Basin in November 2007 is of major concern. Besides, high abundances were reported from fjord areas in Denmark (Riisgård et al. 2007) and from the northern Baltic Sea (Lehtiniemi et al. 2007). It is possible that these areas will act as donor areas, allowing *M. leidyi* to spread into the important fish spawning ground in the Basin centre. Such an expansion from coastal to offshore waters was observed in the Black Sea. Here abundance and biomass of *M. leidyi* was initially highest in inshore areas, which warm up earlier and/or are subjected to higher eutrophication. Subsequent increases of temperatures in offshore waters caused the expansion of populations into the central parts of the Black Sea (Mutlu 1999).

Despite the low present predation impact by *M. leidyi* on zooplankton, the ctenophore may exert a significant predatory influence on Baltic cod eggs at relatively low abundances due to an overlap in their vertical distribution in the Bornholm Basin. Haslob et al. (2007) observed highest densities of *M. leidyi* in the Bornholm Basin at the same depth range where cod eggs are found, a result that was corroborated by the present study.

The recruitment success of eastern Baltic cod is strongly dependent on increased egg survival due to inflows of high saline, oxygen rich water from the North Sea (Köster et al. 2005). As discussed above, an outbreak of *M. leidyi* in the central Baltic Sea could so far have been restricted by low salinities. Thus, higher survival of cod eggs and larvae after inflow events may be counteracted by an intensified predation impact of *M. leidyi* whose abundances may simultaneously increase due to rising salinities.

Conclusion and recommendation

The abundances of *M. leidyi* in the central Baltic Sea observed in the present study are low compared to the mass occurrences recently reported from neighboring areas. However, the fact that *M. leidyi* is now spread over vast areas of the central Baltic Sea is of major concern due to the ctenophore's ability to survive through the winter in the Baltic Sea, its high potential for explosive population development and its possible negative influences on fish stocks. Therefore, close monitoring of the future development of *M. leidyi* in the Baltic Sea is strongly recommended.

Acknowledgements

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References

Aro E (1989) A review of fish migration patterns in the Baltic. Rapports et procès-verbaux des réunions / Conseil International pour l'Exploration de la Mer 190: 72–96

Boersma M, Malzahn AM, Greve W and Javidpour J (2007) The first occurrence of the ctenophore *Mnemiopsis leidyi* in the North Sea. Helgoland Marine Research 61: 153-155

Faasse MA and Bayha KM (2006) The ctenophore *Mnemiopsis leidyi* A. Agassiz 1865 in coastal waters of the Netherlands: an unrecognized invasion? Aquatic Invasions 1: 270-277

Haslob H, Clemmesen C, Schaber M, Hinrichsen H-H, Schmidt J, Voss R, Kraus G and Köster FW (2007) Invading *Mnemiopsis leidyi* as a potential threat to Baltic fish. Marine Ecology Progress Series 349: 303-306

Hinrichsen H-H, Voss R, Wieland K, Köster FW, Andersen KH and 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

ICES (2007) Report of the Baltic Fisheries Assessment Working Group (WGBFAS), 17 – 26 April 2007, ICES Headquarters. ICES CM 2007/ACFM:15. 727 pp

Janas U and Zgrundo A (2007) First record of *Mnemiopsis leidyi* A. Agassiz, 1865 in the Gulf of Gdańsk (southern Baltic Sea). Aquatic Invasions 2: 450-454

Javidpour J, Sommer U and Shiganova, T (2006) First record of *Mnemiopsis leidyi* A. Agassiz 1865 in the Baltic Sea. Aquatic Invasions 1: 299-302

Kideys AE (2002) Fall and rise of the Black Sea ecosystem. Science 297: 1482-1484

Kideys AE and Niermann U (1993) Intrusion of *Mnemiopsis mccradyi* (Ctenophora; Lobata) into the Mediterranean Sea. Senckenbergiana Maritima 23: 43-47

Kremer P (1994) Patterns of abundance for *Mnemiopsis* in US coastal waters: A comparative overview. ICES Journal of Marine Science 51: 347–354

Kube S, Postel L, Honnef C and Augustin C (2007) *Mnemiopsis leidyi* in the Baltic Sea – distribution and overwintering between autumn 2006 and spring 2007. Aquatic Invasions 2: 137-145

Köster FW and Schnack D (1994) The role of predation on early life stages of cod in the Baltic. DANA 10: 179-201

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 N, Linkowski, T and Beyer JE (2005) Baltic cod recruitment - the impact of climate variability on key processes. ICES Journal of Marine Science 62: 1408-1425

Lehtiniemi M, Pääkkönen J-P, Flinkman J, Katajisto T, Gorokhova E, Karjalainen M, Viitasalo S and Björk H (2007) Distribution and abundance of the American comb jelly (*Mnemiopsis leidyi*) – A rapid invasion to the northern Baltic Sea during 2007. Aquatic Invasions 2: 272-276

Mutlu E (1999) Distribution and abundance of ctenophores and their zooplankton food in the Black Sea. II. *Mnemiopsis leidyi*. Marine Biology 135: 603–614

Möllmann C, Kornilovs G, Fetter M and Köster FW (2005) Climate, zooplankton, and pelagic fish growth in the central Baltic Sea. ICES Journal of Marine Science 62: 1270-1280

Möllmann C and Köster FW (2002) Population dynamics of calanoid copepods and the implications of their predation by clupeid fish in the Central Baltic Sea. Journal of Plankton Research 24: 959-977

Oliveira OMP (2007) The presence of the ctenophore *Mnemiopsis leidyi* in the Oslofjorden and considerations on the initial invasion pathways to the North and Baltic Seas. Aquatic Invasions 3: 185-189

Purcell JE, Breitburg DL, Decker MB, Graham WM, Youngbluth MJ and Raskoff KA (2001a) Pelagic cnidarians and ctenophores in low dissolved oxygen environments: a review. In: Rabalais NN and Turner RE (eds) Coastal Hypoxia: Consequences for Living Resources and Ecosystems, American Geophysical Union, Coastal and Estuarine Studies, vol 58. pp 77–100

Purcell JE, Shiganova TA, Decker MB and Houde ED (2001b) The ctenophore *Mnemiopsis* in native and exotic habitats: U.S. estuaries versus the Black Sea basin. Hydrobiologia 451: 145-176

Purcell JE and Decker MB (2005) Effects of climate on relative predation by scyphomedusae and ctenophores on copepods in Chesapeake Bay during 1987–2000. Limnology and Oceanography 50: 376–387

Riisgård HU, Bøttiger L, Madsen CV and Purcell JE (2007) Invasive ctenophore *Mnemiopsis leidyi* in Limfjorden (Denmark) in late summer 2007 - assessment of abundance and predation effects. Aquatic Invasions 2: 395-401-276

Shiganova TA (1993) Ctenophore *Mnemiopsis leidyi* and ichthyoplankton in the Sea of Marmara in October of 1992. Oceanology 33: 900-903

Shiganova TA (1998) Invasion of the Black Sea by the ctenophore *Mnemiopsis leidyi* and recent changes in pelagic community structure. Fisheries Oceanography 7: 305-310

Shiganova TA, Mirzoyan ZA, Studenikina EA, Volovik SP, Siokou-Frangou I, Zervoudaki S, Christou ED, Skirta AY and Dumont HJ (2001) Population development of the invader ctenophore *Mnemiopsis leidyi*, in the Black Sea and in other seas of the Mediterranean basin. Marine Biology 139: 431-445

Tendal O, Jensen KR and Riisgård HU (2007) Invasive ctenophore *Mnemiopsis leidyi* widely distributed in Danish waters. Aquatic Invasions 2: 272-277

Vinogradov ME, Shushkina EA, Musaeva EI and Sorokin PY (1989) Ctenophore *Mnemiopsis leidyi* (A. Agassiz) (Ctenophora: Lobata) – new settlers in the Black Sea. Oceanology 29: 293-298

Annex 1

Sampling date, sampling position, sampling depth, and abundance of *Mnemiopsis leidyi* sampled with Bongo net

Date	Latitude °N	Longitude °E	Sampling depth [m]	Abundance [ind. m^{-2}]
03.11.2007	55°22.633	15°14.099	0-80	1.21
03.11.2007	55°24.675	15°12.972	0-80	1.53
04.11.2007	55°16.511	16°07.378	0-78	1.29
05.11.2007	55°19.224	16°11.115	0-70	0.92
06.11.2007	55°35.448	14°40.272	0-65	8.10
06.11.2007	55°40.170	14°30.191	0-44	2.34
06.11.2007	55°49.709	14°45.595	0-30	1.08
06.11.2007	55°59.524	15°00.573	0-30	0.00
07.11.2007	55°37.734	15°50.160	0-65	1.32
07.11.2007	55°44.319	15°31.756	0-55	0.76
07.11.2007	55°19.417	14°59.347	0-65	3.30
07.11.2007	55°20.329	14°29.930	0-50	3.71
08.11.2007	55°29.718	14°45.230	0-60	2.27
08.11.2007	55°10.126	14°14.721	0-40	0.35
08.11.2007	55°01.875	14°28.406	0-32	8.92
10.11.2007	54°38.456	14°32.145	0-30	0.00
10.11.2007	54°30.129	14°45.354	0-17	0.00
10.11.2007	54°50.331	15°15.416	0-62	0.55
10.11.2007	55°00.176	15°30.183	0-71	1.57
11.11.2007	55°40.664	16°06.986	0-60	3.43
11.11.2007	55°49.390	16°14.549	0-49	0.58
12.11.2007	56°06.819	17°38.346	0-40	0.00
12.11.2007	56°10.065	17°45.276	0-20	0.00
12.11.2007	56°10.838	16°56.419	0-23	0.00
13.11.2007	55°40.280	16°57.134	0-27	0.00
13.11.2007	55°29.973	17°14.964	0-27	0.00
13.11.2007	55°41.420	17°29.364	0-24	0.00
14.11.2007	55°49.901	17°45.364	0-55	0.00
14.11.2007	55°47.195	18°20.955	0-90	0.00
14.11.2007	55°27.465	18°20.305	0-80	0.00
15.11.2007	55°19.524	17°28.814	0-73	2.86
15.11.2007	55°30.742	17°42.738	0-61	0.14
15.11.2007	55°20.234	16°59.857	0-62	3.17
15.11.2007	55°19.743	16°30.960	0-52	1.41
16.11.2007	55°10.042	16°44.901	0-62	2.24
16.11.2007	55°11.868	17°16.169	0-77	5.53
16.11.2007	55°30.259	16°14.992	0-65	2.62

Annex 2

Sampling date, sampling position, sampling depth, and abundance of *Mnemiopsis leidyi* (> 10 mm) sampled with Isaac-Kidd midwater trawl (IKMT)

Date	**Latitude °N**	**Longitude °E**	**Sampling depth [m]**	**Abundance [ind. m^{-2}]**
03.11.2007	55°10.154	15°15.641	0-57	0.00
03.11.2007	54°50.289	14°45.716	0-35	0.00
04.11.2007	54°40.037	14°59.855	0-55	0.00
04.11.2007	55°10.094	16°15.107	0-55	0.00
04.11.2007	54°59.992	16°00.052	0-55	0.06
05.11.2007	54°49.856	16°14.982	0-35	3.97
05.11.2007	55°00.168	16°29.620	0-25	1.19
05.11.2007	55°19.494	15°30.716	0-60	1.29
05.11.2007	55°29.824	15°15.773	0-60	4.42
05.11.2007	55°40.400	14°59.128	0-60	0.34
06.11.2007	55°40.290	14°29.462	0-45	1.80
06.11.2007	55°50.160	14°45.373	0-30	1.62
06.11.2007	55°59.903	15°00.429	0-30	1.17
06.11.2007	55°59.784	15°28.938	0-40	0.98
07.11.2007	55°50.198	15°44.828	0-40	0.65
07.11.2007	55°19.908	14°59.441	0-60	2.68
07.11.2007	55°20.560	14°30.618	0-40	3.46
08.11.2007	55°30.229	14°45.059	0-55	4.36
08.11.2007	55°10.171	14°14.376	0-40	0.35
08.11.2007	55°00.023	14°29.814	0-20	0.06
10.11.2007	54°50.036	14°15.118	0-20	0.12
10.11.2007	54°40.119	14°30.190	0-30	0.04
10.11.2007	54°30.329	14°45.986	0-15	0.00
10.11.2007	54°50.254	15°15.360	0-50	0.00
10.11.2007	55°00.887	15°31.317	0-50	1.08
10.11.2007	55°10.112	15°45.294	0-55	0.22
11.11.2007	55°40.171	16°30.433	0-55	0.00
11.11.2007	55°49.960	16°14.953	0-50	0.39
12.11.2007	56°00.212	17°00.173	0-30	0.00
12.11.2007	56°10.117	17°46.062	0-20	0.00
12.11.2007	56°00.042	17°30.538	0-32	0.00
12.11.2007	56°09.883	17°12.700	0-21	0.00
12.11.2007	56°09.930	16°53.650	0-23	0.00
13.11.2007	56°00.186	16°27.377	0-45	0.00
13.11.2007	55°50.070	16°44.729	0-38	0.00
13.11.2007	55°50.023	17°14.884	0-27	0.00
13.11.2007	55°39.964	16°59.988	0-27	0.09
13.11.2007	55°30.084	17°14.942	0-28	0.00
13.11.2007	55°40.347	17°31.448	0-26	0.00
14.11.2007	55°49.657	17°46.254	0-55	0.00
14.11.2007	55°49.881	18°14.904	0-55	0.00
14.11.2007	55°27.272	18°20.979	0-55	0.00
14.11.2007	55°09.721	17°45.346	0-40	0.41
14.11.2007	55°20.000	17°30.333	0-60	0.31
15.11.2007	55°30.083	17°45.006	0-60	0.00
15.11.2007	55°20.819	17°00.085	0-55	0.87
15.11.2007	55°19.984	16°31.040	0-50	0.34
16.11.2007	55°10.770	16°45.075	0-60	0.78
16.11.2007	55°10.239	17°15.011	0-60	0.86
16.11.2007	55°30.919	16°14.296	0-50	0.46
16.11.2007	55°39.926	15°29.452	0-60	1.22

Annex 3

Sampling date, sampling position, sampling depth, and density of *Mnemiopsis leidyi* sampled with Multinet (A, B and C refer to locations in Figure 2a)

Multinet A	**Date**	**Sampling depth [m]**	**Density [ind. m^{-3}]**
	15.11.2007	0-10	0.000
		10-20	0.000
Latitude °N	**Longitude °E**	20-30	0.000
55°20.333	16°59.969	30-35	0.000
		35-40	0.000
		40-45	0.042
		45-50	0.063
		50-55	0.071
		55-60	0.010

Multinet B	**Date**	**Sampling depth [m]**	**Density [ind. m^{-3}]**
	11.11.2007	5-15	0.000
		15-25	0.053
Latitude °N	**Longitude °E**	25-35	0.032
55°17.806	15°44.944	35-45	0.063
		45-55	0.044
		55-65	0.099
		65-75	0.022
		75-85	0.010

Multinet C	**Date**	**Sampling depth [m]**	**Density [ind. m^{-3}]**
	07.11.2007	0-15	0.000
		15-25	0.000
Latitude °N	**Longitude °E**	25-35	0.000
55° 20.135	15°00.031	35-45	0.043
		45-55	0.108

PAPER 5

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Short communication

Changes in distribution and lengths of *Mnemiopsis leidyi* in the central Baltic Sea between fall and spring

Marie Storr-Paulsen and Bastian Huwer
DTU Aqua, National Institute of Aquatic Resources, Technical University of Denmark, Charlottenlund Castle, DK-2920 Charlottenlund, Denmark
E-mails: msp@aqua.dtu.dk or bhu@aqua.dtu.dk

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Abstract

In March 2008, we conducted a survey to investigate the distribution and abundance of the invasive ctenophore *Mnemiopsis leidyi* in the Bornholm Basin after the winter period. Compared to the situation in November 2007 the centre of the distribution had shifted towards the deeper parts of the Basin where temperatures were higher than at the surface. Furthermore, we found a decrease in average size from 18.6 mm ± 7.6 SD in November to an average of 10.5 mm ± 4.9 SD in March, which may indicate the emergence of a new generation of *M. leidyi* between the two sampling dates.

Key words: *Mnemiopsis leidyi*, Ctenophora, invasive species, Baltic Sea, Bornholm Basin

Since the first observations of *Mnemiopsis leidyi* A. Agassiz 1865 in Northern Europe (Faasse and Bayha 2006; Hansson 2006; Javidpour et al. 2006; Oliveira 2007), several studies have described occurrences of this invasive lobate ctenophore in the Baltic, spanning from Kattegat to the Bothnian Sea (Haslob et al. 2007; Janas and Zgrundo 2007; Kube et al. 2007; Lehtiniemi et al. 2007; Tendal et al. 2007; Javidpour et al. 2008; Viitasalo et al. 2008). In November 2007, Huwer et al. (2008) investigated the horizontal and vertical distribution of *Mnemiopsis leidyi* in the central Baltic Sea. The studied area covered the Bornholm Basin, an important spawning ground for cod and sprat (Köster et al. 2005). Four months later, in March 2008, we conducted a survey in the same area to investigate if *M. leidyi* had survived the winter and how the distribution and abundances of this invasive species had changed during wintertime.

M. leidyi were sampled during a cruise with the Danish research vessel 'DANA' from March 1st to 17th 2008, on a station grid covering the Bornholm Basin. Additional sampling was conducted on a transect through the Arkona Basin consisting of 6 stations (Figure 1). To assess abundances and the horizontal distribution of *M. leidyi*, hauls with a Bongo net were taken on a total of 75 stations. The gear was equipped with two nets of different mesh size (335 µm and 500 µm) and with flowmeters to measure the volume of filtered water. Double oblique hauls from the surface to 2 meter above the seafloor were conducted at a towing speed of 3 knots.

Upon retrieval of the gear, specimens of *M. leidyi* were immediately sorted from the samples, counted and the body oral-aboral length of each individual was measured to the nearest 1.0 mm with a sliding caliper. All samples were analysed within 30 minutes after capture. Counts of

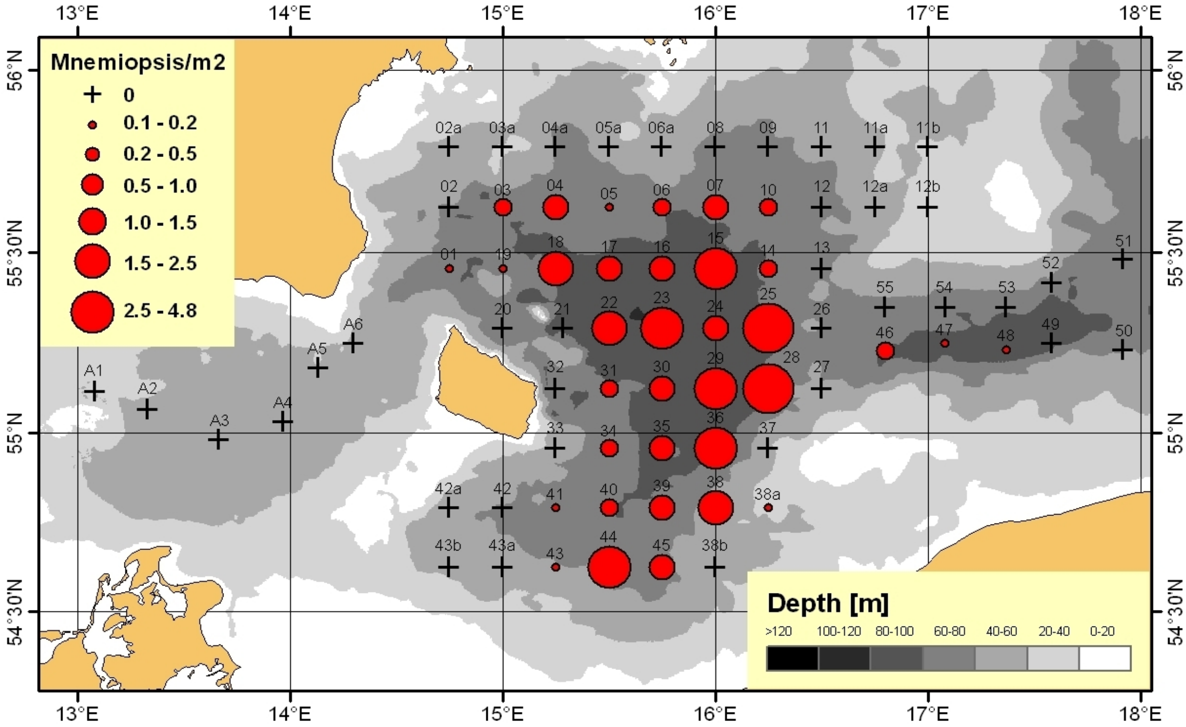

Figure 1. *M. leidyi*. Horizontal distribution and abundances (ind. m^{-2}) sampled with a Bongo net in March 2008. Station numbers are identical with the numbers in Annex 1

M. leidyi were standardised to 1 m^2 surface area by accounting for the filtered water volume and the maximum depth of the tow.

A total of 208 and 261 specimens of *M. leidyi* were caught in the 335 µm and 500 µm net, respectively. There was no significant difference ($P = 0.634$) between the size ranges of specimens caught with the two different mesh sizes, as average lengths were 10.2 mm ± 4.6 SD and 10.7 mm ± 5.1 SD for the 335 µm and 500 µm net, respectively. Accordingly, samples from the two nets have been pooled in the further analysis.

For a comparison of length distributions of *M. leidyi* between fall and spring, length data from November 2007 were used. The sampling procedure for these data is described in Huwer et al. (2008).

Horizontal distribution and abundance

Low temperatures have been found to be a limiting factor for the distribution and growth of *M. leidyi* (Kremer 1994; Mutlu 1999; Purcell et al. 2001; Shiganova et al. 2001; Purcell and Decker 2005). Therefore, we were interested in investigating the abundance and distribution of *M. leidyi* in the central Baltic after the winter period.

Huwer et al. (2008) found *M. leidyi* to be present over large areas of the central Baltic Sea in November 2007. In the present study in March 2008 the species was again distributed over large parts of the area. However, in comparison to the situation in fall 2007, the centre of the distribution had shifted to the deeper central parts of the Bornholm Basin (Figure 1). During the present study in spring 2008, no ctenophores were found on the 18 stations with depths <50 meters. The abundances of *M. leidyi* increased with increasing depth and almost 90% of the specimens were registered on stations with depths >70 meter (Table 1).

A possible reason for this change may be colder winter temperatures above the halocline in the Bornholm Basin. Figure 2 shows temperature and salinity profiles from a station in the central Bornholm Basin (Station 23 in Figure 1 and Annex 1; 55.292°N, 15.750°E) in November 2007 and March 2008. The situation in March showed a well mixed surface layer with a temperature of 4°C, and higher temperatures of 6 to 8°C in the bottom layer below 50 m depth. In November no such distinct temperature difference was detected and the surface water was much warmer with temperatures of about 9.5°C. In contrast to temperature, salinity did not seem to have an influence on the change in distribution in the present study. The salinity profiles showed little differences between fall and spring due to the permanent halocline in the Bornholm Basin.

Kube et al. (2007) have shown that *M. leidyi* was able to survive the winter in the Baltic Sea. Even though abundances at a sampling station in the Bornholm Basin were generally low, they found a decrease in abundances from February to May.

Table 1. Abundances of *M. leidyi* at different depth strata in March 2008

Depth	Stations (n)	*M. leidyi* (n)	*M. leidyi* (%)	Average *M. leidyi* m^{-2}
< 50 m	18	0	0%	0
50-59 m	12	18	3.8%	0.12±0.36
60-69 m	16	41	8.7%	0.19±0.44
70-79 m	17	178	38.0%	0.68±1.19
> 80 m	12	232	49.4%	1.37±0.98

Length distribution

Specimens of *M. leidyi* were significantly (P<0.001) larger in November 2007 than in March 2008. *M. leidyi* between 6-59 mm (average 18.6 mm ± 7.6 SD) and 3-27 mm (average 10.5 mm ± 4.9 SD) were caught in November 2007 and March 2008, respectively (Figure 3). Javidpour et al. (2008) investigated seasonal changes and population dynamics of *M. leidyi* in Kiel Fjord in the western Baltic Sea. Abundance peaks were observed in late summer-early autumn, which is in good correspondence to population dynamics in native habitats of *M. leidyi* (Kremer 1994). Javidpour et al. (2008) further describe seasonal shifts in the dominant size classes and conclude that peak reproduction in Kiel Fjord takes place in late summer and fall. However, their finding of a higher larvae: adult ratio from October 2006 to January 2007 may also indicate some reproduction in the winter period. In the present study, occurrence of smaller individuals in spring could be interpreted as the outcome of a new generation during fall or winter. This may indicate that successful reproduction and overwintering also occurs in the Bornholm Basin. However, because ctenophores can hardly be aged and are known to shrink at low food abundances (Reeve et al. 1989, Purcell et al. 2001), smaller size ranges in March could be due to starvation during wintertime. Another possible explanation for the shift in the length distribution may be passive transport of smaller individuals into the Bornholm Basin. A drift modeling study has shown that such a transport, e.g. from areas in the western Baltic, could be possible within few months (Postel et al. 2007).

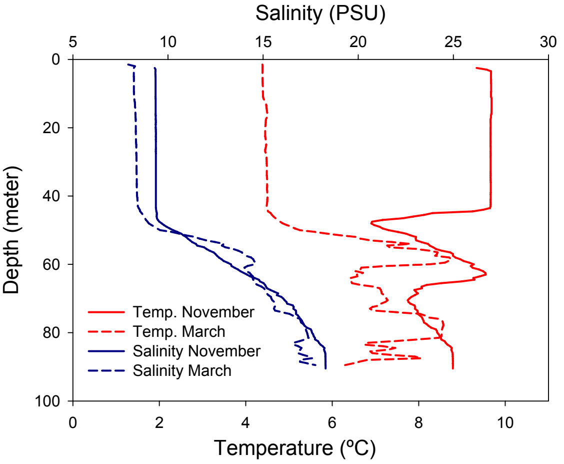

Figure 2. Temperature and salinity profiles in the central Bornholm Basin (station 23 in Figure 1 and Annex 1) in November 2007 and March 2008

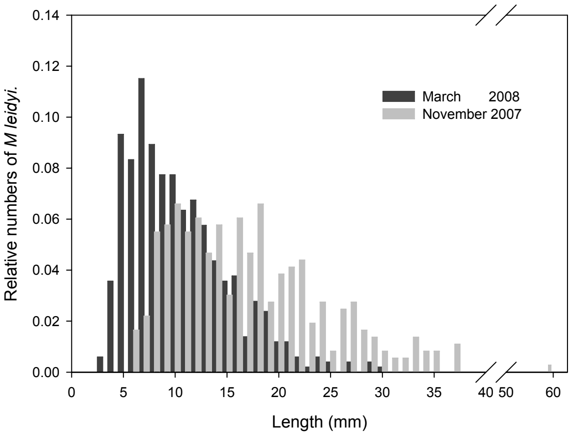

Figure 3. *M. leidyi.* Relative size distribution of ctenophores sampled in March 2008 (dark grey bars, n=469) and November 2007 (light grey bars, n=364; from Huwer et al. 2008)

The maximum abundance of *M. leidyi* in the Bornholm Basin in November 2007 was 8.92 ind. m^{-2}, with an average level of 1.58 ± 2.12 ind. m^{-2} (Huwer et al. 2008). In the present study four months later, abundances were lower with a maximum abundance of 4.83 ind. m^{-2}, and an average level of 0.43 ± 0.86 ind. m^{-2}.

However, even though abundances had decreased from fall to spring, *M. leidyi* has survived the second winter after its introduction to the central Baltic.

Conclusions

It can be concluded that *M. leidyi* was still present in the Bornholm Basin after the winter 2007/2008 and that the size distribution had shifted to smaller specimens, which may indicate the emergence of a new generation. Furthermore, there has been a shift in the horizontal distribution towards deeper parts of the Basin from fall to spring. Accordingly, *M. leidyi* may migrate from the colder surface layer to the warmer deep water during winter, while expanding its distribution to warmer upper layers and coastal areas during summer and fall. A similar temperature dependent vertical distribution was reported by Javidpour et al. (2008) for the *M. leidyi* population in Kiel Fjord. Other possible reasons for the changing distribution might be passive advection or differences in food availability. Thus, the present study provides further support for the hypothesis that *M. leidyi* uses the deep layers of the Bornholm Basin as overwintering refuge (Kube et al. 2007; Huwer et al. 2008).

However, to obtain a better understanding of *M. leidyi* distribution and population dynamics in the central Baltic, a temporally explicit monitoring is highly advisable. *M. leidyi* is known to prey on fish eggs and larvae (Cowan and Houde 1993; Purcell and Arai 2001; Purcell et al. 2001) and to compete with fish for zooplankton prey. Therefore, the seasonal development of this invasive predatory species receives special interest in the light of spatio-temporal interactions with ichthyoplankton in the Bornholm Basin (Haslob et al. 2007; Huwer et al. 2008). This area is at present the most important spawning ground for Eastern Baltic cod, a fish stock already suffering from unfavorable environmental conditions and heavy exploitation (Köster et al. 2005).

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References

Claussen DL, Hopper RA, Sanker AM (2000) The effects of temperature, body size, and hydration state on the terrestrial locomotion of the crayfish *Orconectes rusticus*. Journal of Crustacean Biology 20: 218-223

Cowan JH Jr., Houde ED (1993) Relative predation potentials of scyphomedusae, ctenophores and planktivorous fish on ichthyoplankton in Chesapeake Bay. Marine Ecology Progress Series 95: 55-65

Faasse MA, Bayha KM (2006) The ctenophore *Mnemiopsis leidyi* A. Agassiz 1865 in coastal waters of the Netherlands: an unrecognized invasion? Aquatic Invasions 1: 270-277

Hansson HG (2006) Ctenophores of the Baltic and adjacent Seas – the invader *Mnemiopsis* is here! Aquatic Invasions 1: 295-298

Haslob H, Clemmesen C, Schaber M, Hinrichsen H-H, Schmidt J, Voss R, Kraus G, Köster FW (2007) Invading *Mnemiopsis leidyi* as a potential threat to Baltic fish. Marine Ecology Progress Series 349: 303-306

Huwer B, Storr-Paulsen M, Riisgård H-U, Haslob H (2008) Abundance, horizontal and vertical distribution of the invasive ctenophore *Mnemiopsis leidyi* in the central Baltic Sea, November 2007. Aquatic Invasions 3: 113-124

Janas U, Zgrundo A (2007) First record of *Mnemiopsis leidyi* A. Agassiz, 1865 in the Gulf of Gdańsk (southern Baltic Sea). Aquatic Invasions 2: 450-454

Javidpour J, Sommer U, Shiganova, T (2006) First record of *Mnemiopsis leidyi* A. Agassiz 1865 in the Baltic Sea. Aquatic Invasions 1: 299-302

Javidpour J, Molinero J C, Peschutter J, Sommer U, Shiganova T (2008) Seasonal changes and population dynamics of the ctenophore *Mnemiopsis leidyi* after its first year of invasion in the Kiel Fjord, Western Baltic Sea. Biological Invasions. DOI 10.1007/s10530-008-9300-8

Kremer P (1994) Patterns of abundance for *Mnemiopsis* in US coastal waters: A comparative overview. ICES Journal of Marine Science 51: 347-354

Kube S, Postel L, Honnef C, Augustin C (2007) *Mnemiopsis leidyi* in the Baltic Sea – distribution and overwintering between autumn 2006 and spring 2007. Aquatic Invasions 2: 137-145

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 N, Linkowski T, Beyer JE (2005) Baltic cod recruitment - the impact of climate variability on key processes. ICES Journal of Marine Science 62: 1408-1425

Lehtiniemi M, Pääkkönen J-P, Flinkman J, Gorokhova E, Karjalainen M, Viitasalo S, Björk H (2007) Distribution and abundance of the American comb jelly (*Mnemiopsis leidyi*) – A rapid invasion to the northern Baltic Sea during 2007. Aquatic Invasions 2: 272-276

Mutlu E (1999) Distribution and abundance of ctenophores and their zooplankton food in the Black Sea. II. *Mnemiopsis leidyi*. Marine Biology 135: 603-614

Oliveira OMP (2007) The presence of the ctenophore *Mnemiopsis leidyi* in the Oslofjorden and considerations on the initial invasion pathways to the North and Baltic Seas. Aquatic Invasions 3: 185-189

Postel L, Kube S, Hammer C, Zimmermann C, Sommer U, Javidpour J, Clemmesen C, Boersma M (2007) Die Invasion der räuberischen Rippenqualle *Mnemiopsis leidyi* in der Ostsee. Final Report, November 2007. IOW - Leibniz Institute for Baltic Sea Research, Warnemünde

Purcell JE, Arai MN (2001) Interactions of pelagic cnidarians and ctenophores with fish: A review. Hydrobiologia 451: 27–44

Purcell JE, Shiganova TA, Decker MB, Houde ED (2001) The ctenophore *Mnemiopsis* in native and exotic habitats: U.S. estuaries versus the Black Sea basin. Hydrobiologia 451: 145-176

Purcell JE, Decker MB (2005) Effects of climate on relative predation by scyphomedusae and ctenophores on copepods in Chesapeake Bay during 1987–2000. Limnology and Oceanography 50: 376-387

Reeve MR, MA Syms, Kremer P (1989) Growth dynamics of a ctenophore (*Mnemiopsis*) in relation to variable food supply. I. Carbon biomass, feeding, egg production, growth and assimilation efficiency. Journal of Plankton Research 11: 535-552

Shiganova TA, Mirzoyan ZA, Studenikina EA, Volovik SP, Siokou-Frangou I, Zervoudaki S, Christou ED, Skirta AY, Dumont HJ (2001) Population development of the invader ctenophore *Mnemiopsis leidyi*, in the Black Sea and in other seas of the Mediterranean basin. Marine Biology 139: 431-445

Tendal O, Jensen KR, Riisgård HU (2007) Invasive ctenophore *Mnemiopsis leidyi* widely distributed in Danish waters. Aquatic Invasions 2: 272-277

Viitasalo S, Lehtiniemi M, Katajisto T (2008) The invasive ctenophore *Mnemiopsis leidyi* overwinters in high abundances in the subarctic Baltic Sea. Journal of Plankton Research 30: 1431-1436

Annex 1

Station number, position, sampling date, depth and abundance of *Mnemiopsis leidyi* caught with 335 µm and 500 µm Bongo nets, respectively. The station numbers refer to Figure 1

Station	Geographic coordinates		Date	Sampling depth (m)	Abundance (ind. m^{-2}) 335 µm	Abundance (ind. m^{-2}) 500 µm
	Latitude, °N	Longitude, °E				
A1	54.817	13.083	16.03.2008	0- 35	0.00	0.00
A2	55.067	13.333	16.03.2008	0- 41	0.00	0.00
A3	54.983	13.667	16.03.2008	0- 45	0.00	0.00
A4	55.033	13.967	16.03.2008	0- 46	0.00	0.00
A5	55.183	14.133	16.03.2008	0- 45	0.00	0.00
A6	55.250	14.300	16.03.2008	0- 45	0.00	0.00
1	55.458	14.750	13.03.2008	0- 69	0.12	0.12
2	55.625	14.750	06.03.2008	0- 66	0.00	0.00
02a	55.792	14.750	06.03.2008	0- 47	0.00	0.00
3	55.625	15.000	13.03.2008	0- 75	0.33	0.11
03a	55.792	15.000	06.03.2008	0- 37	0.00	0.00
4	55.625	15.250	12.03.2008	0- 76	0.50	1.49
04a	55.792	15.250	06.03.2008	0- 51	0.00	0.00
5	55.625	15.500	12.03.2008	0- 67	0.13	0.13
05a	55.792	15.500	06.03.2008	0- 59	0.00	0.00
6	55.625	15.750	12.03.2008	0- 70	0.42	0.00
06a	55.792	15.750	06.03.2008	0- 42	0.00	0.00
7	55.625	16.000	08.03.2008	0- 73	0.83	0.69
8	55.792	16.000	07.03.2008	0- 61	0.00	0.00
9	55.792	16.250	07.03.2008	0- 60	0.00	0.00
10	55.625	16.250	08.03.2008	0- 72	0.43	0.57
11	55.792	16.500	07.03.2008	0- 56	0.00	0.00
11a	55.792	16.750	07.03.2008	0- 47	0.00	0.00
11b	55.792	17.000	07.03.2008	0- 37	0.00	0.00
12	55.625	16.500	07.03.2008	0- 62	0.00	0.00
12a	55.625	16.750	07.03.2008	0- 44	0.00	0.00
12b	55.625	17.000	07.03.2008	0- 26	0.00	0.00
13	55.458	16.500	05.03.2008	0- 59	0.00	0.00

Annex 1 (continued)

Station	Geographic coordinates		Date	Sampling depth (m)	Abundance (ind. m^{-2}) 335 μm	Abundance (ind. m^{-2}) 500 μm
	Latitude, °N	Longitude, °E				
14	55.458	16.250	05.03.2008	0- 73	0.56	0.00
15	55.458	16.000	05.03.2008	0- 84	2.14	2.32
16	55.458	15.750	05.03.2008	0- 87	0.77	0.62
17	55.458	15.500	05.03.2008	0- 84	1.48	0.49
18	55.458	15.250	12.03.2008	0- 87	1.54	0.56
19	55.458	15.000	12.03.2008	0- 76	0.15	0.00
20	55.292	15.000	13.03.2008	0- 71	0.00	0.00
21	55.292	15.283	13.03.2008	0- 77	0.00	0.00
22	55.292	15.500	13.03.2008	0- 93	1.59	0.87
23	55.292	15.750	14.03.2008	0- 95	1.21	1.91
24	55.292	16.000	14.03.2008	0- 90	0.43	0.98
25	55.292	16.250	14.03.2008	0- 74	4.01	5.66
26	55.292	16.500	10.03.2008	0- 63	0.00	0.00
27	55.125	16.500	10.03.2008	0- 52	0.00	0.00
28	55.125	16.250	10.03.2008	0- 81	2.19	5.21
29	55.125	16.000	10.03.2008	0- 90	2.07	2.81
30	55.125	15.750	12.03.2008	0- 90	0.48	0.85
31	55.125	15.500	12.03.2008	0- 67	0.15	0.29
32	55.125	15.250	12.03.2008	0- 58	0.00	0.00
33	54.958	15.250	09.03.2008	0- 45	0.00	0.00
34	54.958	15.500	09.03.2008	0- 75	0.39	0.26
35	54.958	15.750	08.03.2008	0- 80	0.36	1.62
36	54.958	16.000	08.03.2008	0- 74	2.42	1.78
37	54.958	16.250	08.03.2008	0- 53	0.00	0.00
38	54.792	16.000	08.03.2008	0- 53	1.25	1.25
38a	54.792	16.250	08.03.2008	0- 50	0.00	0.20
38b	54.625	16.000	08.03.2008	0- 47	0.00	0.00
39	54.792	15.750	08.03.2008	0- 75	0.19	0.93
40	54.792	15.500	09.03.2008	0- 79	0.17	0.52
41	54.792	15.250	09.03.2008	0- 68	0.00	0.13
42	54.792	15.000	09.03.2008	0- 58	0.00	0.00
42a	54.792	14.750	09.03.2008	0- 46	0.00	0.00
43	54.625	15.250	10.03.2008	0- 58	0.16	0.00
43a	54.625	15.000	10.03.2008	0- 32	0.00	0.00
43b	54.625	14.750	09.03.2008	0- 47	0.00	0.00
44	54.625	15.500	09.03.2008	0- 65	1.44	2.02
45	54.625	15.750	09.03.2008	0- 60	0.50	0.84
46	55.230	16.800	04.03.2008	0- 75	0.34	0.34
47	55.250	17.080	04.03.2008	0- 80	0.00	0.36
48	55.233	17.367	04.03.2008	0- 66	0.00	0.33
49	55.250	17.583	05.03.2008	0- 63	0.00	0.00
50	55.233	17.917	05.03.2008	0- 58	0.00	0.00
51	55.483	17.917	05.03.2008	0- 66	0.00	0.00
52	55.417	17.583	04.03.2008	0- 76	0.00	0.00
53	55.350	17.367	04.03.2008	0- 70	0.00	0.00
54	55.350	17.083	04.03.2008	0- 66	0.00	0.00
55	55.350	16.800	04.03.2008	0- 63	0.00	0.00

PAPER 6

Seasonal distribution patterns of the invasive ctenophore *Mnemiopsis leidyi* in the central Baltic Sea in relation to ichthyoplankton

Matthias Schaber[1,*], Holger Haslob[1,*], Bastian Huwer[2,*], Anne Harjes[1], Hans-Harald Hinrichsen[1], Friedrich W. Köster[2], Marie Storr-Paulsen[2], Jörn O. Schmidt[3], Rüdiger Voss[3]

[1] Leibniz Institute of Marine Sciences, IFM-GEOMAR, Düsternbrooker Weg 20, 24105 Kiel, Germany
[2] National Institute of Aquatic Resources, Technical University of Denmark, Charlottenlund Castle, Jaegersborg Allé 1, 2920 Charlottenlund, Denmark
[3] Sustainable Fishery, Department of Economics, University of Kiel, Wilhelm-Seelig Platz 1, 24118 Kiel, Germany
* These authors contributed equally to this work

ABSTRACT

The invasive ctenophore *Mnemiopsis leidyi* was recorded for the first time in the Western Baltic in autumn 2006. As *M. leidyi* has been shown to be an important predator on early life stages of fishes in other regions, similar effects on fish populations in the Baltic cannot be rejected. An eastward propagation of the ctenophore into important spawning grounds of major Baltic fish stocks as well as predation on fish eggs was observed in the Bornholm Basin in 2007. The aim of the present study was to investigate the temporal and spatial overlap of *M. leidyi* and Baltic sprat (*Sprattus sprattus*) and cod (*Gadus morhua*) eggs and larvae as necessary prerequisite for predation. We conducted 7 research cruises covering the Bornholm Basin and adjacent areas from May 2007 to November 2008. To obtain horizontal and vertical distribution patterns of ctenophores as well as ichthyoplankton, standard Bongo-nets and multiple opening-closing nets were deployed. Results show different inter-seasonal distribution and overlap characteristics and thus different threat-scenarios for cod and sprat eggs and larvae. The overall potential impact of *M. leidyi* on the corresponding fish species was low for most of the period observed. However, we detected some scenarios with exceptionally high overlaps and signs for mass occurrences. Besides, a future population explosion can not be ruled out. Therefore, a further monitoring of the development of *M. leidyi* in the Baltic Sea is highly recommended.

Keywords: ctenophore, predator-prey overlap, cod, sprat, *Gadus morhua*, *Sprattus sprattus*, Bornholm Basin

INTRODUCTION

Accidentally or deliberately introduced alien species have the potential to significantly alter food webs, species composition and complete structures of established ecosystems (Levine 2008). The majority of biological invasions in marine systems are mediated through ballast-water with the number of recognized invasions from this origin increasing throughout the world (Carlton 1985, Carlton & Geller 1993).

During recent years, an invasion of the zooplanktivorous lobate ctenophore *Mnemiopsis leidyi,* native on the east coasts of North and South America (Purcell et al. 2001), to northern Europe has taken place – most probably also due to ballast-water. An almost simultaneous observation of *M. leidyi* at several locations in northern Europe took place in autumn 2006 (Faasse & Bayha 2006, Boersma et al. 2007, Oliveira 2007, Tendal et al. 2007) including initial evidence from the southwestern Baltic (Javidpour et al. 2006). A further proliferation into the central Baltic Sea between autumn 2006 and fall 2007 was reported (Kube et al. 2007, Huwer et al. 2008).

M. leidyi is known to voraciously prey on zoo- as well as ichthyoplankton (Purcell & Decker 2005, Costello et al. 2006). Thus, earlier observations from ecosystems invaded by *M. leidyi* gave rise to severe apprehensions concerning the state of fish stocks and the ecosystem as a whole. In the early 1980s, *M. leidyi* was accidentally introduced into the Black Sea. Here, *M. leidyi* showed a massive population explosion until the late 1980s with concentrations of up to 1.5 kg m^{-2} (Vinogradov et al. 1989). A following massive decline in the landings of the important anchovy (*Engraulis encrasicolus*) fishery could be related to *M. leidyi* as predator on eggs and larvae of *E. encrasicolus*, thus influencing the stock already affected by heavy fishing pressure (Bilio & Niermann 2004). Additionally, prey competition with zooplanktivorous fish stocks has been observed, intensifying potential negative effects on these fish stocks (Vinogradov et al. 1989, Daskalov & Mamedov 2007).

Consequently, much attention was led on the potential impact of *M. leidyi* in the Baltic since its first sighting (e.g. Haslob et al. 2007, Kube et al. 2007, Huwer et al. 2008, Javidpour et al. 2009), especially, because semi-enclosed seas like the Baltic are known to have higher sensitivity to the impact of invasive species (Caddy 1993).

In the Baltic, cod and sprat are the two dominating fish stocks, both having pelagic early life history stages (eggs and larvae). The spawning activity is concentrated in spring (sprat) and summer (cod) in the deep basins of the Baltic Sea (Aro 1989). During this part of the year the Bornholm Basin is characterized by a seasonal thermocline at approximately 20 to 30 m depth and a permanent halocline at between 50 to 75 m depth (Kullenberg & Jacobsen 1981, Møller & Hansen 1994). Ephemeral inflows of well oxygenated saline water from the North Sea replenish oxygen in the deep layers which is lost due to the breakdown of organic material by bacteria (Matthäus & Franck 1992). Contrary to other areas where salinities are sufficient to keep eggs floating in the surface layer, cod and sprat eggs in the Baltic Sea occur exclusively in the intermediate layers, concentrating within or below the halocline (Kändler 1944, Wieland & Jarre-Teichmann 1997). Depending on the prevailing ambient hydrographic conditions eggs can sink to layers with ambient oxygen concentration too low to allow successful development. For example for Baltic cod eggs, oxygen concentrations of less than 2 $ml*l^{-1}$ are considered critical (Wieland et al. 1994). A few days after hatch, the larvae begin to migrate vertically through the halocline into less saline, shallower water layers to feed (Grønkjær & Wieland 1997, Voss et al. 2007).

Apart from ambient hydrography, egg predation (Köster & Möllmann 2000) as well as larval starvation (Voss et al. 2003, Dickmann et al. 2007) have been discussed as major sources of mortality during the early life of Baltic sprat and cod. In contrast to other systems where a multitude of vertebrate and invertebrate predators on fish eggs and larvae can be found (e.g. California current and Baja Califonia: Alvariño 1980, Western North Atlantic: Turner et al. 1985, Gulf of Alaska: Brodeur & Merati 1993, or see Bailey & Houde 1989 for general review), the only identified significant ichthyoplankton predators in the corresponding depth layers in the central Baltic were, until recently, the clupeid fish species sprat (*Sprattus sprattus*) and herring (*Clupea harengus*) (Köster & Schnack 1994). With *M. leidyi*, another source of potential predation has been introduced into the Baltic Sea. The ctenophore could also indirectly affect fish larval mortality via competition for food resources and thus intensify larval starvation. As a matter of fact, for both, sprat as well as cod larvae indications for potential food limitation in the larval stage exist (Voss et al. 2006, Hinrichsen et al. 2002). Larval starvation due to food limitation might depend on the temporal coupling or decoupling of the production maxima of fish larvae and their prey organisms, as originally formulated in Cushing's 'match-mismatch' hypothesis (Cushing 1974, 1990). Both processes, predation as well as starvation, are strongly mediated in their importance by a highly variable overlap between predator and prey (comparable to a 'match-mismatch' concept). In any case, spatial and temporal overlap are necessary prerequisites for predation or competition to actually occur. The recent invasion of *M. leidyi* might influence both processes, but the focus of this work lies on spatio-temporal overlap of adult *M. leidyi* as potential predator and ichthyoplankton as prey.

Haslob et al. (2007) observed a vertical overlap of *M. leidyi* and ichthyoplankton and provided evidence for *M. leidyi* predation on fish eggs in the central Bornholm Basin. However, their study was restricted to one sampling period and did not take the seasonal changes in abundance and distribution patterns of *M. leidyi* and its potential ichthyoplanktonic prey into account. A better temporal coverage seems indispensable, especially as a sudden and brief occurrence of carnivore gelatinous plankters is not an anomaly but an adaptation that takes advantage of fluctuating resource availability (Boero et al. 2008).

In the present study we investigated seasonal changes in the abundance and distribution of *Mnemiopsis leidyi* in relation to early life stages of cod (*Gadus morhua*) and sprat (*Sprattus sprattus*) from April 2007 to November 2008. The sampling was concentrated on the Bornholm Basin area as it presently represents the only suitable spawning ground for the Eastern Baltic cod stock (Köster et al. 2005, Hinrichsen et al. 2007). In addition, it also serves as a major spawning ground for Baltic sprat (Aro 1989). The objective of this study was to assess the spatial overlap of predator and prey during different seasons and in relation to ambient hydrography.

Given the danger of a de-evolution of high-energy food chains back to medusozoan dominance (e.g. Boero et al. 2008), such understanding of ecological dynamics of gelatinous plankton might become an impelling priority in marine biology as well as conservation.

MATERIAL AND METHODS

Sampling

Sampling was conducted on six cruises onboard the German research vessel “Alkor” and on three cruises onboard the Danish research vessel “Dana” from April 2007 to November 2008. Table 1 provides a detailed overview of cruises and applied gears. In May and August 2007 and March, April, May and August 2008 sampling covered the entire Bornholm Basin (11800 km^2) on a 45-station grid with approximately 10 nautical mile grid-point distances plus 6 further stations in the easterly adjacent Slupsk Furrow (Fig. 1). Station depth ranges from 60 m at the margins of the basin to 100 m in the centre. The station grid was chosen to best account for differences and variability of the hydrography. A slightly different station grid was covered in November 2007 and 2008 (Fig.6 c and h). On some cruises additional stations were covered in the Arkona Sea (Fig. 6a – h). To obtain the horizontal distribution of *M. leidyi* and ichthyoplankton on each station one double oblique tow with a bongo net, equipped with 335 µm and 500 µm mesh sizes, was performed from 5 m above the bottom to the surface. This type of sampling does not account for patchiness on a smaller scale than the station grid, but gives a reliable estimate of the average abundance of species in the investigation area. Starting from April 2007, the vertical distribution of both *M. leidyi* and ichthyoplankon was investigated with a towed multiple opening-closing net on selected stations in the Bornholm Basin with high numbers of *M. leidyi* as seen from Bongo net sampling (Fig. 1).

On RV “Alkor”, the gear in use was a HYDROBIOS MAXI-type net (Hydrobios, Holtenau, Germany) with a net mouth opening of 0.5 m^2 equipped with 9 nets of 335 µm mesh size. On each corresponding station, at least three profiles from the surface down to near bottom were sampled in 5 m depth intervals. On RV “Dana”, the multinet used was a HYDROBIOS MIDI-type net (Hydrobios, Holtenau, Germany) with a net mouth opening of 0.25 m^2 equipped with 5 nets of 335 µm mesh size. With this net, one profile per corresponding station was sampled in 5 m depth intervals. Due to technical restrictions in November 2007, the depth intervals were 10 m. In November 2008, no vertically resolved sampling was possible due to extremely bad weather and resulting time constraints. All nets were equipped with a flowmeter to obtain the filtered volume of water.

Table 1: Cruises and sampling methods applied for the detailed resolution of spatial distribution of *Mnemiopsis leidyi* and ichthyoplankton. HD – Sampling of horizontal distribution; VD – Sampling of vertical distribution (* - ichthyoplankton samples analyzed). (HLN – Helgoländer Larvennetz).

Year	Month	HD	VD	Gear	Remarks
2007	April	-	x*	CTD, MN Maxi	
	May	x*	x*	CTD, MN Maxi, Bongo	
	August	x*	x*	CTD, MN Maxi, Bongo	HLN & WP-2 in Arkona Basin
	November	x*	x	CTD, MN Midi, Bongo	not on regular grid
2008	March	x*	x*	CTD, MN Midi, Bongo	
	April	x	x	CTD, MN Maxi, Bongo	
	May	x	x	CTD, MN Maxi, Bongo	
	August	x	x	CTD, MN Maxi, Bongo	
	November	x	-	CTD, Bongo	not on regular grid

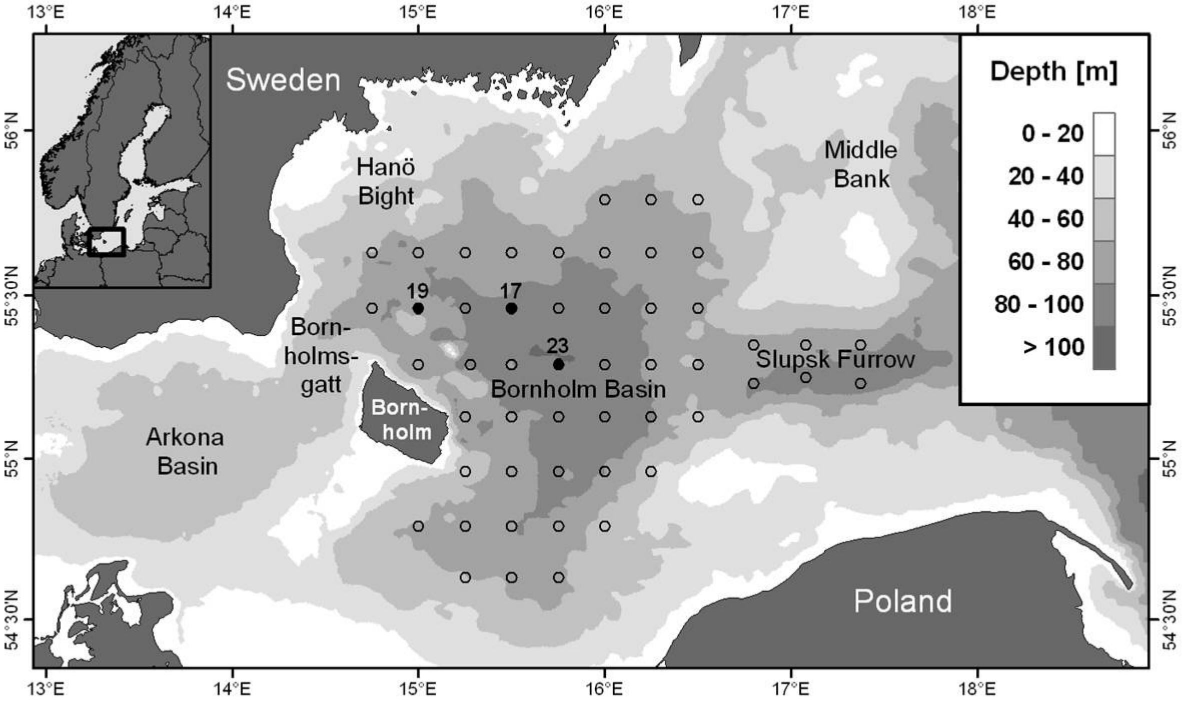

Fig. 1: Overview of the sampling area. Circles represent the regular station grid as sampled with CTD and Bongo-nets. Highlighted stations (17, 19, 23) show positions of multinet casts for the resolution of vertical distribution of *M. leidyi* and ichthyoplankton prey organisms. Additional stations sampled in adjacent areas (Arkona Basin, margins of the Bornholm Basin, Hanö Bight, Middle Bank) on several cruises are depicted on the corresponding panels in Fig. 6.

Temperature (°C), salinity (practical salinity unit, PSU) and oxygen content (ml l^{-1}) were measured concurrently on each station using an AMD-CTD (Sea and Sun Technology, Trappenkamp, Germany). In August 2007, additional stations in the Arkona Basin were sampled with a Helgolaender Larvae Net (HLN) with an opening of 2 m and 300 µm mesh and a WP-2 with 60 cm opening and 200 µm mesh which were deployed four times on each station from 4 m above the bottom to the surface.

Handling of the samples and laboratory analyses

As *M. leidyi* quickly dissolves in formaldehyde, prior to any fixation, all ctenophores from the Bongo- and Multinets were immediately collected from the samples, counted and measured on board. On the additional stations sampled with HLN and WP-2 nets, subsamples for length measurements were taken. As the lobes proved to be very susceptible to mechanical impact of sampling gear and therefore often were damaged or missing, length measurements were conducted on the central oral-aboral axis to the lower mm excluding the lobes. Afterwards, the remaining plankton sample from the 500µ Bongo-net was fixed in a 4 % formaldehyde-sea water solution.

As mechanical stress imposed through standard sampling gear can result in damage of soft-bodied plankton rendering identification impossible (Boero et al. 2008), the correct taxonomic identification of *M. leidyi* was confirmed on two sampling dates in 2007. Primers targeting the highly variable spacer region (ITS1) of ribosomal DNA genes, situated between 18S and 5.8S rDNA were used. Primers were designed such that they only fitted on *M. leidyi*, but not on any other co-occurring ctenophore. Moreover, four highly species specific microsatellite primer pairs desinged for *M. leidyi* were fully functional for 12 and 9 specimens in April and May 2007 (TBH Reusch, M Sparwel, unpublished data).

Ichthyoplankton was analysed in the lab using a stereomicroscope. Eggs and larvae were sorted from the whole sample, counted, and at least 200 eggs and larvae per sample were identified to species level. Due to time constraints all Bongo samples from May, August and November 2007 and March 2008 were analysed to cover a one-year period, whereas the samples from April, May, August and November 2008 remained unanalyzed with respect to ichthyoplankton. Vertically resolved ichthyoplankton samples from multinet casts were analyzed from April, May and August 2007 as well as March 2008.

Overlap calculation

To quantify and assess the potential impact of *M. leidyi* on ichthyoplankton throughout the season, a relative coefficient of overlap was calculated for the horizontal as well as the vertical distribution patterns of the ctenophore and its potential prey.

This coefficient C (Horn 1966) is 0 when there is no overlap and 1 at concurrent distributions of predator and prey:

$$C = 2\sum_{i=1}^{n}(A_i \times B_i) / \left(\sum_{i=1}^{n} A_i^{2} + \sum_{i=1}^{n} B_i^{2}\right) \qquad (1)$$

where for the vertical overlap calculation n is the number of (depth) strata covering the water column and A and B are the relative abundances of predator (*M. leidyi*) and prey organisms (different early life stages of cod (*G. morhua*) and sprat (*S. sprattus*)) per stratum. For the horizontal overlap calculation n is the number of stations covered and A and B are the relative abundances of predator (*M. leidyi*) and prey (ichthyoplankton).

Quotient plot analysis and statistical evaluation

In the highly stratified central Baltic Sea, the ambient hydrographic conditions experienced by *M. leidyi* can change significantly with only small vertical movements. Despite the known tolerance of *M. leidyi* towards a wide range of abiotic conditions (e.g. Purcell et al. 2001), it is desirable to identify habitat preferences in newly invaded areas. Thus, quotient curves were analyzed to identify and statistically evaluate the preferred habitat of the ctenophore in the area and to delimit environmental thresholds. These curves allow an assessment of selection or avoidance of habitats with certain properties. All curves were derived from vertically resolved abundance data and ambient environmental parameters (water depth, temperature, salinity and oxygen) on each station sampled with a multinet. The quotient (Q_c) of the percentage of total densities of *M. leidyi* within each environmental parameter c ($\%M_c$) and the percentage frequency of occurrence of each environmental parameter c ($\%e_c$) was calculated. The analysis covered the whole water column. According to different multinet sampling strategies, the vertical depth resolution was 5 m and 10 m respectively.

$$Q_c = (\%M_{c)} / (\%e_c) \qquad (2)$$

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 (for a detailed description of underlying calculations, see van der Lingen et al. 2001). Statistical evaluation was performed by applying the adapted R (R Development Core Team 2008) library “Shachar” (M Bernal). This library 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. Quotient values outside the corresponding confidence limits can be considered statistically significant. To test for possible combined effects of temperature, salinity and oxygen on the vertical distribution of *M. leidyi* a stepwise algorithm was applied to identify the best fitting model using the Akaike Information Criterion. This algorithm is part of the adapted "MASS"-package for R (Venables & Ripley 2002).

RESULTS

Hydrography

The seasonal development of the hydrographic situation showed the typical pattern expected for the Bornholm Basin, with a permanent halocline at ca. 50-60 m depth and a temporal thermocline developing during summer due to surface heating. All measurements of vertical hydrography profiles shown in Fig. 2 were conducted on Station 23 in the central Bornholm Basin (bottom depth 95 m), with the exceptions of August 2007 (Station 19, bottom depth 76 m) and August 2008 (Station 17, bottom depth 84 m).

Vertical temperature profiles showed a typical seasonal trend over the sampling period (Fig. 2). In April 2007, the water column was well mixed above 60 m depth with water temperatures of ca. 5 °C. Below 60 m, temperature increased towards the bottom with values reaching approximately 9 °C in the deepest layers (Fig. 2a). From late spring to summer, a distinct warming of the surface layers occurred (Fig. 2b and c). Layers forming the intermediate winter water (40 - 60 m) remained at lower temperature levels with minimum values of ca. 4 and 6 °C in May and August, respectively. In late fall, the upper water column was well mixed with temperatures close to 10 °C (Fig. 2d). During winter, the surface layer above the permanent halocline remained homogenous and well mixed with temperatures decreasing to 4-5 °C in March and April 2008 (Figs. 2e and f). The 2008 season showed a very similar temperature development (Figs. 2f-i). Surface temperatures gradually increased from April to August, while the below-halocline layers stayed relatively constant at temperatures of 6-8 °C. By November 2008, the water column above the halocline was well mixed again with a temperature of approx. 10°C.

Vertical profiles of salinity generally showed very similar pictures over the whole period sampled with a low-saline surface layer (ca. 7 – 8 psu) and a distinct halocline in ca. 50-60 m depth. Below that halocline, salinity levels showed a continuous increase towards maximum levels of ca. 16 psu at the sea bed.

Oxygen concentration profiles also showed little variation over the observation period. Overall oxygen levels were highest (6-8 ml l^{-1}) in the well-mixed surface and intermediate layers down to ca. 60 m depth. Below, distinct oxygen depletion had occurred. Generally, ambient oxygen concentrations below 2 ml l^{-1} are considered critical for cod egg survival as the development of cod eggs is known to cease at a very early stage below this oxygen threshold (Wieland et al. 1994). In 2007, oxygen conditions below the halocline degraded over the season. In April, the 2 ml l^{-1} oxygen threshold was reached in 70 m depth, gradually decreasing to 0 ml l^{-1} below 85 m (fig. 2a). In August 2007, the 2 ml l^{-1} threshold had risen to 65 m depth and water masses below 75 m were anoxic (Fig. 2c).

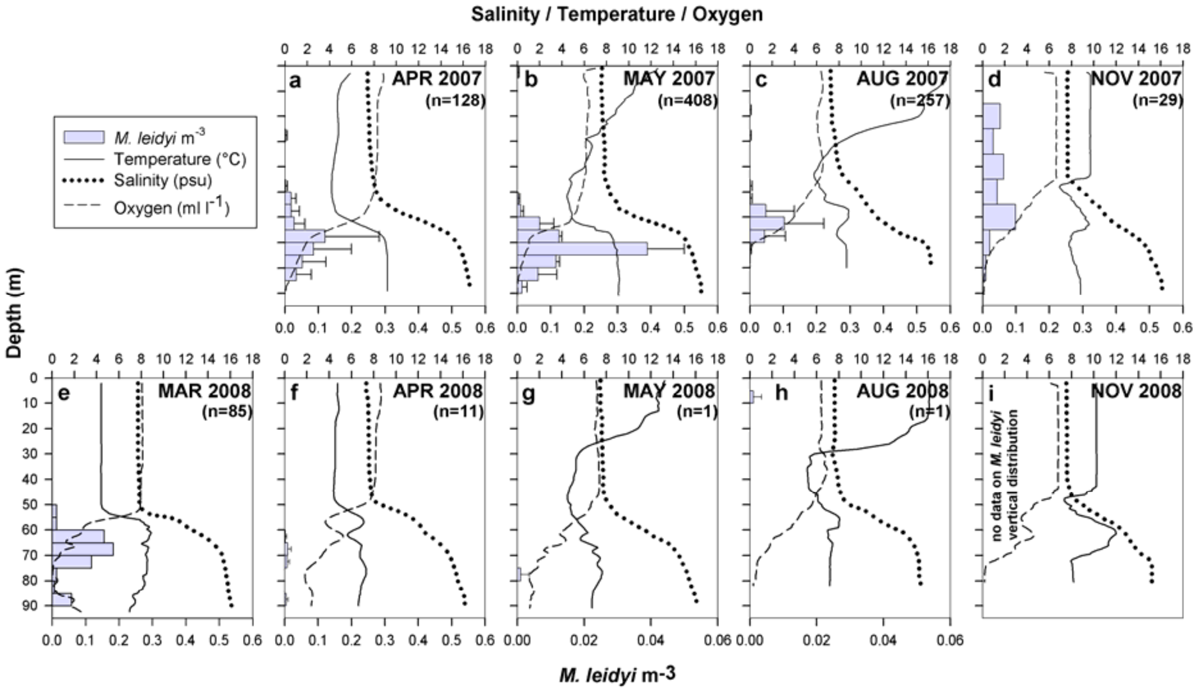

Fig. 2: *Mnemiopsis leidyi*. Vertical distribution (mean + sd) and corresponding hydrography profiles in the Bornholm Basin throughout the sampling period from April 2007 to November 2008. Note different scale of x-axis in Fig. g and h.

In March 2008, an anoxic region between 75 and 85 m was observed. Below this anoxic layer, oxygen concentration showed an increase towards ca. 2.5 ml l^{-1} between 85 m and the sea floor, indicating a limited inflow of oxygen-rich water (Fig. 2e). In April 2008, oxygen conditions further improved with minimum levels not falling below 2 ml l^{-1}. By May and August 2008, the oxygen situation close to the seafloor had deteriorated again with ambient oxygen concentration falling well below 2 ml l^{-1} and reaching anoxic conditions in August and November 2008 (Figs. 2g-h).

Vertical distribution of *Mnemiopsis leidyi*

The vertical distribution of *Mnemiopsis leidyi* was found to be strongly dependent on the ambient hydrography. In both years, in the majority of months sampled, the vertical distribution of *M. leidyi* was almost exclusively constrained to water layers below the permanent halocline. Maximum abundances were observed below 60 m in salinities >8 psu (Fig. 2). In May and August 2008 overall densities were, however, too low to allow for conclusive results. Quotient plot analysis showed a positive selection of salinity levels >10.5 psu (Fig. 3a). On deep stations, *M. leidyi* was distributed down to 90 m depth showing tolerance towards oxygen depleted conditions (cf. April and May 2007). However, no clear avoidance or preference of certain oxygen concentration levels was obvious from quotient plot analysis (not shown). Vertical distribution in relation to temperature as tested by quotient plot analysis showed significant ($p < 0.05$) avoidance of temperatures lower than 6.5 °C and positive selection of temperature levels of about 8.5 °C (Fig. 3b). The only exception to the observation that *M. leidyi* was exclusively distributed below the halocline was detected in November 2007 in the central Bornholm Basin where *M. leidyi* was almost evenly distributed throughout the water column (Fig. 2d).

As temperature and salinity as well as salinity and oxygen were significantly dependent variables, only a possible combined effect of temperature and oxygen on the vertical distribution of *M. leidyi* could be tested. The test revealed no significant interaction of temperature and oxygen on the vertical distribution of the ctenophore (p = 0.1). Thus, we regard temperature to be the main factor determining the vertical distribution of *M. leidyi*.

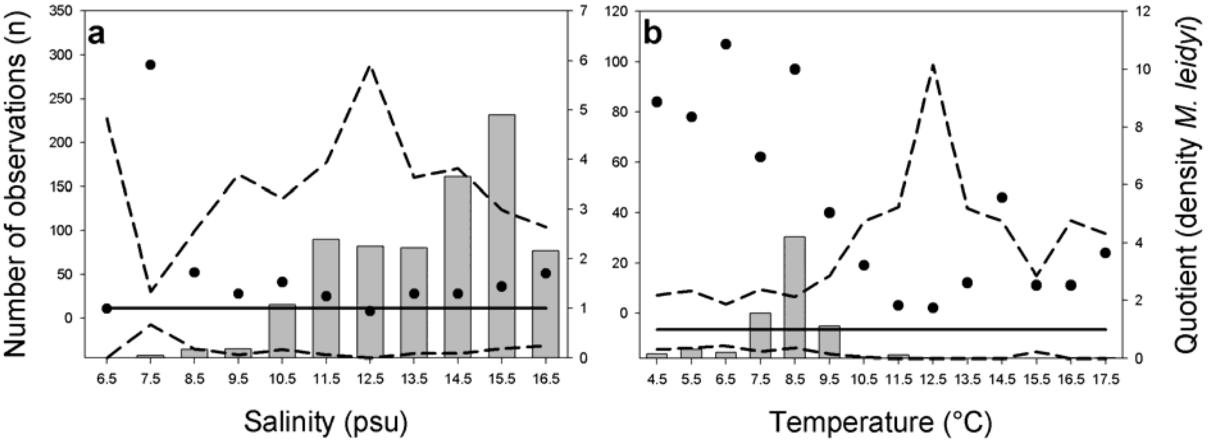

Fig. 3: *Mnemiopsis leidyi*. Quotient rule analysis of distribution of *M. leidyi* in relation to ambient salinity (a) and temperature (b). Dots: number of observations of corresponding abiotic parameter. Bars: *M. leidyi* quotient curve. Dashed lines: 95% confidence interval. Solid line: quotient value 1 (marking random selection of habitat).

Vertical distribution of ichthyoplankton

For both sprat (*Sprattus sprattus*) and cod (*Gadus morhua*), marked differences in the vertical distribution of eggs and larvae were found, with eggs generally showing a deeper distribution than larvae. Sprat eggs were recorded in a wide depth range between 12.5 and 87.5 m in April 2007. Highest densities with a maximum mean of 5.4 ind. m^{-3} were found below the halocline in 62.5 m (Fig. 4a). Considerably higher densities were observed in May 2007 (Fig. 4b). The vertical distribution pattern was similar to the situation in April, but the maximum average density (12.6 ind. m^{-3}) was found at 57.5 m depth, i.e. slightly shallower than in April 2007. No sprat eggs were retrieved from vertical multinet casts in August 2007 (Fig. 4c). In March 2008, again, there was a distinct peak below the halocline with a maximum mean density of 15.5 ind. m^{-3} in 62.5 m (Fig. 4d).

Sprat larvae were retrieved from all depths sampled from close to the surface to 87.5 m in April 2007 (Fig. 4a). Mean density clearly peaked in 12.5 m (1.4 ind. m^{-3}). In May 2007, larvae showed a bimodal distribution with two distinct abundance maxima at the surface (2.5 m) and between 67.5 and 72.5 m (Fig. 4b).

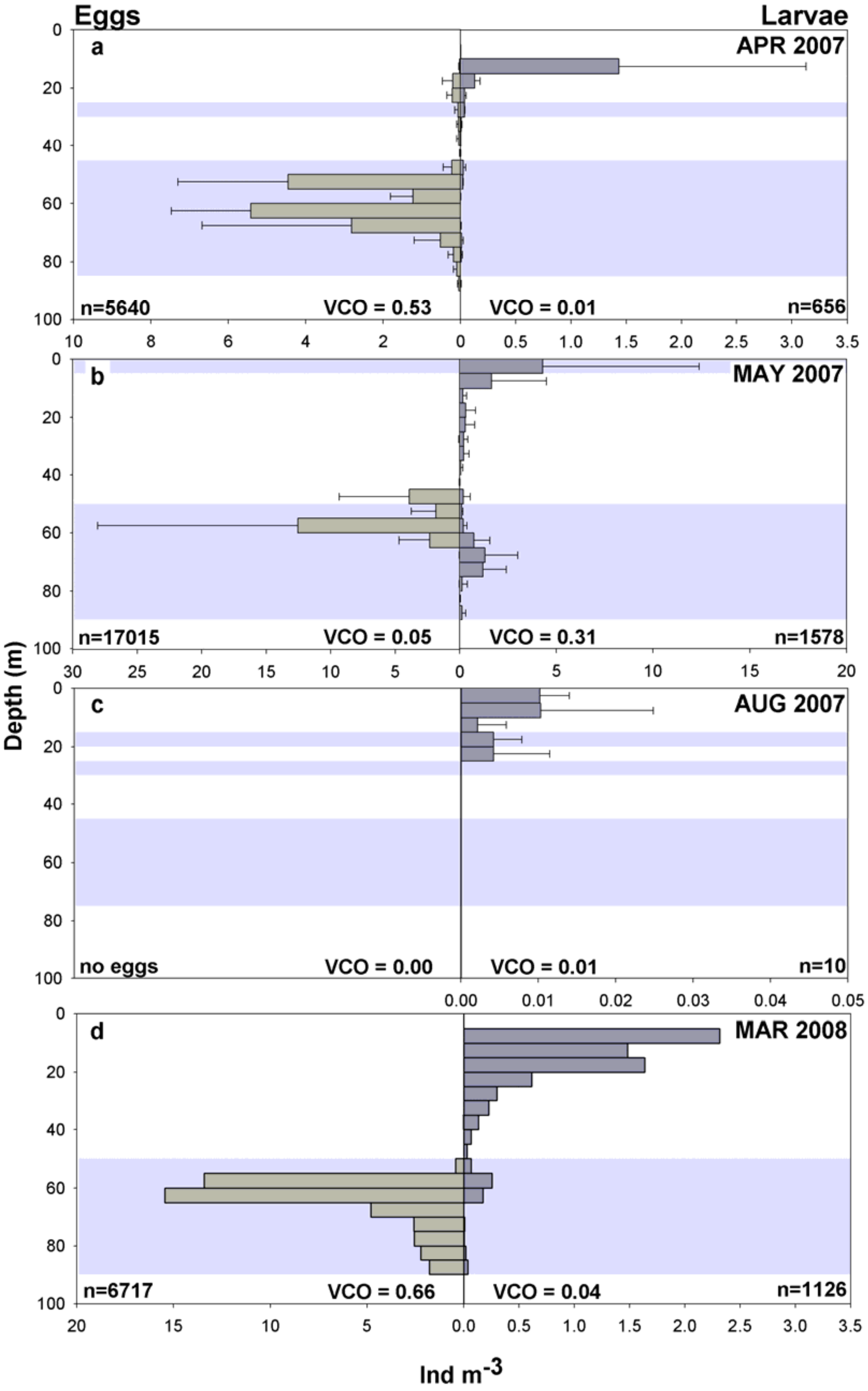

Fig. 4: *Sprattus sprattus*. Vertical distribution (mean + sd) of eggs (left) and larvae (right) in the Bornholm Basin in April 2007 (a), May 2007 (b), August 2007 (c) and March 2008 (d). Areas highlighted in grey represent vertical distribution range of *Mnemiopsis leidyi*. VCO = Vertical Coefficient of Overlap of *M. leidyi* and corresponding ichthyoplankton prey organism. Note different scales of x-axis.

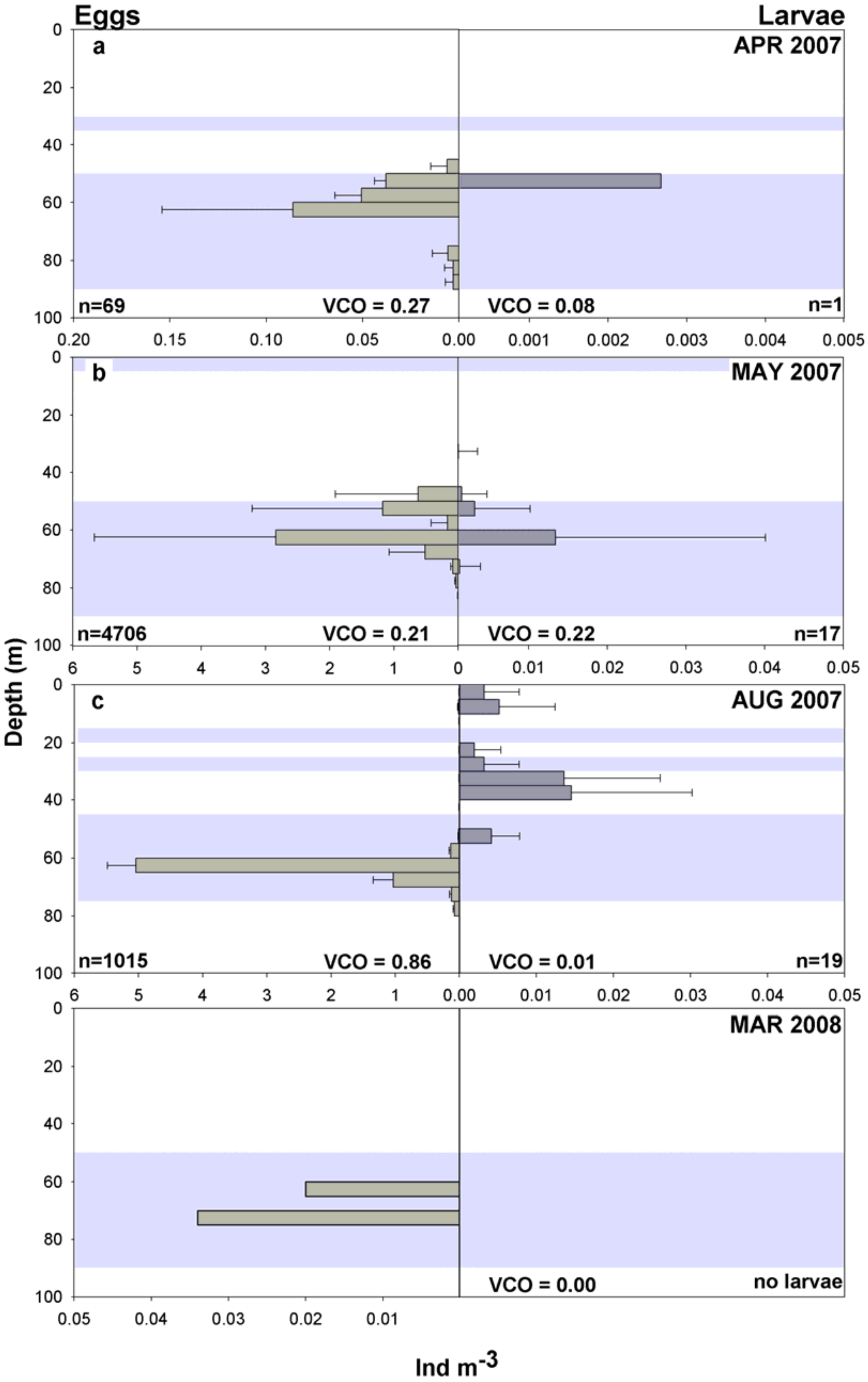

Fig. 5: *Gadus morhua*. Vertical distribution (mean + sd) of eggs (left) and larvae (right) in the Bornholm Basin in April 2007 (a), May 2007 (b), August 2007 (c) and March 2008 (d). Areas highlighted in grey represent vertical distribution range of *Mnemiopsis leidyi*. VCO = Vertical Coefficient of Overlap of *M. leidyi* and corresponding ichthyoplankton prey organism. Note different scales of x-axis.

In August 2007, sprat larvae were again only retrieved in near-surface samples (Fig. 4c). As in May 2007, a second, smaller mode in vertical sprat larvae distribution was observed below the halocline in March 2008.

Cod eggs were found in all vertically resolved samplings (April, May & August 2007, March 2008, Figures 5a, b, c and d), corresponding to the protracted spawning period of Baltic cod. In April and May 2007, cod eggs were observed below the halocline at depths >45 m. In both months, mean maximum densities were highest in 62.5 m (0.09 and 2.8 ind. m^{-3} respectively). In August 2007, the overall vertical distribution range was broader than in the preceding months. However, as before mean maximum densities were highest below the halocline. In March 2008, cod eggs were only observed in 62.5 and 72.5 m depth in very low densities (0.02 and 0.03 ind. m^{-3} respectively).

Densities of cod larvae were negligible in April 2007 (Fig. 5a). In May 2007, only relatively low densities of cod larvae were observed between 32.5 and 72.5 m depth (Fig. 5b). In August 2007, cod larvae were most abundant and inhabited shallower layers between 2.5 and 52.5 m depth (Fig. 5c). Multinet casts in March 2008 did not retrieve any cod larvae.

Horizontal distribution of *Mnemiopsis leidyi*

The horizontal distribution and abundance of *Mnemiopsis leidyi* were found to change considerably throughout the season. In May 2007, highest abundances of up to 7.4 ind. m^{-2} were recorded in the central Bornholm Basin (water depth >60m) with declining densities towards its margins (Fig. 6a). Eastward, high densities were also found in the Slupsk Furrow, a region with water depths of more than 60 m. A totally different distribution pattern was found a few months later. On most of the stations sampled in the Bornholm Basin in August, no *M. leidyi* could be detected and distinct aggregations of up to 2.0 ind. m^{-2} were only observed in the north-western part of the Basin (Fig. 6b). However, on additional sampling stations in the adjacent Bornholmsgatt, a connection of the Arkona Basin and the Bornholm Basin, extremely high densities of *M. leidyi* were observed with numbers partially exceeding 500 ind. m^{-2}. These observations however were made from samples collected with different gear (Helgoländer Larvennetz HLN and WP-2 net) than used for the standard sampling in the Bornholm Basin. In November of the same year, *M. leidyi* was sampled in several regions of the central Baltic Sea including the Arkona Basin, the Bornholmsgatt, the Bornholm Basin and its margins, coastal areas of Sweden and the Slupsk Furrow. Abundances were rather evenly distributed throughout these areas with maximum abundances occurring northwest of Bornholm island and in the Slupsk Furrow (Fig. 6c, Huwer et al. 2008).

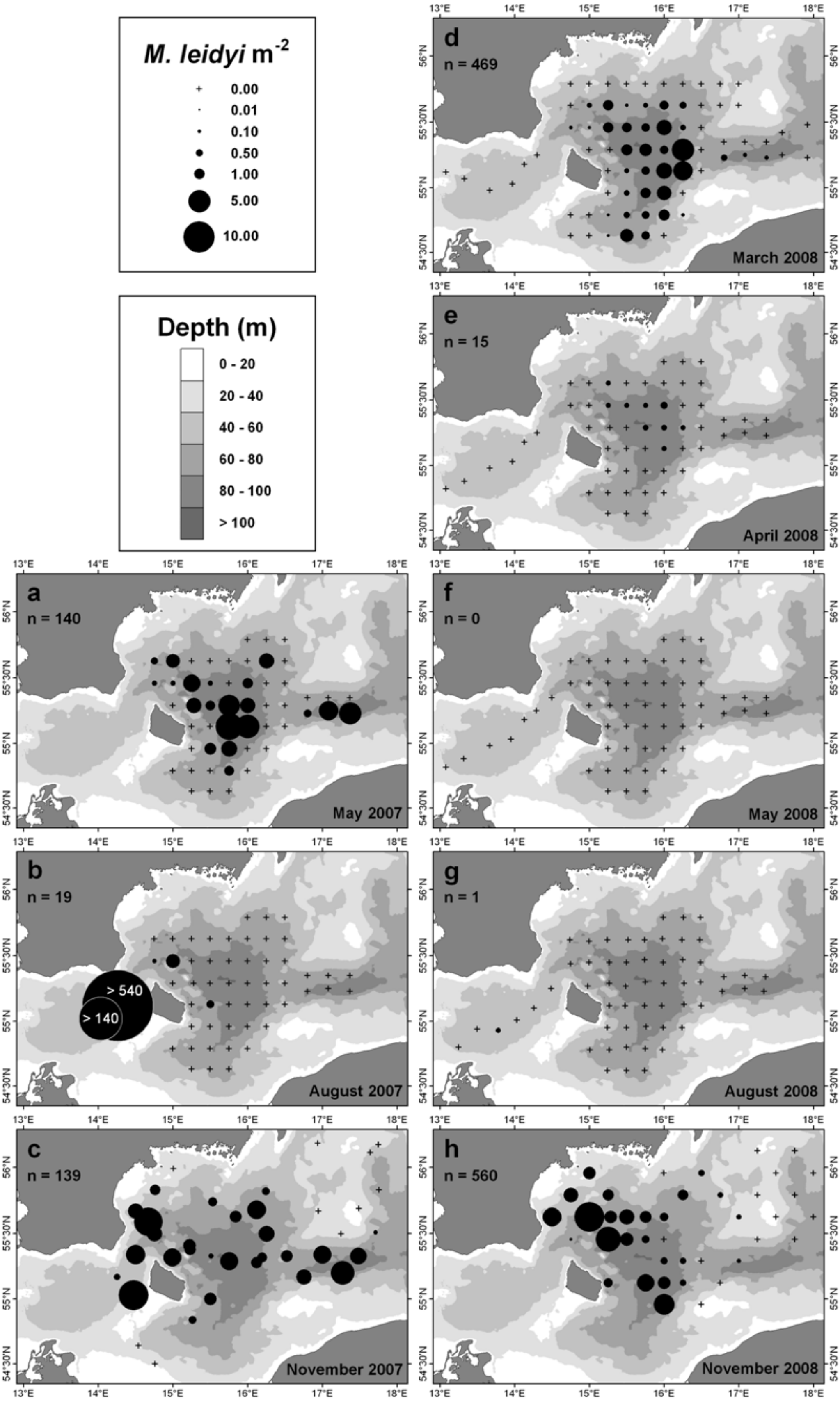

Fig. 6: ***Mnemiopsis leidyi*****. Horizontal distribution in the Bornholm Basin and adjacent areas in May (a), August (b) and November (c) 2007 as well as in March (d), April (e), May (f), August (g) and November (h) 2008. (Note: Numbers (n=19) in Figure b) relate to Bongo-net sampling on the regular station grid. High numbers in the adjacent Bornholmsgatt were sampled with different gear (HLN, WP-2).**

The distribution pattern changed again over winter and similar to the distribution in May 2007 *M. leidyi* was mainly found in the central Bornholm Basin in March 2008 (Fig. 6d). In April 2008, densities had distinctly declined since March to numbers not exceeding 0.5 ind. m^{-2}. *M. leidyi* was restricted to the central parts of the Bornholm Basin and no specimens were caught towards the margins of the Basin and in the southern part (Fig. 6e). In contrast to May 2007, *M. leidyi* had virtually disappeared from the Bornholm Basin in May 2008. It was not possible to retrieve specimens on the regular Bongo-grid (Fig. 6f). The same situation was observed in August 2008 where only one specimen was caught with a Bongo net in the Arkona Basin (Fig. 6g).

However, in November 2008, *M. leidyi* of a broad size range had reappeared on stations sampled in the Hanö Bight northwest of the Bornholm Basin as well as the northwestern and southeastern part of the Bornholm Basin indicating presence of the ctenophore in the whole area. Highest densities were recorded in the northwestern part of the Bornholm Basin. No *M. leidyi* were retrieved on stations covering the shallow Middle Bank between the Bornholm Basin and the southern Gotland Basin (Fig. 6h).

Horizontal distribution of ichthyoplankton

Varying abundances of early life stages of sprat and cod were recorded during the sampling period from May 2007 to March, reflecting the different species specific peak spawning periods. In November 2007, densities of relevant ichthyoplankton organisms were negligible as spawning activity of both species had ceased by that time of the year.

Sprat eggs were retrieved in May 2007 and March 2008 (Figures 7a & c). In both years, distribution was relatively similar with highest densities of up to 2129 ind. m^{-2} (March 2007) in the central part of the Bornholm Basin. Sprat larvae were recorded in May and August 2007 and March 2008 in the deeper areas of the Bornholm Basin and the Slupsk Furrow (Figures 7d, e & f). Highest densities of 425 ind. m^{-2} were sampled in the southern Bornholm Basin in May 2007. In August 2007, after spawning of Baltic sprat had ceased, maximum densities had declined to 2 ind. m^{-2}. In March 2008, larvae were distributed rather equally throughout the Bornholm Basin and adjacent areas with highest densities of 113 ind. m^{-2} in the central Bornholm Basin.

Cod eggs were recorded in May 2007 with a maximum of 683 ind. m^{-2}. The distribution was rather patchy and highest abundances were recorded in the southern and western part of the central Bornholm Basin (Fig. 7g). In August 2007, cod eggs were distributed more evenly in the whole central basin with densities reaching up to 144 ind. m^{-2} (Fig. 7h). In March 2008, generally low densities (max. 9 ind. m^{-2}) were recorded in the central Bornholm Basin and the Slupsk Furrow (Fig. 7i). The highest abundances of cod larvae were recorded in May 2007 with 6 ind. m^{-2} (Fig. 7j). Larvae were concentrated in the southern central Bornholm Basin and along the margins of the basin. In August 2007, cod larvae were evenly distributed throughout the basin with densities similar to May. In March 2008, no cod larvae were recorded.

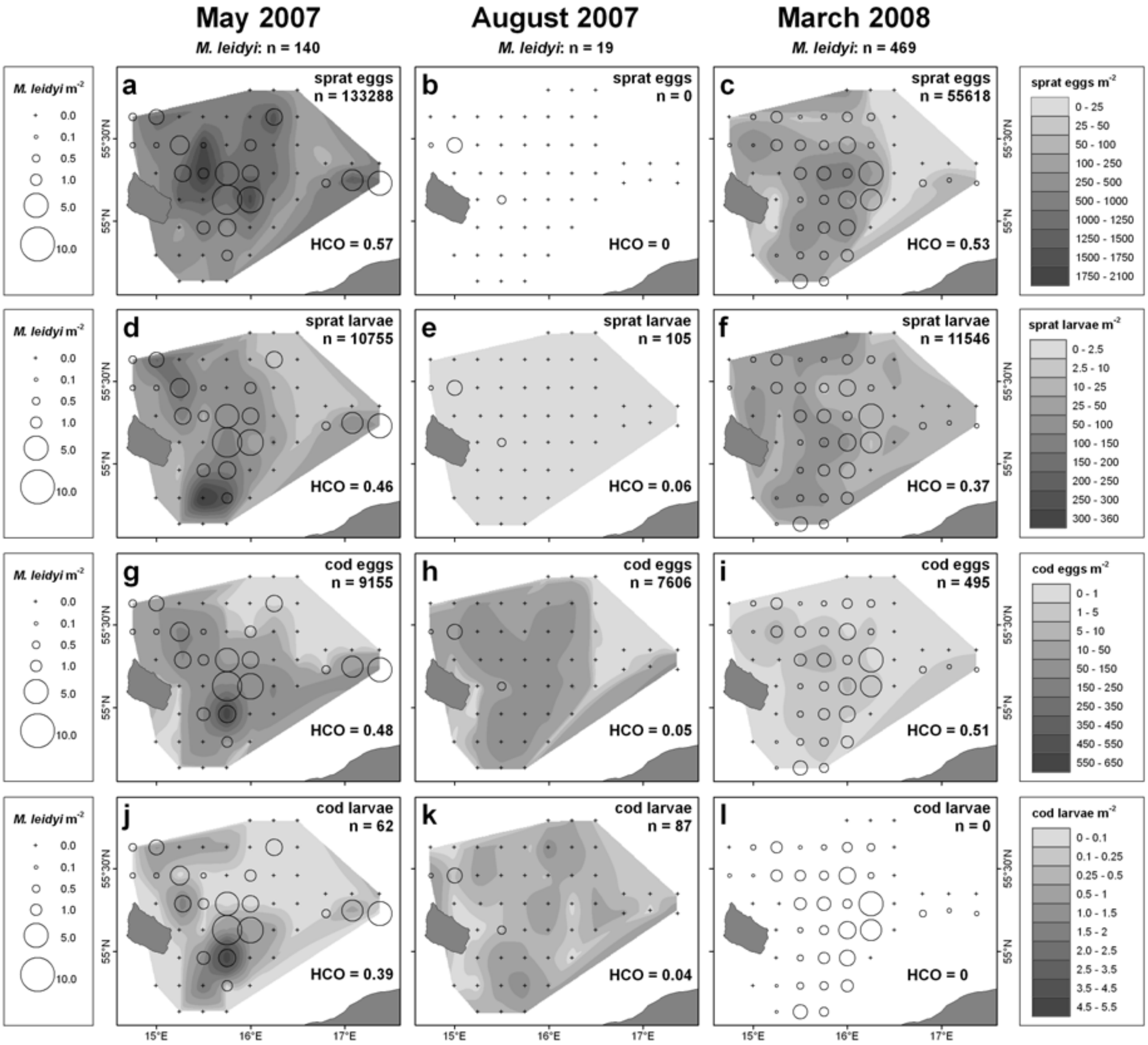

Fig. 7: *Sprattus sprattus* & *Gadus morhua*. Horizontal overlap of ichthyoplankton (contours) and the ctenophore *Mnemiopsis leidyi* (open circles) in the Bornholm Basin in May (left column) and August (middle column) 2007 and March 2008 (right column) for sprat eggs (a-c), sprat larvae (d-f), cod eggs (g-i) and cod larvae (j-l). HCO = Horizontal Coefficient of Overlap of predator (*M. leidyi*) and prey (eggs and larvae).

Length-frequency distributions of *Mnemiopsis leidyi*

Length distributions of *Mnemiopsis leidyi* measured from multinet (335 µm) samples were rather similar for the majority of samplings (Fig. 8). In April, May and November 2007 as well as in March, April and November 2008 the length distribution ranged from 0.3-3 cm, with median values between 1.0-1.7 cm. Only in August 2007, the size range was much broader with a minimum length of 0.7 cm, maximum lengths > 6 cm, and a median length of 2.6 cm (Fig. 8c). Measurements from samples collected in the same cruise in the adjacent Bornholmsgatt with WP-2 and HLN nets (200 µm and 300 µm respectively) however contained distinct fractions of small specimens with a length range of 0.2 to 4.3 cm and median lengths of 1.0 and 1.8 cm respectively (Fig. 8i). Only one specimen was sampled in May (1.8 cm) and August (5.0 cm) 2008, respectively (no figure).

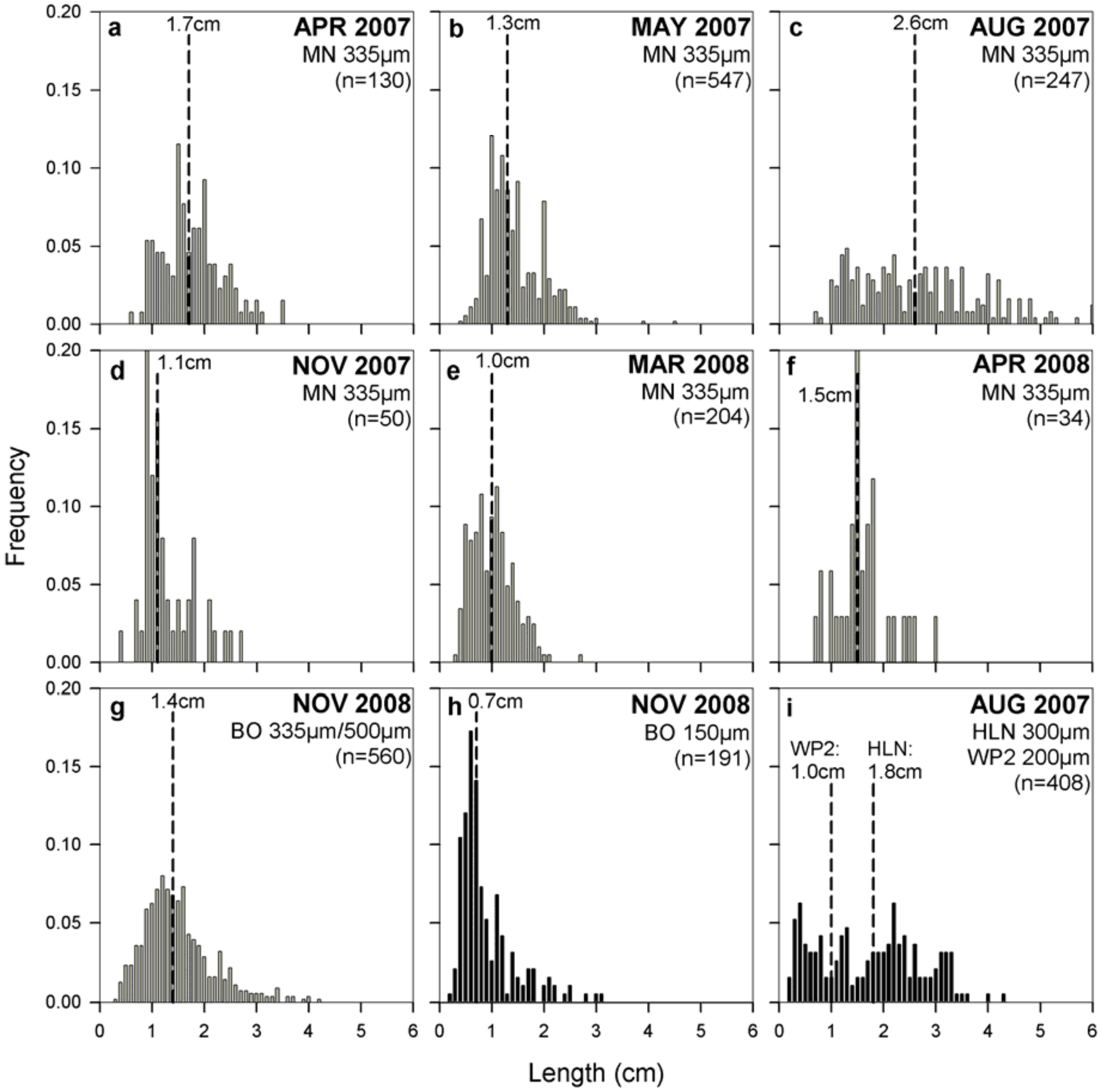

Fig. 8: *Mnemiopsis leidyi*. Seasonal length-frequency distributions (1 mm size classes) sampled in the Bornholm Basin and adjacent areas with different gear in 2007 and 2008. (MN = Multinet, BO = Bongo, HLN = Helgoländer Larvennetz, WP2 = WP-2). Dashed lines mark the medians of the length distributions.

In November 2008, length frequencies were derived from samples caught with Bongo-nets (335 µm and 500 µm). The median length was 1.4 cm. The overall length distribution was broader than that measured in March with lengths ranging from 0.3 to 4.2 cm (Fig. 8g). Samples collected in the same month with a Bongo-net with a smaller meshsize (150 µm) however contained a large fraction of relatively small specimens (median length 0.7 cm) with an overall size range of 0.2 to 3.1 cm (Fig. 8h). Length measurements were taken from all sampled specimens, and the total numbers are given in each figure. Exceptions are the samplings with HLN and WP-2 nets (Fig. 8i), where only a random subsample was measured due to the high number of specimens. Overall, apart from November 2008, modal lengths of *M. leidyi* measured over the sampling period were within a range where *M. leidyi* is known to already be capable of preying upon ichthyoplankton (Monteleone & Duguay 1988).

Overlap

Spatio-temporal changes in abundance and distribution of both *Mnemiopsis leidyi* and the investigated ichthyoplankton organisms resulted in distinct differences in horizontal and vertical overlap indices and, accordingly, in different scenarios of potential predation mortality for eggs and larvae of sprat and cod (Table 2).

Table 2: Horizontal (HCO) and vertical (VCO) coefficients of overlap (HORN 1966) of the invasive ctenophore *Mnemiopsis leidyi* as predator and potential ichthyoplankton prey organisms sprat (*Sprattus sprattus*) and cod (*Gadus morhua*) in the Bornholm Basin.

Species	**Stage**	**HCO**	**VCO**	**Date**
Sprat *(Sprattus sprattus)*	eggs	**-**	0.53	April 2007
		0.57	0.05	May 2007
		0.00	0.00	August 2007
		0.53	0.66	March 2008
	larvae	-	0.01	April 2007
		0.46	0.31	May 2007
		0.06	0.01	August 2007
		0.35	0.04	March 2008
Cod *(Gadus morhua)*	eggs	-	0.27	April 2007
		0.48	0.21	May 2007
		0.05	0.86	August 2007
		0.51	0.58	March 2008
	larvae	-	0.08	April 2007
		0.39	0.22	May 2007
		0.04	0.01	August 2007
		0.00	0.00	March 2008

For sprat eggs, the highest horizontal coefficient of overlap (HCO) was estimated in the spring months, i.e. the peak spawning period (0.57 in May 2007, 0.53 in March 2008). Vertical coefficients of overlap (VCO) were highest in early spring (March and April) and decreased in May. In August, no overlap coefficient could be calculated as sprat spawning had ceased. The same trend was obvious for sprat larvae with relatively high HCO values of 0.46 in May 2007 and 0.35 in March 2008. VCO values for sprat larvae, however, peaked in May. In August, both overlap coefficients were considerably lower.

For cod eggs, a very high VCO was calculated in August, but the horizontal overlap was low. In March 2008, the overlap was relatively high in both dimensions. Lower overlap values were found for April and May 2007, but they were still on medium levels. For cod larvae, a combination of high overlap coefficients in both dimensions was only found in May 2007.

DISCUSSION

Due to the different seasonal timing of peak spawning of the major Baltic fish stocks cod (*Gadus morhua*) and sprat (*Sprattus sprattus*) and variable abundance and distribution characteristics of ichthyoplankton and the invasive planktivore ctenophore *Mnemiopsis leidyi* in both horizontal and vertical plane, different impact scenarios of the ctenophore on ichthyoplankton organisms are obvious. The predation risk exerted by *M. leidyi* on cod and sprat eggs and larvae is apparently dependent on the different abundances of the ctenophore as observed throughout the sampling period and also on the present hydrographic situation with main impact on vertical overlap of predator and prey.

Our results show that the distribution and abundance of *Mnemiopsis leidyi* in the Bornholm Basin is highly variable throughout the season. For example, in August 2007 the ctenophore had largely disappeared from the Bornholm Basin with merely sporadic observations near the western margins of the Basin. A shift to larger length classes from May to August indicates that the specimens remaining in August are survivors originating from the cohorts observed in May. In the Bornholmsgatt, an area located to the west of the Bornholm Basin, remarkably high abundances comparable to local mass occurrences in the Black Sea (Kideys & Romanova 2001, Shiganova et al. 2001) were observed. These densities were lower than those observed during contemporary blooms in coastal areas of the western Baltic (Javidpour et al. 2009) or in earlier observations of peak abundances in native or invaded habitats (Purcell et al. 2001, Sullivan et al. 2001, Riisgård et al. 2007). However, we cannot exclude an underestimation of the actual abundances in the Bornholm Basin as length frequency data from the sampling gear operated in the Bornholmsgatt contained high numbers of small specimens that possibly were not caught with the Bongo- and Multinets operated in the Bornholm Basin. This assumption can be supported by the fact that a high fraction of very small specimens were collected in small-meshed Bongo samples (150 µm) in the central Basin in late fall 2008 while considerably fewer small individuals were caught with simultaneously deployed 335 µm and 500 µm Bongo nets. A similar bias can not be excluded for vertical abundances analyzed by two different multinet types. However, as the meshsize of both nets deployed as well as the sampling procedure were identical, the relative overall vertical distribution patterns derived from the multinet catches can be regarded comparable and representative.

We are aware of the shortcoming that no quantitative stomach contents data were analyzed for this manuscript. Proper analyses of stomach contents were precluded by the severe impact on the body structure of soft-bodied plankton through mechanical stress imposed by the plankton gear (compare Boero et al. 2008), which in our case would clearly have biased quantitative diet composition investigations on *M. leidyi*. However, on specimens in relatively good condition, we were able to conduct qualitative observations of stomach contents. Amongst copepods, cladocerans and other zooplankton, we observed fish eggs in a number of the investigated specimens. Additionally, we assume that the potential for predation on ichthyoplankton was given for the majority of sampled specimens as (apart from November 2008) the modal lengths measured throughout the sampling period were in a range in which *M. leidyi* is known to already be capable of preying upon fish eggs and larvae (Monteleone & Duguay 1988).

The vertical distribution of *Mnemiopsis leidyi* in the Bornholm Basin was influenced by salinity and to a higher extent by temperature conditions. Quotient plot analysis showed a preference for salinities >10.5 psu. It is known that the ctenophore is able to tolerate ambient salinity levels ranging from 2 – 38 psu. The distribution pattern therefore might also be influenced by ambient temperature. Even though the temperature in the upper water layers was well within the range known to be tolerable for *M. leidyi* (Purcell et al. 2001) throughout the observation period, the ctenophore was only found in deeper layers below the halocline in layers with comparatively warm water. A thermal barrier on the vertical distribution of *M. leidyi* in the Bornholm Basin was hypothesized by Storr-Paulsen & Huwer (2008). Based on the comprehensive coverage of the area with seasonal samplings in the present study, this hypothesis could now be validated and a threshold level of 6.5 °C was specified by quotient plot analysis. In the majority of months observed, the intermediate water layers were colder than that threshold level and thus constituted a vertical barrier for *M. leidyi*. The ctenophores observed below the halocline in the Bornholm Basin had most likely been transported into the Basin by advection of high saline deep water from the Arkona Basin (e.g. Lehmann & Hinrichsen 2002, Lehmann et al. 2008) and subsequently been trapped below the cold intermediate water layer. This observation was supported by a different hydrographic situation in November 2007 and November 2008 where intermediate layers and the upper water column were warmer than 6.5 °C. In November 2007, *M. leidyi* was found in almost all water layers sampled. Although vertically resolved sampling was not feasible in November 2008, the extended horizontal distribution of *M. leidyi* into shallow areas suggests a similar situation as in November 2007.

Diurnal vertical migration of *Mnemiopsis sp.* has been observed in other regions (Zaika & Ivanova 1992, Mutlu 1999). In the Bornholm Basin, such vertical migration behavior was apparently prevented by adverse hydrographic conditions constituting a thermal barrier.

Ambient oxygen concentration in our study was of minor importance on vertical distribution of *Mnemiopsis leidyi*. Tolerance of small specimens towards hypoxic conditions has been described by Purcell et al. (2001). The ctenophores in our study tolerated very low levels of oxygen but avoided layers with total oxygen depletion. These findings were corroborated by the distribution pattern observed in March 2008. Then, a distinct decline in abundance was observed along an oxygen gradient towards deeper layers. However, increasing oxygen concentration right above the seafloor gave an indication of a recent intrusion of oxygenated water. Here, a distinct increase of abundance of the ctenophore was observed. Whether *M. leidyi* had actively migrated vertically into that layer or had been enclosed in the intruding water masses from westerly adjacent regions could not be identified. In any case, consumption rates of *M. leidyi* do not decrease in low oxygen conditions (Decker et al. 2004).

Eastward proliferation of the high numbers of ctenophores observed in the Bornholmsgatt into the Bornholm Basin is likely, as regional inflow events of the ambient water body from the northwestern margin of the basin can be observed during westerly and easterly winds. Predominant westerly winds lead to a transport of the upper water layers towards the east into the Bornholm Basin whereas easterly winds lead to a compensatory inflow of water masses from deeper layers of adjacent westerly areas (Krauß & Brügge 1991). Thus, the ctenophores observed in the Bornholmsgatt in August 2007 could be the initial population for the regular occurrence of *Mnemiopsis leidyi* in the Bornholm Basin and Slupsk Furrow area observed in November 2007. A similar situation with a depopulated central basin in August and regular occurrence of *M. leidyi* in November has been observed in 2008. However, no distinct accumulations of the ctenophore in the westerly adjacent Bornholmsgatt and Arkona Basin were observed in August 2008.

Horizontal distribution was more extended in both autumn 2007 and 2008 compared to the preceding months. In conjunction with the observed temperature-dependent patterns in vertical distribution, this autumnal range extension can be explained with higher surface and intermediate water temperatures in November 2007 and 2008. As there was no thermal threshold barrier in the corresponding months preventing vertical migration into shallower layers, *Mnemiopsis leidyi* could spread into shallower water over a wide area. In the other months observed, the ctenophore was restricted to the deep areas of the central Bornholm Basin and the Slupsk Furrow due to the low temperatures in intermediate water layers and thus could not propagate to shallower adjacent areas.

Even though signs of a mass occurrence of *Mnemiopsis leidyi* were found in the Bornholmsgatt in August 2007, no mass occurrence has been observed yet in the Bornholm Basin. This, together with obvious fluctuations in distribution and abundance, indicates environmental limitations of the ctenophore in the area investigated. Warm surface waters are regarded to increase metabolic rates of *M. leidyi* and thus have boosted an expansion of the ctenophore in the Black Sea (Anninsky & Abolmasova 2000). Comparable conditions were well present in the summer months in upper water layers of the Bornholm Basin. A lack of a bloom of the ctenophore in that area may have resulted from the thermal separation of *M. leidyi* in the intermediate layers from warm surface layers. Although overall ambient hydrographic parameters recorded during the observation period were well within the limits known to be tolerated by *M. leidyi*, the experienced temperature conditions were not suitable to boost reproductive output which is restricted to temperatures >10-15 °C (Purcell et al. 2001).

Additional possible constraints for a population outbreak are predation pressure or food competition mediated by other gelatinous zooplankton or zooplanktivorous fishes as well as food limitation. The moon jellyfish, *Aurelia aurita*, as possible intraguild competitor usually is present in high densities in the area during the summer months but abundance maxima are known to appear in the upper water layers (Barz & Hirche 2005). High densities of *Aurelia aurita* have been observed in the surface layers in summer 2008 by the authors (unpublished data). Thus, a vertical overlap of the moon jellyfish with the distribution of *M. leidyi* observed in summer 2007 (this study) is unlikely. The only likely jellyfish predator in the area that is capable to feed on *M. leidyi* (e. g. Purcell 1991) and also on ichthyoplankton (Lischka 1999) is the lion´s mane jellyfish *Cyanea capillata*. However, this jellyfish underlies strong seasonal differences in occurrence and distribution and generally only appears sporadically and in low densities (Barz & Hirche 2005).

As the ctenophore has been shown to be trapped in the deep parts of the central Basin by cold intermediate water layers, food limitation in that depth is another possible reason for the decline of *M. leidyi* in the area over the summer months. *M. leidyi* has been shown to severely affect zooplankton communities in the southern Caspian Sea by reducing total number and biomass of zooplankton species in that region through predation (Roohi et al. 2008). The long-term dynamics of the most abundant mesozooplankton species in the area (copepods *Pseudocalanus elongatus*, *Temora longicornis*, *Acartia spp.*, *Centropages hamatus* and different cladocerans) show a clear maximum in production in the warm summer months (Möllmann et al. 2000). However, as shown by Schmidt (2006), the majority of species and their developmental stages are distributed above the halocline. Thus, due to the missing vertical overlap, they are not contributing to the available prey field of *M. leidyi*.

Lack of food competition due to severely depleted zooplanktivorous anchovy (*Engraulis encrasicolus*) stocks in the Black Sea has been postulated as reason for the massive population outbreak of *Mnemiopsis leidyi* in the 1980s and 1990s (Purcell et al. 2001). Huwer et al. (2008) hypothesized, that the presently high sprat (*Sprattus sprattus*) stock in the Baltic Sea exerts a strong food competition pressure on *M. leidyi* and thus prevents the local population from excessive outbreaks. Möllmann et al. (2005) have shown that the stock is currently on such high levels that intra-stock competition for food resources already led to a general decline in condition of Baltic sprat. Another possible explanation for the obvious disappearance of *M. leidyi* from the central Bornholm Basin from spring to summer could be predation by adult cod (*Gadus morhua*). During this time, cod migrate into the central basin for spawning (Aro 1989, Wieland et al. 2000). *M. leidyi* is known to be preyed upon by several fish species (e.g. Link & Ford 2006). For example, it is of primary importance as prey item for rock cod (*Patagonotothen ramsayi*) on the Patagonian shelf (Laptikhovsky & Arkhipkin 2003), and predation on *M. leidyi* by butterfish (*Peprilus triacanthus*) is assumed to be a reason for local population declines in Narragansett Bay, Rhode Island, in late summer and early fall (Oviatt & Kremer 1977). Additionally, Mianzan et al. (1996) reported 20 different fish species from Argentine coastal waters that were found preying on ctenophores. Atlantic cod (*G. morhua*) is also known to prey upon ctenophores in Greenland waters (Hansen 1949). During spawning time, adult cod are almost exclusively distributed below the halocline in the Bornholm Basin (Schaber et al. 2009) and thus overlap with the residence depths of the ctenophore. In August 2007, stomach content analysis of cod caught in the vicinity of stations with evidence of *M. leidyi* revealed that 11 % of stomachs analyzed by the authors contained one or more specimen of the ctenophore (unpublished data). This observation is supported by recreational fishers reporting frequent catches of cod in the Øresund that regurgitated high numbers of the ctenophore after being hauled on deck (JH Hansen, pers. comm.).

Altogether, these factors could lead to the contrasting abundance dynamics of *Mnemiopsis leidyi* in the central Baltic Sea compared to native temperate and other exotic habitats. Lobate stages display an abundance maximum over the summer months in native north American habitats (Sullivan et al. 2001, Purcell et al. 2001) and in exotic habitats like the Black Sea, although peak blooms can vary in their seasonal timing (Purcell et al. 2001). In coastal habitats of the Baltic Sea, two peak blooms of *M. leidyi* have been observed by Javidpour et al. (2009) in June and August/September. Those blooms were dominated by small (<1 mm) stages. As our sampling method did not retain those small stages, direct comparison is not possible. Nevertheless, the unique ambient conditions experienced by the ctenophore in the Bornholm Basin as discussed above are the most likely reason for differences in peak abundance.

The influence of ambient hydrography on the vertical distribution of both predator and prey is reflected by variable spatial overlap coefficients leading to different impact scenarios of *M. leidyi* on ichthyoplankton. For example, a vertical shift of the 6.5 °C temperature threshold led to a deeper distribution maximum of the ctenophore in May 2007 and thus reduced the overlap with sprat eggs although both overall abundance and egg production were higher than in other months. This highlights the sensitivity of the potential impact of *M. leidyi* on ichthyoplankton to minor changes in ambient hydrography. A considerable overlap of the ctenophore and sprat larvae was observed in May 2007. The majority of larvae was distributed locally and high abundances were observed in the region of main ctenophore densities. Although direct predation of *M. leidyi* on Baltic sprat larvae has not yet been observed, these larvae can be considered vulnerable to predation (e.g. Purcell & Arai 2001). For both cod eggs and larvae, maximum overlap values and abundance maxima did not occur simultaneously. Thus, for the period observed, the overall impact of *M. leidyi* on cod can be regarded as minor.

CONCLUSION

Mnemiopsis leidyi has been observed preying upon ichthyoplankton in the Bornholm Basin in an earlier study (Haslob et al. 2007). In the present study, we have shown that distribution and abundance of the invasive ctenophore *Mnemiopsis leidyi* and thus predation risk on ichthyoplankton in the Bornholm Basin underlie strong seasonal variations. A “match” situation according to Cushing´s match-mismatch hypothesis (1990) requires a high temporal and spatial (both horizontal and vertical) overlap as well as sufficiently high abundances of both predators and prey. A comparatively high overlap of the ctenophore with sprat eggs was observed in spring 2008 when sprat displayed intensive spawning activity. However, maximum overlap values were identified outside the peak spawning periods of both sprat and cod. In combination with low abundances of *M. leidyi* compared to other areas, leading to a mismatch-situation, the overall predation risk on ichthyoplankton and the influence on fish stock recruitment can presently be regarded as limited.

A back-shift of Baltic cod peak spawning time to earlier months in the season, for which indications exist in our data, could lead to a more pronounced overlap between *M. leidyi* and cod early life stages in the future and thus to a significant impact of the ctenophore on the recruitment success of the Eastern Baltic cod stock. This situation would be even more severe if *M. leidyi* displayed a massive population explosion as observed in other areas, e.g. the Black Sea. Population outbreaks in previously invaded ecosystems occurred some years after the initial introduction and identification of *M. leidyi* in the respective areas (Purcell et al. 2001). Thus, as the introduction of the ctenophore into the Baltic Sea occurred only two years ago, intensive monitoring is suggested to follow the population dynamics of *M. leidyi* in the central Baltic Sea and to timely identify possible population outbreaks with potentially severe impact on local fish stocks.

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LITERATURE CITED

Alvariño A (1980) The relation between the distribution of zooplankton predators and anchovy larvae. CalCOFI Rep 21:150-160

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

Bailey KM, Houde ED (1989) Predation on eggs and larvae of marine fishes and the recruitment problem. Adv Mar Biol 25:1-83

Barz K, Hirche HJ (2005) Seasonal development of scyphozoan medusae and the predatory impact of *Aurelia aurita* on the zooplankton community in the Bornholm Basin (central Baltic Sea), Mar Biol 147:465-476

Bilio M, Niermann U (2004) Is the comb jelly to blame for it all? *Mnemiopsis leidyi* and the ecological concerns about the Caspian Sea. Mar Ecol Prog Ser 269:173–183

Boero F, Bouillon J, Gravili C, Miglietta MP, Parsons T, Piraino S (2008) Gelatinous plankton: irregularities rule the world (sometimes). Mar Ecol Prog Ser 356:299-310

Boersma M, Malzahn AM, Greve W, Javidpour J (2007) The first occurrence of the ctenophore *Mnemiopsis leidyi* in the North Sea. Helgoland Mar Res 61:153-155

Brodeur RD, Merati N (1993) Predation on walleye pollock (*Theragra chalcogramma*) eggs in the western Gulf of Alaska: The roles of vertebrate and invertebrate predators Mar Biol 117(3):483-493

Caddy JF (1993) Toward a comparative evaluation of human impacts on fishery ecosystems of enclosed and semienclosed seas. Rev Fish Sci 1:57–95

Carlton JT (1985) Transoceanic and interoceanic dispersal of coastal marine organisms: the biology of ballast water. Oceanogr Mar Biol Ann Rev 23: 313–371

Carlton JT, Geller JB (1993) Ecological Roulette: The Global Transport of Nonindigenous Marine Organisms. Science 261(5117):78-82

Costello JH, Sullivan BK, Gifford DJ, Van Keuren D, Sullivan LJ (2006) Seasonal refugia, shoreward thermal amplification and metapopulation dynamics of the ctenophore *Mnemiopsis leidyi* in Narragansett Bay, Rhode Island. Limnol Oceanogr 51:1819-1831

Cushing DH (1974) The natural regulation of fish populations. In: Harden Jones FR (ed) Sea fisheries research. Paul Elek, London, p 399–412

Cushing DH (1990) Plankton production and year-class strength in fish populations: An update of the match/mismatch hypothesis. Adv Mar Biol 26:249–294

Daskalov GM, Mamedov EV (2007) Integrated fisheries assessment and possible causes for the collapse of anchovy kilka in the Caspian Sea. ICES J Mar Sci 64(3):503-511

Decker MB, Breitburg DL, Purcell JE (2004) Effects of low dissolved oxygen on zooplankton predation by the ctenophore *Mnemiopsis leidyi*. Mar Ecol Prog Ser 280:163-172

Dickmann M, Möllmann C, Voss R (2007) Feeding ecology of Central Baltic sprat *Sprattus sprattus* larvae in relation to zooplankton dynamics: implications for survival. Mar Ecol Prog Ser 342:277–289

Faasse MA, Bayha KM (2006) The ctenophore *Mnemiopsis leidyi* A. Agassiz 1865 in coastal waters of the Netherlands: an unrecognized invasion? Aquat Invasions 1:270-277

Grønkjær P, Wieland K (1997) Ontogenetic and environmental effects on vertical distribution of cod larvae in the Bornholm Basin, Baltic Sea. Mar Ecol Prog Ser 154:91-105

Hansen PM (1949) Studies on the biology of the cod in Greenland waters. Rapp P-v-Réun Cons Int Expl Mer, 123

Haslob H, Clemmesen C, Schaber M, Hinrichsen HH, Schmidt JO, Voss R, Kraus G, Köster FW (2007) Invading *Mnemiopsis leidyi* as a potential threat to Baltic fish. Mar Ecol Prog Ser 349:303–306

Hinrichsen HH, Möllmann C, Voss R, Köster FW, Kornilovs G (2002) Biophysical modeling of larval Baltic cod (*Gadus morhua*) growth and survival. Can J Fish Aquat Sci 59(12):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. Mar Ecol Prog Ser 345:245–254

Horn HS (1966) Measurement of overlap in comparative ecological studies. Am Nat 100:419–424

Huwer B, Storr-Paulsen M, Riisgård HU, Haslob H (2008) Horizontal and vertical distribution of the invasive ctenophore *Mnemiopsis leidyi* in the central Baltic Sea, November 2007. Aquat Invasions 3:113–124

Ivanov V, Kamakin AM, Ushivtzev VB, Shiganova TA, Zhukova O, Aladin N, Wilson SI, Harbison GR, Dumont HJ (2000) Invasion of the Caspian Sea by the comb jellyfish *Mnemiopsis leidyi* (Ctenophora). Biol Invasions 2:255–258

Javidpour J, Sommer U, Shiganova T (2006) First record of *Mnemiopsis leidyi* A. Agassiz 1865 in the Baltic Sea. Aquat Invasions 1:299-302

Javidpour J, Molinero JC, Peschutter J, Sommer U (2009) Seasonal changes and population dynamics of the ctenophore *Mnemiopsis leidyi* after its first year of invasion in the Kiel Fjord, Western Baltic Sea. Biol Invasions 11:873-882

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

Kideys AE, Romanova Z (2001) Distribution of gelatinous macrozooplankton in the southern Black Sea during 1996-1999. Mar Biol 139(3):535-47

Köster FW, Schnack D (1994) The role of predation on early life stages of cod in the Baltic. Dana 10:179–201

Köster FW, Möllmann C (2000) Trophodynamic control by clupeid predators on recruitment success in Baltic cod? ICES J Mar Sci 57(2):310–323

Köster FW, Möllmann C, Hinrichsen HH, Wieland K, Tomkiewicz J, Kraus G, Voss R, Markarchouk A, MacKenzie BR, St. John MA, Schnack D, Rohlf N, Linkowski T, Beyer JE (2005) Baltic cod recruitment - the impact of climate variability on key processes. ICES J Mar Sci 62(7):1408–1425

Krauß W, Brügge B (1991) Wind-produced Water Exchange between the Deep Basins of the Baltic Sea. J Phys Oceanogr 21(3):373-384

Kube S, Postel L, Honnef C, Augustin C (2007) *Mnemiopsis leidyi* in the Baltic Sea – distribution and overwintering between autumn 2006 and spring 2007. Aquat Invasions 2:137-145

Kullenberg G, Jacobsen TS (1981) The Baltic Sea: an Outline of its Physical Oceanography. Mar Pollut Bull 12(6):183-186

Laptikhovsky VV, Arkhipkin AI (2003) An impact of seasonal squid migrations and fishing on the feeding spectra of subantarctic notothenioids *Patagonotothen ramsayi* and *Cottoperca gobio* around the Falkland Islands. J Appl Ichthyol 19:35-39

Lehmann A, Hinrichsen HH (2002) Water, heat and salt exchange between the deep basins of the Baltic Sea. Boreal Env Res 7:405-415

Lehmann A, Javidpour J, Clemmesen C, Petereit C, Schmidt JO (2008) *Mnemiopsis leidyi*, a new invader to the Baltic Sea: possible pathways of distribution. BALTEX Newsletter 1:13-15

Levine JM (2008) Biological invasions. Curr Biol 18(2):R57-R60

Link JS, Ford MD (2006) Widespread and persistent increase of Ctenophora in the continental shelf ecosystem off NE USA. Mar Ecol Prog Ser 320:153-159

Lischka M (1999) Abundanz, Verteilung und Nahrungsökologie von Scyphomedusen in der zentralen Ostsee. MS Thesis, Christian-Albrechts University, Kiel, Germany

Matthäus W, Franck H (1992) Characteristics of major Baltic inflows – a statistical analysis. Cont Shelf Res 12:1375-1400

Mianzan HW, Mari N, Prenski B, Sanchez F (1996) Fish predation on neritic ctenophores from the Argentine continental shelf: A neglected food resource? Fish Res 27(1-3):69-79

Møller JS, Hansen IS (1994). Hydrographic processes and changes in the Baltic Sea. Dana 10:87-104

Möllmann C, Kornilovs G, Sidrevics L (2000) Long-term dynamics of main mesozooplankton species in the central Baltic Sea. J Plankton Res 22(11):2015–2038

Möllmann C, Kornilovs G, Fetter M, Köster FW (2005) Climate, zooplankton, and pelagic fish growth in the central Baltic Sea. ICES J Mar Sci 62(7):1270-1280

Monteleone DM, Duguay LE (1988) Laboratory studies of predation by the ctenophore *Mnemiopsis leidyi* on the early stages in the life history of the bay anchovy, *Anchoa mitchilli*. J Plankt Res 10(3):359-372

Mutlu E (1999) Distribution and abundance of ctenophores and their zooplankton food in the Black Sea. II. *Mnemiopsis leidyi.* Mar Biol 135:603–613

Oliveira OMP (2007) The presence of the ctenophore *Mnemiopsis leidyi* in the Oslofjorden and considerations on the initial invasion pathways to the North and Baltic Seas. Aquat Invasions 3:185-189

Oviatt CA, Kremer PM (1977) Predation on the Ctenophore, *Mnemiopsis leidyi*, by Butterfish, *Peprilus triacanthus*, in Narragansett Bay, Rhode Island. Chesap Sci 18:236-240

Purcell JE (1991) A review of cnidarians and ctenophores feeding on competitors in the plankton. Hydrobiologia 216/217:335-342

Purcell JE, Arai MN (2001) Interactions of pelagic cnidarians and ctenophores with fish: a review. Hydrobiologia 451:27–44

Purcell JE, Shiganova TA, Decker MB, Houde ED (2001) The ctenophore *Mnemiopsis* in native and exotic habitats: U.S. estuaries versus the Black Sea basin. Hydrobiologia 451:145-176

Purcell JE, Decker MB (2005) Effects of climate on relative predation by scyphomedusae and ctenophores on copepods in Chesapeake Bay during 1987-2000. Limnol Oceanogr 50:376-387

R Development Core Team (2008) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Riisgård HU, Bøttiger L, Madsen CV, Purcell JE (2007) Invasive ctenophore *Mnemiopsis leidyi* in Limfjorden (Denmark) in late summer 2007 - assessment of abundance and predation effects. Aquat Invasions 2(4):395-401

Roohi A, Yasin Z, Kideys AE, Hwai ATS, Khanari AG, Eker-Develi E (2008) Impact of a new invasive ctenophore (*Mneniopsis leidyi*) on the zooplankton community of the Southern Caspian Sea. Mar Ecol 29(4):421-434

Schaber M, Hinrichsen HH, Neuenfeldt S, Voss R (2009) Hydroacoustic resolution of small-scale vertical distribution of Baltic cod (*Gadus morhua* L.) – habitat choice and limits during spawning. Mar Ecol Prog Ser 377:239-253

Schmidt JO (2006) Small and meso-scale distribution patterns of key copepod species in the Central Baltic Sea and their relevance for larval fish survival. PhD Thesis, Christian-Albrechts University, Kiel, Germany

Shiganova TA, Mirzoyan ZA, Studenikina EA, Volovik SP, Siokou-Frangou I, Zervoudaki S, Christou ED, Skirta AY, Dumont HJ (2001) Population development of the invader ctenophore *Mnemiopsis leidyi*, in the Black Sea and in other seas of the Mediterranean basin. Mar Biol 139:431-445

Storr-Paulsen M, Huwer B (2008) Changes in distribution and lengths of *Mnemiopsis leidyi* in the central Baltic Sea between fall and spring. Aquat Invasions 3(4):429-434

Sullivan BK, Keuren DV, Clancy M (2001) Timing and size of blooms of the ctenophore *Mnemiopsis leidyi* in relation to temperature in Narragansett bay, RI. Hydrobiologia 451(1-3):113-20

Tendal O, Jensen KR, Riisgård HU (2007) Invasive ctenophore *Mnemiopsis leidyi* widely distributed in Danish waters. Aquat Invasions 2(4):455-460

Turner JT, Tester PA, Hettler WF (1985) Zooplankton feeding ecology: a laboratory study of predation on fish eggs and larvae by the copepods *Anomalocerata ornata* and *Centropages typicus*. Mar Biol 90:1-8

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: Kruse GH, Bez N, Booth T, Dorn M, Hills S, Lipcius RN, Pelletier D, Roy C, Smith SJ, Witherell D (eds) Spatial processes and management of marine populations. University of Alaska Sea Grant, Fairbanks, p 185-209

Venables WN, Ripley BD (2002) Modern Applied Statistics with S. Springer, New York

Vinogradov ME, Shushkina EA, Musaeva EI, Sorokin PY (1989) Ctenophore *Mnemiopsis leidyi* (A. Agassiz) (Ctenophora: Lobata) – new settlers in the Black Sea. Oceanology 29: 293-298

Voss R, Köster FW, Dickmann M (2003) Comparing the feeding habits of co-occurring sprat (*Sprattus sprattus*) and cod (*Gadus morhua*) larvae in the Bornholm Basin, Baltic Sea. Fish Res 63(1):97–111

Voss R, Clemmesen C, Baumann H, Hinrichsen HH (2006) Baltic sprat larvae: coupling food availability, larval condition and survival. Mar Ecol Prog Ser 308:243–254

Voss R, Schmidt JO, Schnack D (2007) Vertical distribution of Baltic sprat larvae: changes in patterns of diel migration? ICES J Mar Sci 64(5):956–962

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, Jarre-Teichmann A (1997) Prediction of vertical distribution and ambient development temperature of Baltic cod, *Gadus morhua* L., eggs. Fish Oceanogr (3):172-187

Wieland K, Jarre-Teichmann A, Horbowa K (2000) Changes in the timing of spawning of Baltic cod: possible causes and implications for recruitment. ICES J Mar Sci 57(2):452-464

Zaika VE, Ivanova NI (1992) *Mnemiopsis mccradyi* in the autumn hyponeuston of the Black Sea. Ekol Morya 42:6-10


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