

BONUS BIO-C3

Biodiversity changes: causes, consequences and management implications

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BIO-C3 overview

The importance of biodiversity for ecosystems on land has long been acknowledged. In contrast, its role for marine ecosystems has gained less research attention. The overarching aim of BIO-C3 is to address biodiversity changes, their causes, consequences and possible management implications for the Baltic Sea. Scientists from 7 European countries and 13 partner institutes are involved. Project coordinator is the GEOMAR Helmholtz Centre for Ocean Research Kiel, Germany, assisted by DTU Aqua, National Institute of Aquatic Resources, Technical University of Denmark.

Why is Biodiversity important?

An estimated 130 animal and plant species go extinct every day. In 1992 the United Nations tried countering this process with the "Biodiversity Convention". It labeled biodiversity as worthy of preservation – at land as well as at sea. Biological variety should not only be preserved for ethical reasons: It also fulfils key ecosystem functions and provides ecosystem services. In the sea this includes healthy fish stocks, clear water without algal blooms but also the absorption of nutrients from agriculture.

Biodiversity and BIO-C3

To assess the role of biodiversity in marine ecosystems, BIO-C3 uses a natural laboratory: the Baltic Sea. The Baltic is perfectly suited since its species composition is very young, with current salt level persisting for only a few thousand years. It is also relatively species poor, and extinctions of residents or invasions of new species is therefore expected to have a more dramatic effect compared to species rich and presumably more stable ecosystems.

Moreover, human impacts on the Baltic ecosystem are larger than in most other sea regions, as this marginal sea is surrounded by densely populated areas. A further BIO-C3 focus is to predict and assess future anthropogenic impacts such as fishing and eutrophication, as well as changes related to global (climate) change using a suite of models.

If talking about biological variety, it is important to consider genetic diversity as well, a largely neglected issue. A central question is whether important organisms such as zooplankton and fish can cope or even adapt on contemporary time scales to changed environmental conditions anticipated under different global change scenarios.

BIO-C3 aims to increase understanding of both temporal changes in biodiversity - on all levels from genetic diversity to ecosystem composition - and of the environmental and anthropogenic pressures driving this change. For this purpose, we are able to exploit numerous long term data sets available from the project partners, including on fish stocks, plankton and benthos organisms as well as abiotic environmental conditions. Data series are extended and expanded through a network of Baltic cruises with the research vessels linked to the consortium, and complemented by extensive experimental, laboratory, and modeling work.

From science to management

The ultimate BIO-C3 goal is to use understanding of what happened in the past to predict what will happen in the future, under different climate projections and management scenarios: essential information for resource managers and politicians to decide on the course of actions to maintain and improve the biodiversity status of the Baltic Sea for future generations.

Table of Contents

I. Executive Summary	4
II. Introduction	5
<i>References.....</i>	<i>6</i>
III. Core Activity.....	7
1. <i>Mapping present connectivity and dispersal barriers in the whole Baltic Sea seascape</i>	<i>7</i>
2. <i>Mapping variation in connectivity in the whole Baltic seascape</i>	<i>10</i>
3. <i>Mapping future connectivity in the whole Baltic seascape.....</i>	<i>11</i>
4. <i>Mapping connectivity in a high resolution model of Gulf of Riga</i>	<i>13</i>
5. <i>Dispersal and survival of fish eggs and larvae in the Baltic Sea.....</i>	<i>16</i>
6. <i>Connectivity between Eastern” and “Western” Baltic cod populations.....</i>	<i>16</i>
7. <i>Connectivity of larval cod in the transition area between North Sea and the western Baltic Sea</i>	<i>17</i>
8. <i>Connectivity between offshore areas and inshore lagoons: The example of the Atlantic herring in the Western Baltic Sea</i>	<i>18</i>
9. <i>Connectivity and seed areas of the invasive comb jelly Mnemiopsis leidyi in the Baltic Sea</i>	<i>22</i>
10. <i>Can passive larval drift shape the genetic structure of Baltic Mytilus populations?.....</i>	<i>24</i>
IV. Appendices	25

I. Executive Summary

All organisms move during some stage(s) in their life-cycle. Movement can be inter-generational dispersal by eggs, spores or larvae/juveniles, or it may be migrations during the adult stage, e.g. to feeding or spawning areas. On an evolutionary timescale also genes move through space from one generation to the next, also known as gene flow. The movement of organisms connects different parts of a metapopulation in the land/sea-scape, and different habitats/environments may also be viewed as connected through the exchange of organisms. Dispersal between populations and habitats as well as inter-population migrations have far-reaching consequences for the ecology and evolution of species. Examples are resilience to disturbances, recruitment patterns, transport of biomass, risk of species invasions, and potential for local adaptations. Understanding the connectivity in the seascape is also essential for informed management and conservation strategies, e.g. stock-separated management of fisheries, and design of marine protected areas to conserve biodiversity.

The task 3.3. 'Connectivity' in BONUS BIO-C3 aimed for an extensive study of the biological connectivity within the Baltic Sea. The task covered a range of species from macro-algae to fish and native and non-native species. Studies included large-scale analyses of the whole Baltic Sea as well as detailed, highly-resolved studies of sub-basins. The general tool used was bio-physical modelling, which is suitable for biological dispersal that is highly influenced by the physical water transport in ocean circulation. A case where connectivity is largely controlled by organism migration was also covered where empirical methods of acoustic surveys, trawling and stomach analysis were used. The task 3.3 also included an analysis of potential changes of connectivity assuming a changing climate using scenario modelling.

A biophysical model covering the whole Baltic sea showed that there are large geographic differences of dispersal distance in the Baltic seascape. Distances become shorter in the Gulf of Bothnia and in the Gulf of Finland compared to the Baltic proper. Dispersal distances also significantly depend on the dispersal strategy where pelagic larval duration and drift depth are important traits. Based on modelled connectivity it was possible to identify the major dispersal barriers in the Baltic Sea showing that connectivity along coasts within sub-basins is generally high but that there exist several inter-basin barriers. This indicates the scale of local adaptations and possible management units. Another study focusing on the variability of Baltic Sea connectivity between years showed that there are several consistent patterns across years, which suggests that it is meaningful to generalize connectivity also over longer time scales. This insight is important for including connectivity into management strategies.

Since dispersal and connectivity are important drivers of biodiversity the task 3.3 also included an attempt to explore possible changes in connectivity caused by climate-driven changes of the environment. Based on future predictions of ocean circulation and temperature bio-physical and metabolic modelling suggested that dispersal distance may on average increase, especially in the southern Baltic. Generally, the local retention is expected to decrease while export to other sub-basins may increase. This may increase stock mixing and also the spread of non-native species.

In addition to the large-scale general model predictions of Baltic Sea connectivity a number of focus studies were included in task 3.3. A detailed, high-resolution bio-physical model of the Gulf of Riga showed that dispersal distances of bivalve larvae are on average 34 km and

that settlement areas varied significantly between years. The intensity of larval settlement in the region was strongly correlated with food availability and dispersal duration. The model suggests that there is significant local retention on the scale of the Gulf of Riga, which may guide implementation of protected areas.

The dispersal of fish eggs and larvae, e.g. of flounder and cod, is particularly sensitive to water density and the occurrence of hypoxic areas. Bio-physical modelling showed that ocean circulation together with egg buoyancy and bathymetry may act to reduce connectivity between the basins in central and eastern Baltic, which supports actions to consider these as separate management units. Also from otolith and model studies of the potential mixing between the Eastern and Western cod stocks it was concluded that egg and larval connectivity was low between the areas mainly because of low survival of immigrants. In contrast, modelled dispersal of cod eggs and larvae showed that connectivity is high within the transition zone between Kattegat and the Baltic Sea. The cod in this area is likely demographically correlated.

Movement of organisms may constitute a significant flow of biomass between environments and also change the intensity of ecological interactions like competition and predation. This type of habitat connectivity was studied within task 3.3 with herring as a model where spawning individuals migrate from offshore feeding areas to coastal spawning beds. Acoustic and trawling surveys showed that often sensitive inshore waters may be highly important for offshore fish, and that the temporary spawning population may transfer massive biomass. Surprisingly, the predation rate was found to be low on herring larvae within inshore waters. However, a novel finding was that adult herring consumed large number of estuarine fish, mainly gobies, highlighting the potential food-web consequences of mass migrations.

A bio-physical model was also used to test hypotheses about sources of invasive species, here the comb-jelly *Mnemiopsis leidyi*. Results suggested that the transition between the North Sea and the Baltic Sea within Limfjorden may act as a refuge and may re-seed Kattegat and the southern Baltic after years with local extinction.

Finally, task 3.3 also included one study about evolutionary consequences of connectivity. A combined approach using a population genetic analysis and a larval dispersal model was used to understand the processes responsible for the hybrid zone of the blue mussel species *Mytilus trossulus* and *M. edulis*. Results suggested that dispersal distances of larvae are generally too short to explain the extended cline in allele frequencies across the Kattegat-Baltic Sea transition.

In summary, task 3.3 presents maps of how connectivity of eggs, spores and larvae are expected to vary within the Baltic Sea, and also how dispersal distance is expected to change in the future. This general information is complemented with a number of focus studies exploring in detail how dispersal and connectivity may affect patterns of recruitment, stock separation, transport of biomass, and invasion routes of non-native species. The information generated with task 3.3 is partly used in habitat prediction within task 3.4, and also form an important contribution to the assessment of marine protected areas in task 5.2 and evaluation of management strategies in task 5.3.

II. Introduction

Most species occur as metapopulations (Levins 1970, Hanski 1999) where more or less spatially separated subpopulations interact through dispersal. We here use dispersal in a

broad sense including organism movements that may affect either demography or gene flow. The dispersal between subpopulations determines their connectivity where immigration may lead to new colonization, density-dependent competition, and gene flow if immigrants are reproductively successful. On ecological time scales dispersal reduces the risk of local extinctions and on evolutionary time scales the realized gene flow affects genetic diversity and evolution of local adaptations (Sanford and Kelly 2011). Metapopulation dynamics is particularly relevant in spatial management of harvested stocks and conservation, e.g. through marine protected areas (MPA) where it is assumed that populations will persist in often small and widely separated habitats, preferably also with a positive effect on unprotected areas (Jonsson et al. 2016). The Baltic Sea has a complex circulation pattern with multiple basins and connectivity in the Baltic seascape is presently poorly known. The Baltic Sea is also expected to be particularly impacted by global change (e.g. Kotta et al. 2014) and an important question is if this may also change connectivity (e.g. Gerber et al. 2014).

Within WP 3.3 we aimed to estimate connectivity and its variability on the scale of the whole Baltic sea as well as with a detailed study of the Gulf of Riga. This was carried out for a selection of species including macroalgae, invertebrates, fish and one invasive species. WP 3.3 also includes predictions of future connectivity based on climate scenario models. Most studies are based on bio-physical modelling (e.g. Hinrichsen et al. 2016), but also empirical studies using acoustic sampling of fish was used.

The overall objectives were to understand how different parts of the Baltic Sea may be linked through dispersal and where we may expect dispersal barriers, and how this differs for species with different dispersal strategies. Examples are studies of relative effects of habitat quality, larval dispersal and food availability for bivalve recruitment, stock mixing of cod, connectivity between coast and offshore for herring, and spread of an invasive comb-jelly. This information is important when identifying management and evolutionary significant units. Results from WP 3.3 are also used within WP 3.4 to combine connectivity and habitat/species distribution models into model predictions of metapopulation persistence. The estimates of connectivity within WP 3.3 is also essential in the assessment of marine protected areas (MPAs) and network properties in WP 5.2.

The WP 3.3 produced many different studies and many extensive datasets. The main results are highlighted in the section III Core Activities, while more detailed descriptions are provided as appendices.

References

- Gerber LR, Mancha-Cisneros MDM, O'Connor MI, Selig ER. 2014. Climate change impacts on connectivity in the ocean: Implications for conservation. *Ecosphere* 5:33
- Hanski I. 1999. *Metapopulation Ecology*. Oxford University Press, New York
- Hinrichsen HH, Lehman A, Petereit C, Nissling A, Ustups D, Bergström U, Hüsey K. 2016a. Spawning areas of eastern Baltic cod revisited: Using hydrodynamic modelling to reveal spawning habitat suitability, egg survival probability, and connectivity patterns. *Progress in Oceanography* 143: 13-25

- Jonsson PR, Nilsson Jacobi M, Moksnes PO (2016a) How to select networks of marine protected areas for multiple species with different dispersal strategies. *Diversity and Distributions* 22:161-173
- Kotta J, Möller T, Orav-Kotta H, Pärnoja M. 2014. Realized niche width of a brackish water submerged aquatic vegetation under current environmental conditions and projected influences of climate change. *Marine Environmental Research* 102: 88-101
- Levins R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America* 15:237-240
- Sanford E, Kelly MW. 2011. Local adaptation in marine invertebrates. *Annual Review of Marine Science* 3:509-535

III. Core Activity

1. Mapping present connectivity and dispersal barriers in the whole Baltic Sea seascape

Abstract: A bio-physical model was used to simulate dispersal distance and connectivity in the whole HELCOM area. Dispersal distance varies considerably among areas and for different dispersal strategies. Most sub-basins show high local retention and only moderate inter-basin connectivity. The novel approach to identify partial dispersal barriers indicate that there may be a few strong barriers that impede gene flow and facilitate local adaptations, and that there may be several areas that are sufficiently demographically independent to justify separate management units.

Progress: All work completed and we refer to the detailed report by Jonsson et al. (2016a) in the Appendix.

Deviations: No deviations from work plan.

Introduction: Dispersal and connectivity are today recognized as key factors for local population dynamics and population persistence. Dispersal between subpopulations determines their connectivity where immigration may lead to new colonization, density-dependent competition, and gene flow. On ecological time scales dispersal reduces the risk of local extinctions and on evolutionary time scales the realized gene flow affects genetic diversity and evolution of local adaptations. Understanding dispersal and the source-sink dynamics of metapopulations are important for conservation and restoration of marine populations, and an important conservation criterion when selecting marine protected areas (MPAs). In this study the aim was to map dispersal, connectivity and dispersal barriers in a geographically explicit way.

Methods and Results: The present study uses bio-physical modelling to estimate dispersal and connectivity in the seascape of the Baltic Sea including the whole HELCOM area. The bio-physical model combines a hydrodynamic model of the ocean circulation with

Lagrangian particle tracking simulations where biological traits like spawning time, PLD, and vertical behavior were implemented. From a large number of dispersal trajectories we constructed connectivity matrices specifying dispersal probabilities between all areas in the model domain between 0 and 100 m depth. Based on the connectivity matrices we employed a new method to identify partial dispersal barriers in the Baltic seascape that may indicate separate management or evolutionary significant units. Maps of spatially resolved dispersal distance for a range of generic dispersal strategies show that there are large geographic differences in the Baltic seascape (Fig. 1). There is a general trend that dispersal distances become shorter in the Gulf of Bothnia and in the Gulf of Finland. Dispersal distances are also very dependent on the pelagic larval duration, as well as the depth interval in which propagules are drifting. Based on dispersal trajectories connectivity matrices were calculated and a new approach was employed to identify partial dispersal barriers for a range of allowed maximum dispersal among areas (Fig. 2)

Recommendations: There is no sub-basin that is totally isolated although most dispersal occurs within sub-basins, indicating that basin-scale is of the same magnitude as the tail of the dispersal distance distribution in most cases. The area-specific dispersal distance will also guide the design of MPAs where mean dispersal distance will indicate the MPA size resulting in sufficient local retention and recruitment. The analysis of partial dispersal barriers may indicate the presence of unique local adaptations to different regions in the strong Baltic Sea environmental gradients. Barriers may also slow down recolonization and reduce resilience to regional disturbances, and barriers may impede range shifts as a response to future climate.

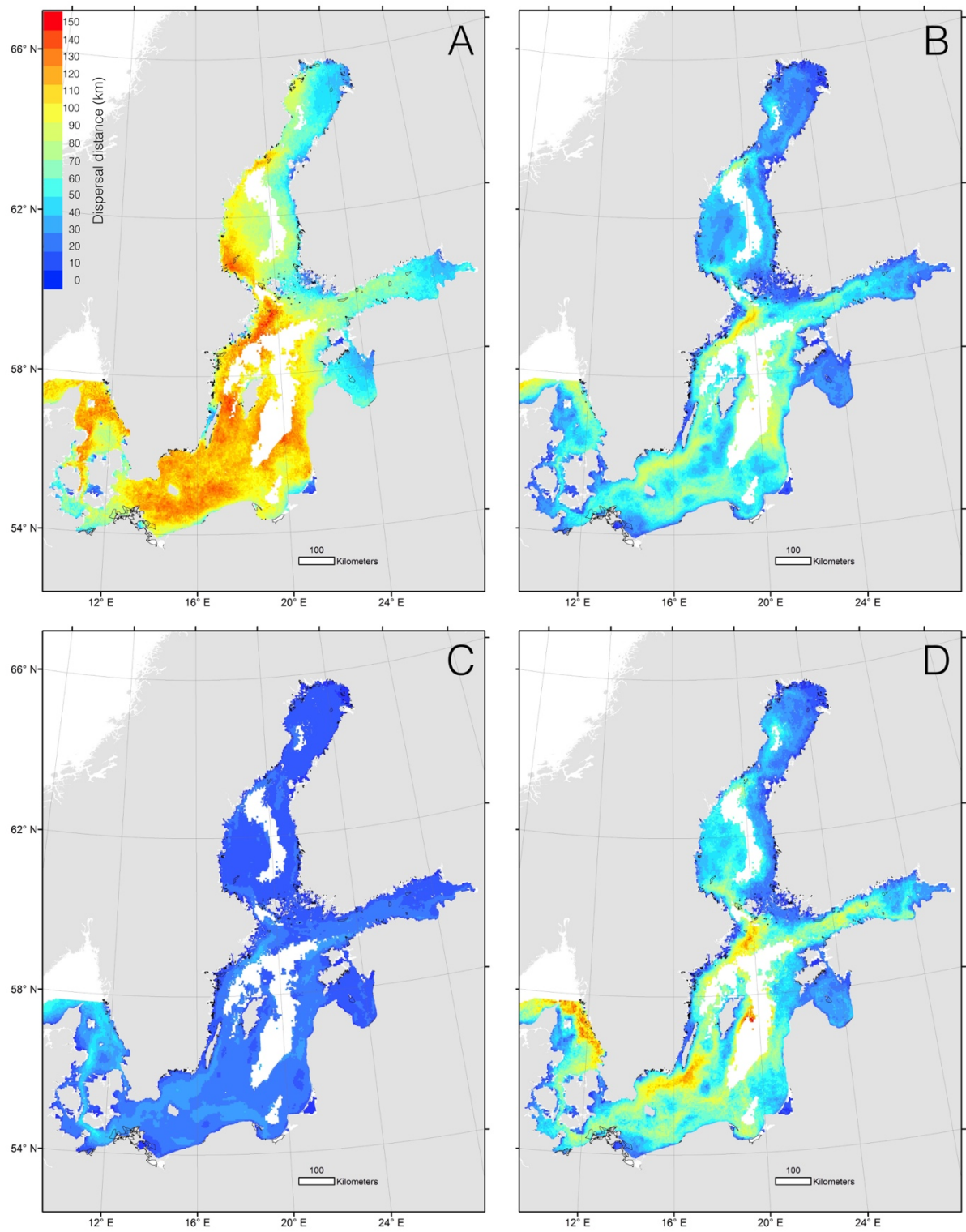


Figure 1. Modelled area-specific dispersal distance for four generic dispersal strategies. **(A)** Spawning time: 25% for each of the months May to August, Pelagic larval duration (PLD): 60 days, Drift depth: 0-2 m. **(B)** Spawning time: 25% June and 75% July, PLD: 30 days, Drift depth: 25% at 0-2 m, 50% at 10-12 m, 25% at 24-26 m. **(C)** Spawning time: 16% for each month between April and September, PLD: 5 days, Drift depth: 100% at 0-2 m.

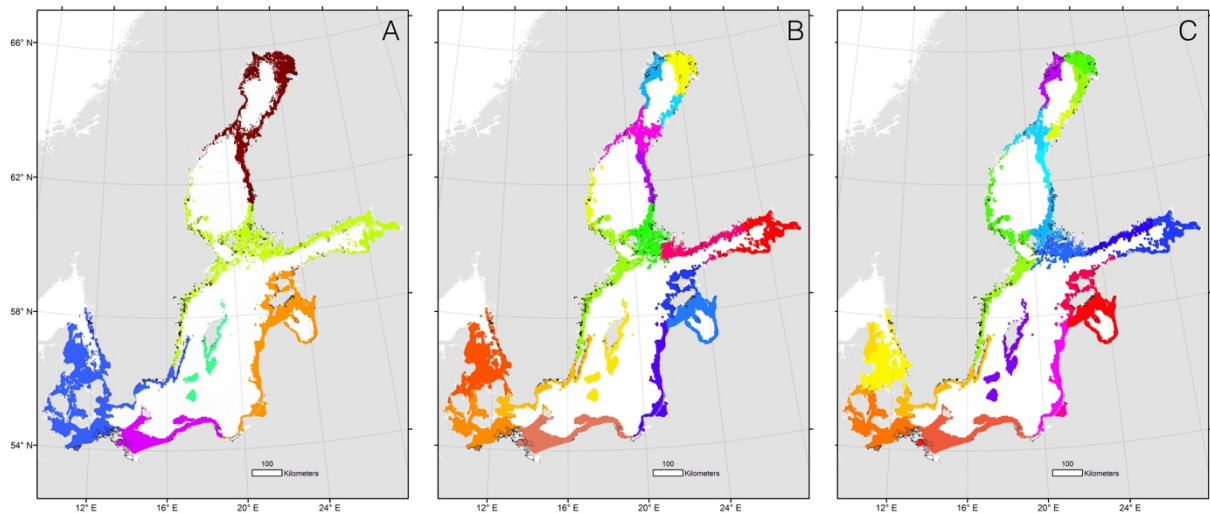


Figure 2. Examples of the identification of dispersal barriers for one dispersal strategy and a habitat specified by the depth interval 0-10 m. (A) Low allowed dispersal between areas producing 6 clusters. (B) Medium allowed dispersal between areas producing 20 clusters. (C) High allowed dispersal between areas producing 28 clusters.

2. Mapping variation in connectivity in the whole Baltic seascape

Abstract: Dispersal distance in the Baltic Sea was estimated using a bio-physical model with the aim to find consistent patterns and quantify inter-annual variability.

Progress: All work completed and manuscript ready for submission (Hinrichsen et al. 2016a in manus).

Deviations: No deviations from work plan.

Introduction: There is no information about how consistent dispersal and connectivity patterns between years are in the Baltic Sea. If patterns across the Baltic seascape are consistent this may affect short-term variability of species distributions, evolution of local adaptations, but also facilitate spatial management.

Methods and Results: A bio-physical model based on an oceanographic model produced spatially and temporally resolved long-term averages of dispersal distances of Lagrangian particles calculated for the whole Baltic Sea. These dispersal patterns are based on the long-term wind driven and thermohaline circulation calculated by using a coupled sea ice-ocean model of the Baltic Sea for a 40-year time period. These average dispersal distances are available on decadal quarterly time scale basis for specific subareas (50 km x 50 km) in the Baltic Sea. The average dispersal distances cover temporal windows ranging from 5 to 50 days resolved at 5-day intervals and are available for the upper 100 m of the water column. Furthermore, in order to assess the importance of MPA networks, positions of important dispersal corridors and connectivity hot-spots in offshore areas were calculated. From the model runs there is a clear evidence of persistent dispersal patterns which comprise mostly the basin-like structure of the Baltic Sea with less transport between the basins (Fig. 3). The mean geographic distances suggest a very stable cyclonic circulation cell in the eastern Gotland Basin with recirculation towards the west in the northern part which extended in the south to the Bornholm Basin and the Gdansk Deep

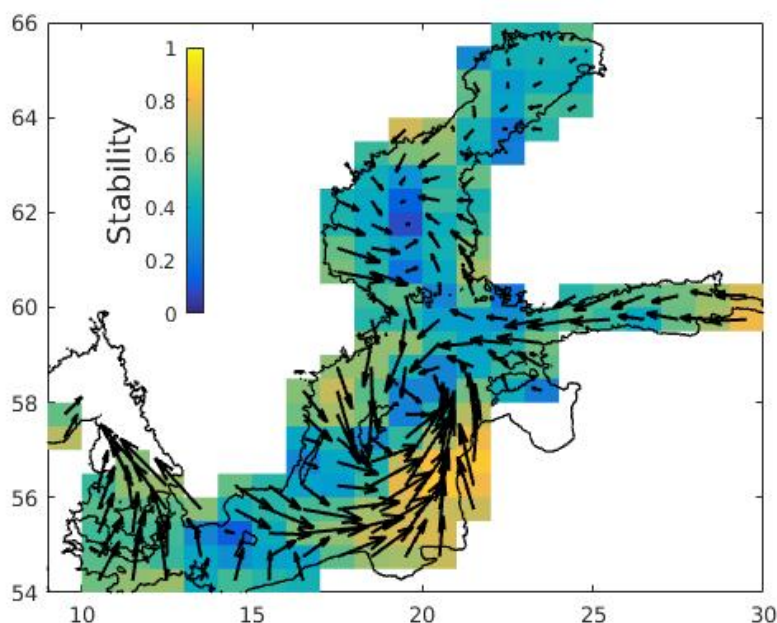


Figure 3. Ocean current based mean geographic distances and stability, 2.5, depth level, 1.quarter decade 1981-1990, drift duration 50 days (from Hinrichsen et al. in manus).

Recommendations: This study shows that large-scale connectivity patterns are consistent between years. The reduced connectivity between sub-basins indicates that these may form separate management units. Within sub-basins connectivity is generally high and indicates significant local retention.

3. Mapping future connectivity in the whole Baltic seascape

Abstract: Future dispersal and connectivity was estimated from particle tracking using velocity fields from a climate scenario model. On average future circulation is expected to lead to longer dispersal distances and this effect is strongest in the southern Baltic Sea. The effect of increasing seas-surface temperature was also assessed and indicates that the resulting acceleration of larval development partly counteract the circulation-based increase in dispersal distance. However, this effect is rather weak in the southern Baltic Sea. The increase in dispersal distance in a future climate may call for changes in management units and MPA size.

Progress: All work completed and we refer to the detailed report by Jonsson et al. (2016b) in the Appendix.

Deviations: No deviations from work plan.

Introduction: One important consequence of global changes in the environment is that population connectivity may change with effects on metapopulation persistence, range shifts and spread of non-native, invasive species. Multiple factors may change marine connectivity, including changes in circulation, habitat distribution, phenology and temperature-dependent development. The net effect on future connectivity is very difficult to predict, and to our knowledge there is yet no explicit spatial modelling of future connectivity based on scenario simulations of ocean circulation. In this study we aimed at

the first attempt to model the future connectivity in the HELCOM area.

Methods and Results: We set up a unique model of spatially explicit dispersal under future climate conditions in the Baltic Sea using projected ocean velocity fields from scenario models based on the IPCC emission scenarios A1b and A2. In addition to effects of ocean circulation we also assessed the effect of temperature change on dispersal and connectivity through the accelerated larval development reducing the pelagic larval duration. Results show that mean dispersal distance will on average increase, caused by changes in the circulation. This effect is, however, very dependent on geographic area and is particularly large in the southern Baltic Sea (Fig. 4). The changes in dispersal distance translate into a reduced local retention in many of the southern Baltic sub-basins and increased inter-basin connectivity. The effect of increasing sea-surface temperature will lead to more rapid larval development reducing the pelagic larval duration and thus dispersal distance. However, this effect is strongest in the northern Baltic Sea and weaker in the southern Baltic Sea where the effect of circulation change is expected to dominate.

Recommendations: The future mean increase in dispersal distance, mainly in the southern Baltic Sea will affect local retention and connectivity between sub-basins in the Baltic Sea. Generally, the local retention is expected to decrease while export to other sub-basins may increase. This may increase stock mixing and also the spread of non-native species. The increased dispersal distance in many areas may also cause lower local retention within MPAs, and may call for an extension of some MPAs.

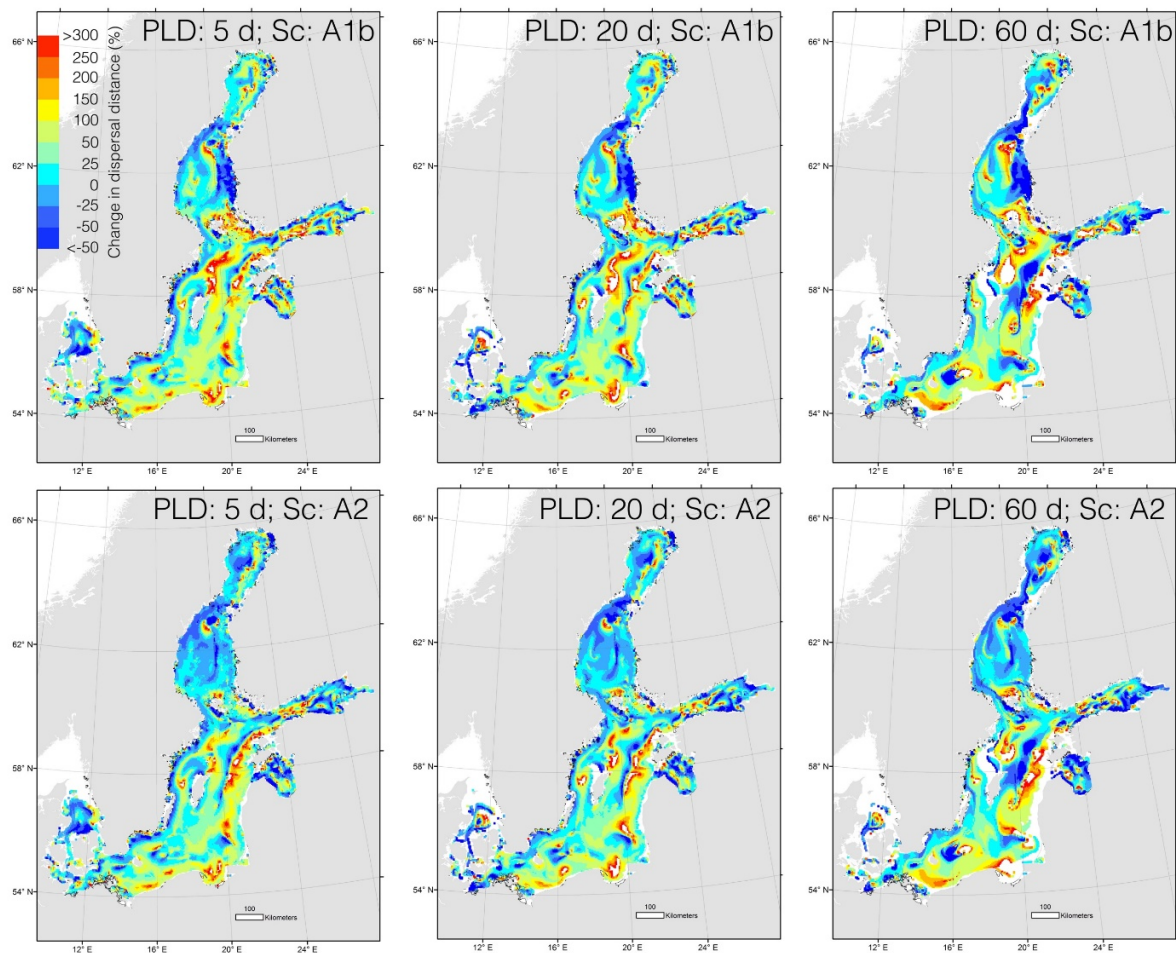


Figure 4. Proportional change (%) in dispersal distance in the Baltic Sea caused by the predicted change in circulation pattern. Data are shown for three pelagic larval durations (PLD) 5, 20 and 60 days, and two emission scenarios (Sc) A1b and A2.

4. Mapping connectivity in a high-resolution model of Gulf of Riga

Abstract: The dispersal of larvae depends on a number of physical and biological factors as the duration of the larvae phase, the local hydrodynamics, and food availability e.g. temperature- and nutrient-dependent growth dynamics of phytoplankton as well as growth and mortality of the larvae. In this study, we have applied a combination of hydrodynamic modelling, ecosystem modelling and agent-based modelling to analyze the importance of fine scale dispersal patterns, identify important source and sink areas and estimate the importance of hydrodynamics, temperature and food availability for larvae dispersal.

Progress: Fine-scale connectivity modelling and reporting is finalised and a manuscript (Middelboe et al.) is in preparation.

Deviations: No derivation from work plan.

Introduction: The dispersal patterns of planktonic phases creates the fundamental properties of connectivity between benthic communities that affect the risk of local extinctions, genetic diversity and evolution of local adaptations. The dispersal of larvae depends on a number of physical and biological factors including the duration of the larvae phase, the hydrodynamics at the local spawning site, food availability (temperature- and nutrient-dependent growth dynamics of phytoplankton) as well as growth and mortality of the larvae. Knowledge about connectivity between populations and about the importance of factors determining the dispersal patterns of key benthic species are central for our ability to quantify and predict impacts on the benthic community structure and resilience from natural and anthropogenic pressures. *Mytilus edulis* is a key benthic fauna species in the Kattegat-Baltic sea area being the dominating fauna on the hard bottoms. It's a character species for reefs protected via EUs habitat directive and a main source of food for wintering water birds occurring in numbers of international importance in bird protection areas around the Baltic Sea (e.g. Gulf of Riga area). This study aims to analyse fine-scale connectivity patterns between *Mytilus* populations in the Gulf of Riga area.

Methods and Results: In this study, we applied a combination of hydrodynamic modelling, ecosystem modelling and agent-based modelling to analyze fine scale dispersal patterns of *Mytilus* larvae in the Gulf of Riga area during a 38 years period (1971-2007). An agent based model (ABM) was developed for modelling *Mytilus edulis* larvae dispersal based on spawning conditions (density and conditions of adult mussels), modelled hydrodynamics, temperature- and food dependent growth and mortality rates as well as substrate dependent settlement. The model complex was used to map the importance of areas as source and sink, estimate the importance variability in current speed, temperature and food availability for year-to-year variability in number of larvae settled, larval dispersal distance and dispersal time. The average relative importance of the areas as spawning (source) and settlement (sink) areas was spatial variability in the study area. The areas most important as source area were the more sheltered areas: the Pärnu Bay area, off the south-east coast of the island Saaremaa, in the strait between Saare and the main land of Estonia and in the Irbe Strait (Figure 1). The important sink areas was mainly found within the Gulf of Riga; especially the Pärnu Bay area and off the south-east coast of the island Saaremaa. There were relatively large year-to-year variations as illustrated by the minimum and maximum importance of the areas as source or sink in the study periode (Figure 1). Especially the importance of sinks was variable as the max relative importance showed large values over large areas, suggesting that the number of larvae settled, in some areas are highly variable between years. This results may indicate that maintenance of some local populations may rely on conditions that occur less frequently than the general pattern suggest.

The overall modelled mean (\pm SD) dispersal distance of *Mytilus* larvae was 34.3 (\pm 6.0) km, with most larvae (ca. 65%) traveling 5-35 km and few traveling long distances of up to 240 km. The year-to-year variability in average dispersal distance was between about 30 km to 50 km. The overall modelled mean dispersal time (\pm SD) was 240.4 (\pm 25.4.0) time steps (each of 3 hours), with most larvae (ca. 60%) traveling 23-34 days (180-260 time steps x 3 hours) before settling. First larvae settlings occurred after ca. 18 days and only a small proportion survived to the defined maximum age of 56 days. The variable that showed the strongest correlation with the number of settled larvae was food availability (r : 0.61-0.81), thus suggesting that high food availability ensure survival of the larvae to competent size. The distance travelled was significantly related to currents speed (r : -0.49 and -0.55) and temperature. Using PLS multiple regressions food availability could, together with currents, explain 69% of the variability between years of the number of larvae settled, the same variable could explain 35% of the variability in time for settlement. 30% of the between year variability in dispersal distance could be explained by currents, temperature and food availability.

Recommendations:

The developed model-complex integrating fine-scale hydrodynamics-, ecological- and agent-based modelling over 38 years can be used as an important basis for management of the large number of sites protected by the EU habitat and bird directives (MPAs) in the study area. Further studies will assess the degree of connectivity and self-recruitment between MPAs as basis for management recommendations.

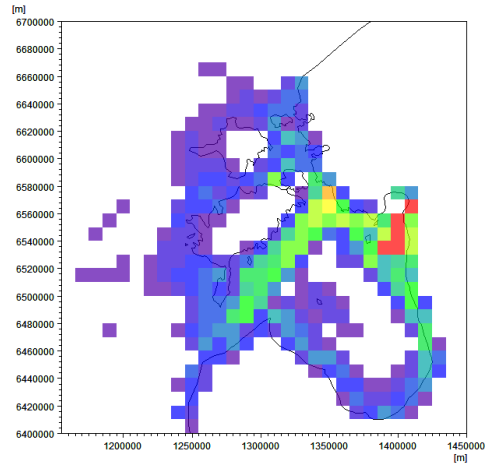
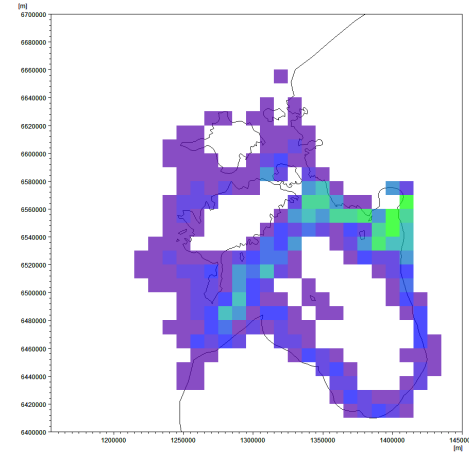
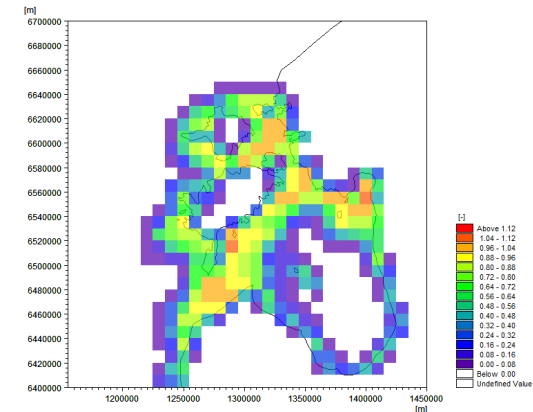
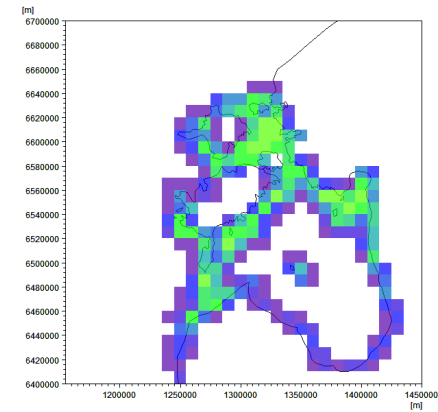
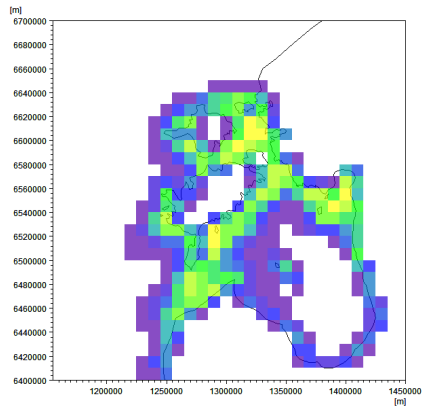
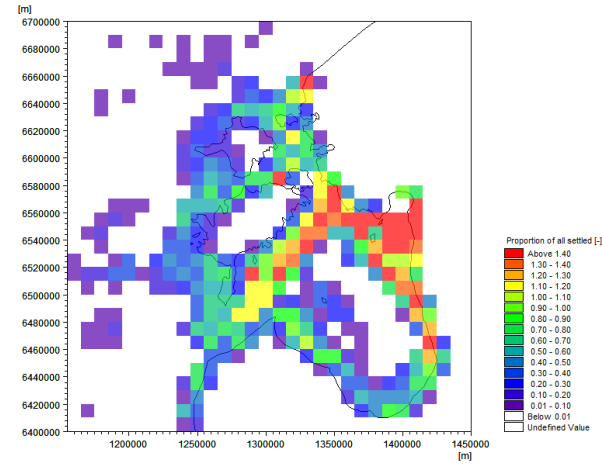
Average**Min****Max**

Figure 1. Importance of areas as sink for larvae settlement expressed as the proportion of all settled larvae (upper) and importance of areas as source expressed as larvae spawned as a proportion of all spawned larvae (lower). Shown are the average (left panel), minimum (middle panel) and maximum (right panel) of the years 1995 to 2007.

5. Dispersal and survival of fish eggs and larvae in the Baltic Sea

Abstract: Bio-physical modelling of dispersal of flounder and cod eggs and larvae combined with survival driven by salinity and oxygen showed that transport of Baltic cod and flounder eggs and could be limited by the poor connectivity of the early life stages between the different basins in the central and eastern Baltic Sea.

Progress: All work completed and we refer to the published papers Hinrichsen et al. (2016b) and Hinrichsen et al. (2016c in press) in the Appendix as well as one manuscript (Hinrichsen et al.) in preparation.

Deviations: No deviations from work plan.

Introduction: The information on temporally and spatially resolved distribution patterns of Baltic fish early life stages (here of flounder and cod) and strong variations in Baltic Sea circulation patterns is necessary to investigate the existence of self-sustaining components and mixed populations across the Baltic seascape. In addition to potential dispersal caused by drift it is important to evaluate realised connectivity tempered by relevant environmental conditions primarily determined by oxygen and salinity.

Methods and Results: A hydrodynamic model combined with a Lagrangian particle tracking technique was utilized to provide long-term knowledge of environmentally-related survival probability and drift of Baltic fish eggs, larvae and juveniles. Simulations were performed to quantify processes generating heterogeneity in spatial distribution of Baltic fish early life stages. We evaluated the environmental conditions in the different subareas of the Baltic Sea for the suitability for spawning, survival probability, settlement and estimated the population connectivity of Baltic cod early life stages between the different subareas. The extent of Baltic cod and flounder eggs is primarily determined by oxygen and salinity conditions and the ability to obtain neutral buoyancy in the water column, which define the habitat requirement to which species' physiology is suited. Eggs initially released as drifters in the westernmost spawning grounds were more affected by sedimentation than those released in the eastern spawning grounds. For all spawning areas within the Baltic Sea temperature dependent mortality was only evident after severe winters. Egg buoyancy in relation to topographic features like bottom sills and strong bottom slopes could appear as a barrier for the transport of Baltic cod and flounder eggs and could potentially limit the connectivity of the early life stages between the different basins in the central and eastern Baltic Sea.

Recommendations: Egg buoyancy in relation to topographic features like bottom sills and strong bottom slopes could appear as a barrier for the transport of Baltic cod eggs and yolk sac larvae and could potentially limit the connectivity of Baltic cod early life stages between the different basins in the western and eastern Baltic Sea. This supports actions to consider these populations as separate management units.

6. Connectivity between Eastern” and “Western” Baltic cod populations

Abstract: The spatio-temporal dynamics of stock mixing between the two genetically distinct cod populations “Eastern” and “Western” Baltic cod was analysed using shape analysis of

archived otolith and a hydrographic drift model. It is concluded that the immigration of “Eastern” cod does not seem to contribute significantly to recruitment of the “Western” cod stock.

Progress: All work completed and we refer to the published paper Hüseyin et al. et al. (2016) in the Appendix.

Deviations: No deviations from work plan.

Introduction: In the Baltic Sea, two genetically distinct cod populations occur, the “Eastern” Baltic cod in ICES SDs 25-32 and the “Western” Baltic cod in SDs 22-24. Since 2006, cod abundance has increased 5-fold in the Arkona Basin in the eastern part of the “Western” cod’s management unit (SD 24), but remained constant in SD 22, presumably due to mixing of the two stocks. The spatio-temporal dynamics of stock mixing were analysed using shape analysis of archived otolith, and the impact of “Eastern” cod’s immigration on recruitment by hydrographic drift modelling.

Methods and Results: The percentage of “Eastern” Baltic cod in the Arkona Basin increased from ca. 20 % before 2005 to > 60 % in recent years. The spatial resolution of stock mixing suggests immigration occurring north of Bornholm, but propagating throughout the Arkona Basin. An age-related trend in immigration was evident, which started with 4-year cod followed by progressively older individuals. The immigration cannot be attributed to spawning migration, as no seasonal trend in stock mixing was observed. Only between 20-50% of the available habitat was suitable for successful spawning of “Eastern” cod, limited by primarily low salinity. Best conditions occurred irregularly in May-end June, interspersed with years where successful spawning was virtually impossible. On average, only 19 % of the eggs survive to the end of the yolk-sac, with mortality primarily after bottom contact due to low salinity. The general drift direction of the surviving larvae was towards the east. Albeit considerable, the immigration of “Eastern” cod does therefore not seem to contribute significantly to western Baltic cod’s recruitment.

Recommendations: The study supports the recent change to stock-specific management rather than management of fixed geographical areas (SD 22-24), and it is recommended that the monitoring of proportion of “Eastern” and “Western” cod populations within the western Baltic Sea is continued.

7. Connectivity of larval cod in the transition area between North Sea and the western Baltic Sea

Abstract: Connectivity of cod between areas in the western Baltic Sea and Kattegat was studied with bio-physical modelling of early life-stages. The transport of larvae showed high temporal variability, but also some consistent patterns of retention within and dispersion to different management areas. The high exchange rates between areas suggest significant demographic correlation in this region.

Progress: All work completed and we refer to the published paper Huwer et al. (2016) in the Appendix.

Deviations: No deviations from work plan.

Introduction: Connectivity of larval fish via transport by ocean currents is of particular interest, as it may affect survival chances of offspring, recruitment success and also mixing of stocks across management units. Based on drift model studies, the transport patterns of exogenously feeding cod larvae in the western and eastern Baltic was investigated in order to i) determine long-term trends and variability in advective transport of larvae from spawning grounds to juvenile nursery areas, ii) estimate the degree of exchange between different management areas and iii) compare the results with spatial distributions of juvenile cod. Additionally, for eastern Baltic cod we have calculated juvenile fish mortality related to oxygen-dependent settlement probability.

Methods and Results: The dispersal of cod eggs and larvae from spawning areas in western Baltic Sea, The Danish Straits and Kattegat was studied with a bio-physical model. The transport of larvae showed a high intra- and inter-annual variability, but also some general, consistent patterns of retention within and dispersion to different management areas. In case of the western Baltic cod stock, good agreement of drifter end positions, representing potential juvenile settlement areas, with actual catches of juveniles from bottom trawl surveys suggests that the drift simulations provide reasonable estimates of early life stage connectivity between cod populations in the investigated areas. High exchange rates of drifters between management areas of up to ca. 70% suggest that cod populations in the investigated areas are demographically correlated.

Recommendations: The high exchange rate of modelled larvae between areas suggest that these are demographically correlated. The combined effects of adult homing and the suggested high exchange of early life stages make spatial management in this region complex. This calls for better understanding of realised connectivity and further development of stock assessment models.

8. Connectivity between offshore areas and inshore lagoons: The example of the Atlantic herring in the Western Baltic Sea

Abstract: Throughout the last years, P11 conducted a variety of different field studies to examine the connectivity of coastal inshore lagoons with the offshore areas of the Baltic Sea. Atlantic herring (*Clupea harengus*) in the Western Baltic Sea undergoes intensive seasonal migrations between offshore feeding grounds and inshore spawning beds and we used this species as an example to analyse interactions between these systems.

Field studies included acoustic surveys in offshore areas close to Rügen Island to gain insights into the herring migration from offshore to inshore and the number of individuals and the corresponding biomass migrating to coastal waters. In inshore habitats one study was based on comprehensive data sets on the abundance of herring larvae and their potential predators within Greifswald Bay to investigate who actually benefits from the migration. In addition, we also investigated the feeding ecology of adult herring during its migration into the inshore ecosystems hypothesizing a differing pattern in feeding behaviour than described for offshore pelagic systems. We combined investigations on herring stomach contents, larval abundance and zooplankton densities conducted in several consecutive years and revealed a so far undescribed feeding behaviour of herring during their stay in the bay.

Progress: All field work completed and one manuscript is submitted (Kotterba et al.) and one manuscript is in preparation (Kotterba et al.), and one poster was presented at the EMBS 2016 (see Appendix).

Deviations: No deviation from the work plan.

Introduction: Although the connectivity between ecosystems has increasingly gained the attention by marine researchers, the actual importance of links between distinct habitats and systems is still unsatisfyingly evaluated in many cases. For example, Atlantic herring (*Clupea harengus*) in the Baltic Sea is a marine species that undergoes intensive migrations between offshore (marine) feeding grounds and inshore (estuarine) spawning sites implying an intensive transfer of biomass and energy between these systems. Particularly in spring, spawning in coastal areas and inshore lagoons can temporarily exceed the autochthonous primary production. However, studies that quantify and characterize the ecologic interactions of the marine herring during its temporarily presence in estuarine waters are rare. We here combined different ecological field study approaches to investigate specific interactions that arise from the herring migration behaviour. Comprehensive acoustic investigations were performed to analyse the herring distribution and spawning migration in the Western Baltic Sea. Data series and field observations on the abundances of herring larvae and their potential predators were combined with stomach content analyses of the latter to investigate predation impacts on larval survival and the potential benefits of increased larvae densities for resident predators. Furthermore, we combined stomach content analyses of adult herring with zooplankton densities and larvae abundances to investigate food consumption by herring during their stay in a coastal inshore lagoon.

Methods and Results:

Herring spring-spawning migration

The study was conducted to gain general insights into the herring migration patterns and the corresponding biomass of herring that migrates towards the coastal waters during the spawning period. Combined with the ICES coordinated acoustic survey in autumn, our survey gives new insights of the herring migration close to Rügen Island. Within the ICES survey numbers of herring were estimated for the whole Baltic on the basis of ICES rectangles. In the western Baltic (SD 21 – 24) a total of 3 707 million herring individuals were estimated (Gröhsler & Schaber 2016) in autumn 2015. Most of the herring occurred in the Øresund (approx. 1 200 million individuals). While highest fish densities in SD 24 were recorded north and east of Rügen Island and in the central parts of the Arkona Sea, resulting in about 140 million herring individuals in ICES rectangle '38G3' which is quite similar to our study area.

We estimated a total of 200 million herring individuals with a total biomass of 8 700 tons for the study area close to Rügen Island in week 6 (Fig. 6). During the following weeks the total biomass and the total number of individuals increased significantly. Between week 11 and week 19 the estimated total biomass of herring is between 39 200 tons and 6 200 tons with the lowest biomass in week 19. There are two peaks observable in week 11 and week 15 with around 39 000 tons of biomass of herring. The estimated total number of individuals increases from 204 million individuals to 672 million in week 15 and decreases in the following weeks to 122 million which is quite similar to the results from the ICES report.

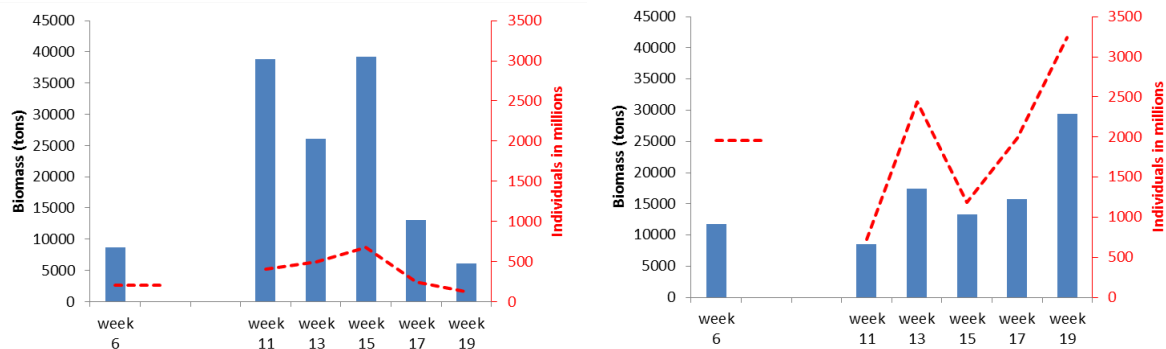


Figure 6. Estimated total biomass and total numbers over time within the three selected rectangles. Left panel: herring; right panel: sprat.

Even if the estimations and the size of the area differ slightly between both studies and the residence time of the individuals is unknown, our results reveal a clear important herring migration to the coastal waters of Rügen Island. Larger individuals arrive at first, which might be related to the speed of migration assuming that larger individuals swim faster compared to smaller conspecifics. However, considering the high proportion of active spawners (80 %) between week 11 and 17, it can be assumed that the herring migration transferred a huge amount of energy from the offshore feeding area to the inshore spawning area. For more details see appendix.

Predator impacts on inshore Baltic herring (*Clupea harengus*) larvae: Lions, tigers and bears – but where?

Bottom-up and top-down driven larval mortality is generally accepted to be a key element controlling the recruitment success and population dynamics of fishes. The majority of studies that examine larval predation have been conducted in offshore and rather oceanic habitats. However, many important spawning beds and larval nursery areas of marine fish species are located in transitional zones such as estuaries and inshore lagoons.

Hypothesizing that the mortality of fish larvae in transitional waters is influenced by another community of predators than in the pelagic offshore habitats, we investigated herring larvae and their potential predators in an important herring spawning area in the western Baltic Sea (Greifswald Bay; 54.2°N, 13.5°E). Combining weekly high-resolution ichthyoplankton survey data on herring larvae abundances with analyses of plankton net bycatches and additional sampling data, we found a spatial overlap between herring larvae and dominant resident predators such as sticklebacks (Fig. 7). However, this spatio-temporal match did not result in a targeted predation on the larvae. Despite very high abundances of herring larvae, we found nearly no larvae in the stomachs of the resident predators. An additional sampling in the very shallow littoral of the lagoon (≤ 1 meter depth) confirmed a coexistence of herring larvae and sticklebacks in this habitat as well, but again not a single larva was found in the examined predator stomachs. Furthermore, we found a remarkable mismatch between herring larvae and gelatinous plankton in the bay since the latter first appear in the area when the majority of the larvae have already emigrated or reached the juvenile stage. This is in contradiction to observations made in other parts of the Baltic Sea, Northern Atlantic and Pacific Ocean, where gelatinous plankton have been demonstrated to be an important predator of fish larvae. However, we found no significant predation impact on herring larvae within the lagoon and conclude that other mechanisms might control herring reproduction

success in these types of nursery grounds. Beyond that, low predation rates might act synergistically with favourable temperature conditions (early increase in spring) and generally high productivities making transitional waters valuable as spawning and nursery grounds for marine fishes (for detailed information see appendix).

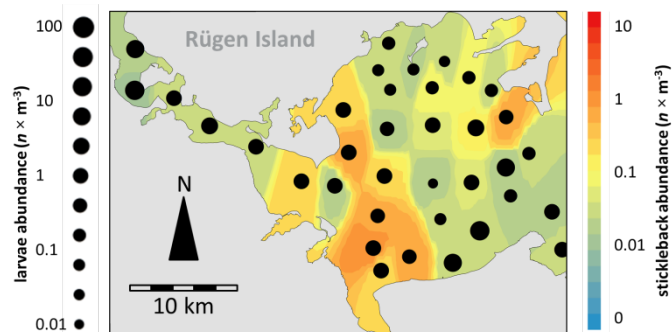


Figure 7. Spatial overlap of herring larvae and threespine stickleback (*Gasterosteus aculeatus*) in May 2011 (calendar week 19) based on the Bongo-net sampling at 36 stations within Greifswald Bay. Larvae abundances are given as black circles (area = proportional to abundance) while the stickleback abundance (color scale) was interpolated using a spatial kriging approach.

A wolf in sheep's clothing – Planktivorous herring as an intense predator of estuarine fish prey

Herring (*Clupea spp.*) is generally considered as a key element in marine food webs in the northern hemisphere linking trophic cascades from zooplankton to higher trophic levels. Besides its prominent ecological importance as so-called “forage fish”, herring has also been an essential marine resource for humans since the Middle Ages. Consequently, intensive research has been focused on herring biology, and the Atlantic herring (*C. harengus*) is considered the world's best studied marine fish species. The text book paradigm of a species almost exclusively feeding on zooplankton, ichthyoplankton and small crustaceans is basically due to many studies on herring feeding behaviour in the open oceans. Hypothesizing that herring is capable to adapt to changing feeding opportunities; we studied a group of herring in the Baltic Sea regularly immigrating into shallow inshore systems. Combining stomach content analyses, zooplankton density estimates and larval abundance examinations from three successive years, we observed a directed and intensive feeding on demersal fishes and benthic crustaceans (Fig. 8) rebutting the so far undisputed conception of a zooplankton feeder constricted to the pelagic food web. We revisited and adjusted the baselines for the present paradigms on the position of herring within marine food webs according to these new findings (for detailed information see appendix).



Figure 8. Stomach content of a single adult herring caught in Greifswald Bay in autumn 2010. The scale in the upper part of the image is divided in cm (labelled ticks) and mm (small ticks). The lower two lines of prey organisms show the remains of goby individuals (*Pomatoschistus* sp.) the uppermost line represents Amphipoda found in the same stomach. On the right edge of the image, the aggregated remains of unidentified fish prey is shown including a remarkable number of small otoliths indicating a high number of gobies that have been consumed by this herring.

*Active habitat selection by Atlantic herring (*Clupea harengus*) larvae*

Furthermore, we had a collaboration with our colleagues at TI-OF that are involved in the BONUS INSPIRE project to analyse data sets on herring larval abundance and distribution within an important retention area of Baltic herring larvae. The work resulted in a manuscript that has been submitted to Scientific reports recently (corresponding author: Patrick Polte, TI-OF). Basically, our results illustrated, that larval herring is characterized by a stage-specific active habitat selection which is contradictive to the general assumptions, that those larvae are primarily dispersed by passive drift mechanisms.

Recommendations: Our results indicate a great importance of inshore waters for the successful reproduction of an ocean-going commercial fish species. Considering the ubiquity of anadromous species among economically and ecologically important fish species, our studies highlight the importance of increasing our knowledge on the functioning and vulnerability of inshore systems in order to establish a sustainable utilisation of these marine resources. Besides the impact on the recruitment of commercial species, the relevance of the connectivity between offshore and inshore systems for the resident communities (including non-commercial but ecologically important species) needs to be evaluated.

9. Connectivity and seed areas of the invasive comb jelly *Mnemiopsis leidyi* in the Baltic Sea

Abstract: A bio-physical model of the drift and dispersal of the invasive comb-jelly *Mnemiopsis leidyi* shows that Limfjorden may act as a refuge during years of local extinction in the Kattegat and the Baltic Sea and start new invasions.

Progress: All work completed and a manuscript (Jaspers et al.) is in preparation.

Deviations: No deviations from work plan.

Introduction: The comb jelly *Mnemiopsis leidyi*, native to the east coast of America and was first recorded in the Baltic Sea in 2006 (Kiel Bay and the Belt Sea) and subsequently spread to

the Gotland Basin and Bay of Puck. From the initial introduction *M. leidy* has occurred erratically in the southwest Baltic Sea during with almost complete disappearance during some years some years (e.g. 2012). However, populations of *M. leidy* has been observed every year in Limfjorden although in low numbers during some years. This study tested the hypothesis that Limfjorden may act as a refuge for *M. leidy* where reproductive rate is high and salinity favorable. This refuge may then act as a source that can re-introduce *M. leidy* to Kattegat and the southern Baltic Sea. The dispersal of *M. leidy* and the connectivity between Limfjorden and nearby areas was tested with a bio-physical model simulating particle trajectories forced by an oceanographic model.

Methods and Results: A bio-physical model of dispersal in surface waters was used to predict patterns of dispersal from the assumed source in Limfjorden. Velocity fields from an oceanographic model spanning 10 years (2001-2010) was used to produce a mean dispersal probability distribution. Figure 9 shows the source at the mouth of Limfjorden and the resulting distribution of particles from model simulations. This preliminary drift model shows that 10 to 20% of the particles released from Limfjorden reach the other side of the Kattegat/Skagerrak within 10 days. From Kattegat many particles also disperse into the Belt Sea and the southern part of the Baltic Sea all the way to the Bornholm Deep.

Recommendations: The drift model results combined with empirical observations suggest that Limfjorden has the potential to act as source region seeding *M. leidy* into the Baltic Sea, hence assuring reinvasions after extinction of local *M. leidy* populations following harsh winter conditions.

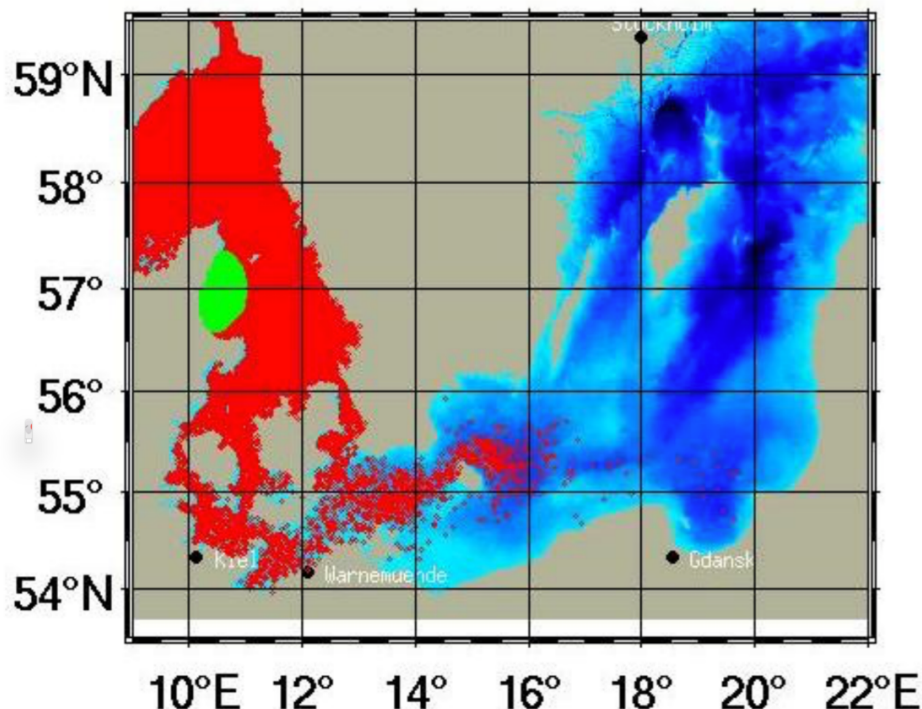


Figure 9. Distribution of particles (red dots) over a 10 year period (2001 – 2010), which have been released at the outlet of Limfjorden (green area). The blue colors indicate bathymetry.

10. Can passive larval drift shape the genetic structure of Baltic *Mytilus* populations?

Abstract: This study aims to understand the mechanisms underlying the discordance in allele frequencies found in the contact zone between *Mytilus edulis* and *M. trossulus* in the Baltic-North Sea transition. Positioning of the cline with genetic methods together with bio-physical modelling showed that dispersal distances are generally too short to explain the present cline in allele frequencies.

Progress: All work completed and we refer to the manuscript Stuckas et al. (in press) in the Appendix.

Deviations: No deviations from work plan.

Introduction: Secondary contact between *Mytilus edulis* and *M. trossulus* in North America results in mosaic hybrid zone formation, so that both species form a hybrid swarm in the Baltic. Exploring mechanisms underlying these contrasting patterns will allow an understanding of processes such as speciation or adaptation to extreme environments (e.g., low salinity). The previous discovery of discordant allele frequency clines across the Baltic secondary contact zone suggested only weak interspecific reproductive barriers resulting in a semi-permeable barrier to gene flow. Recent investigations have tested an alternative hypothesis and asks whether discordant allele frequency clines result from founder events, i.e., long-distance dispersal of passively drifting *Mytilus* larvae beyond a transition zone.

Methods and Results: The study used a combination of population genetic methods and bio-physical modelling of dispersal to test if long-distance dispersal and founder events could explain the cline in allele frequencies within the transition zone between the two *Mytilus* species. Genetic analyses of allele/haplotype frequency clines and Bayesian inference found highest admixture proportions in southern Baltic populations west of Rügen Island. Consequently, a virtual line between this area and the previously characterized admixture zone in the Öresund describes the position of the Baltic *Mytilus* transition zone. Hydrodynamic modelling and Lagrangian particle tracking showed short distance dispersal routes (10 - 30 km) of Baltic *Mytilus* larvae that do not reach far beyond this area (Fig. 10). Consequently, one can reject the possibility that founder events shape discordant allele frequency clines and cause pervasive hybridization. The Baltic *Mytilus* transition zone is characterized by significant environmental changes (e.g., west to east salinity gradient).

Recommendations: It is discussed whether introgressive hybridization of certain alleles/allele combinations is adaptive and whether weak reproductive isolation in combination with reduced post-zygotic incompatibility results in high admixture proportions.

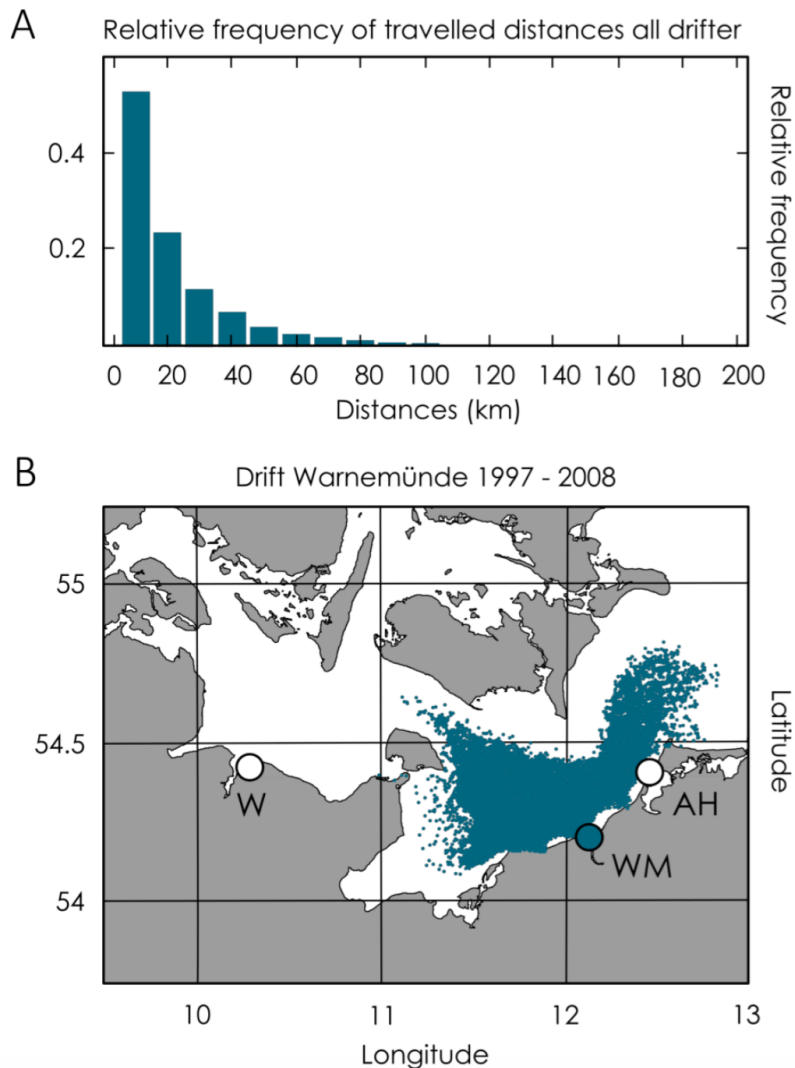


Figure 10. Results of Lagrangian particle tracking. A) Relative frequencies of drifters plotted over the distance travelled from their respective release point to the endpoint. The diagram shows that the majority of drifters move only 20 km or less indicating that that passive drift over long distance may not play a role for dispersal of *Mytilus* spp. in the Baltic area. B) Pictogram showing a qualitative analysis of drifter endpoints that were released at the locality Warnemünde. This example shows how an overall larvae drift patterns was derived based on qualitative analyses of drifter endpoint distributions of 72 localities around the Baltic (from Stuckas et al. in manus).

IV. Appendices

1. Page 1. Jonsson PR, Corell H, Nilsson Jacobi M. 2016. Mapping present connectivity and dispersal barriers in the whole Baltic Sea seascape. Report
2. Page 14. Jonsson PR, Corell H, Kotta J, Andersson H. 2016. Mapping future connectivity in the whole Baltic seascape. Report
3. Page 27. Hinrichsen HH, Lehman A, Petereit C, Nissling A, Ustups D, Bergström U, Hüsey K. 2016b. Spawning areas of eastern Baltic cod revisited: Using hydrodynamic modelling to reveal spawning habitat suitability, egg survival probability, and connectivity patterns. Progress in Oceanography 143: 13-25

4. Page 40. Hinrichsen HH, Petereit C, Nissling A, Wallin I, Ustups D, Florin AB. 2016c Survival and dispersal variability of pelagic eggs and yolk-sac larvae of central and eastern Baltic flounder (*Platichthys flesus*): application of biophysical models. In press. doi:10.1093/icesjms/fsw163
5. Page 55. Hüsey K, Hinrichsen HH, Eero M, Mosegaard H, Hemmer-Hansen J, Lehman A, Lundgaard LS. 2016. Spatio-temporal trends in stock mixing of eastern and western Baltic cod in the Arkona Basin and the implications for recruitment. ICES Journal of Marine Science 73: 293-303
6. Page 66. Huwer B, Hinrichsen HH, Hüsey K, Eero M. 2016. Connectivity of larval cod in the transition area between North Sea and Baltic Sea and potential implications for fisheries management. ICES Journal of Marine Science 73: 1815-1824
7. Page 76. Kotterba P, Moll D, von Nordheim L, Hammer C, Peck MA, Oesterwind D, Polte P. Predator impacts on inshore Baltic herring (*Clupea harengus*) larvae: Lions, tigers and bears – but where? Poster
8. Page 77. Oesterwind D, Kotterba P. Migration of spring spawning herring in the Western Baltic Sea: Acoustic report.
9. Page 85. Stuckas HS, Knöbel LK, Schade H, Breusing CB, Hinrichsen HH, Bartel MB, Langguth KL, Melzner FM. In press. Combining hydrodynamic modelling with genetics: Can passive larval drift shape the genetic structure of Baltic *Mytilus* populations? Molecular Ecology
10. Page 129. Oesterwind D, Polte P. 2014. Hydroacoustic survey for the assessment of small pelagics in the Baltic Sea. Cruise report 279, Thünen Institute of Baltic Sea Fisheries
11. Page 134. Oesterwind D. 2014. Hydroacoustic survey for the assessment of small pelagics in the Baltic Sea. Cruise report 280, Thünen Institute of Baltic Sea Fisheries
12. Page 138. Oesterwind D. 2014. Hydroacoustic survey for the assessment of small pelagics in the Baltic Sea. Cruise report 286, Thünen Institute of Baltic Sea Fisheries
13. Page 140. Oesterwind D. 2015. Hydroacoustic survey for the assessment of small pelagics in the Baltic Sea. Cruise report 699, Thünen Institute of Baltic Sea Fisheries
14. Page 149. Oesterwind D. 2015. Hydroacoustic survey for the assessment of small pelagics in the Baltic Sea. Cruise report 290, Thünen Institute of Baltic Sea Fisheries
15. Page 156. Oesterwind D. 2015. Hydroacoustic survey for the assessment of small pelagics in the Baltic Sea. Cruise report 715, Thünen Institute of Baltic Sea Fisheries

Contributions still under embargo until published

1. Hinrichsen, HH, von Dewitz B, Dierking J. Variability of advective transport-based connectivity in the Baltic Sea (in manus). Under embargo until it has been published. If you are interested in the results or data, please contact the corresponding author: Hans-Harald Hinrichsen, hhinrichsen@geomar.de.
2. Middelboe AL, Potthoff M, Closter RM, Møhlenberg F, Jonsson PR. Fine-resolution modelling of connectivity between *Mytilus* populations in the Gulf of Riga area, Baltic Sea (report). Under embargo until it has been published. If you are interested in the results or data, please contact the corresponding author: Anne-Lise Middelboe, AMI@dhigroup.com.
3. Hinrichsen HH, von Dewitz B, Lehman A, Bergström U, Hüsey K. Spatio-temporal dynamics of juvenile cod's nursery areas in the Baltic Sea (in manus). Under embargo

until it has been published. If you are interested in the results or data, please contact the corresponding author: Hans-Harald Hinrichsen, hhinrichsen@geomar.de.

4. Kotterba, P., Moll, D., von Nordheim, L., Peck, M. A., Oesterwind, D., and Polte, P.: Predation on larval herring (*Clupea harengus*) in inshore waters of the Baltic Sea. *Estuarine and Coastal Shelf Science* (submitted). Under embargo until it has been published. If you are interested in the results or data, please contact the corresponding author: Paul Kotterba, paul.kotterba@thuenen.de.
5. Kotterba P, Paulsen M, Hammer C, Polte P. A wolf in sheep's clothing – Planktivorous herring as an intense predator of estuarine fish prey (in manus). Under embargo until it has been published. If you are interested in the results or data, please contact the corresponding author: Paul Kotterba, paul.kotterba@thuenen.de.
6. Jaspers C, Friis Møller L, Huwer B, Hinrichsen HH. *Mnemiopsis leidyi* in the Baltic Sea region: Reproduction, seasonality and potential seed areas (report). Under embargo until it has been published. If you are interested in the results or data, please contact the corresponding author: Cornelia Jaspers, coja@aqua.dtu.dk.

Mapping present connectivity and dispersal barriers in the whole Baltic Sea seascape

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Introduction

About 70% of marine invertebrates (Thorson 1950) and many demersal fish disperse during early life as small planktonic larvae. Most sedentary marine macroorganisms therefore form partially open local populations (e.g. Kritzer and Sale 2004) connected in metapopulations through dispersal by planktonic spores and larvae (Hanski 1999). Dispersal here includes organism movements that may affect either demography or gene flow. Dispersal and connectivity are today recognized as key factors for local population dynamics (Cowen et al. 2006) and population persistence (Hastings and Botsford 2006). Dispersal between subpopulations determines their connectivity where immigration may lead to new colonization, density-dependent competition, and gene flow if immigrants are reproductively successful. On ecological time scales dispersal reduces the risk of local extinctions and on evolutionary time scales the realized gene flow affects genetic diversity and evolution of local adaptations (Sanford and Kelly 2011). Understanding dispersal and the source-sink dynamics of metapopulations are considered critical for conservation and restoration of marine populations (Botsford et al. 2009), and an important conservation criterion when selecting Marine protected areas (MPAs; Almany et al. 2009).

Dispersal begins with the spawning of gametes or release of larvae, often at some restricted time of the year. Fertilized eggs and larvae are then transported with the ocean circulation for some time known as the pelagic larval duration (PLD) until settlement. The PLD is not fixed but may depend on temperature (O'Connor et al. 2007) and food availability for feeding larvae (Giménez 2010). Settlement of the mature (competent) larvae may also be delayed if suitable habitats are not found (Pechenik 1990). The mortality of larvae is likely high, although still poorly known, and most larvae probably do not survive dispersal transport or the settlement in a suitable site (Rumrill 1990, Hinrichsen et al. 2016), reducing realized connectivity.

It was long assumed that the transport of marine larvae was a product of PLD and typical ocean current speeds resulting in long-distance dispersal, potentially for hundreds of kilometers. However, research the past two decades using new methods, e.g. genetic markers (Hellberg 2009), has substantially diversified this view with reports of high local recruitment (Jones et al. 2009). These recent findings suggest that the mechanisms determining dispersal in the seascape are still poorly understood and this remains a major challenge in ocean ecology.

The present study uses bio-physical modelling to estimate dispersal and connectivity in the seascape of the Baltic Sea. Bio-physical models combine a hydrodynamic model of the ocean circulation with Lagrangian particle tracking simulations where biological traits like spawning time, PLD, and vertical behavior can be implemented (Cowen and Sponaugle 2009, Corell et al. 2012). Our aim was to model dispersal within the whole HELCOM area simulating a range of generic dispersal strategies representing a range of Baltic Sea organisms. From a large number of dispersal trajectories we constructed connectivity matrices specifying dispersal probabilities between all areas between 0-100 m depth. Based on the connectivity matrices we employed a new method to identify partial dispersal barriers in the Baltic seascape that may indicate separate management or evolutionary significant units (Palsbøll et al. 2007).

Methods

Bio-physical model

The dispersal of organisms (eggs, spores, larvae or rafting algae) was modelled with a Lagrangian particle-tracking model driven off-line with flow fields from an ocean circulation model. The off-line working mode enables calculations of a very large number of trajectories. The stored ocean transport data were produced with the BaltiX model (Hordoir, 2013, Moksnes et al. 2014a), a regional configuration of the NEMO ocean engine (Madec 2010) covering the Baltic Sea, the Kattegat, the Skagerrak, and most of the North Sea. It has a horizontal spatial resolution of 2 nautical miles (3.7 km), and 84 levels in the vertical, ranging from 3 m at the surface and 23 m in the deepest parts. The model has open boundaries between Cornwall and Brittany, and between Hebride Islands and Norway. Here tidal harmonics defines the sea surface height (SSH) and velocities, and Levitus climatology defines temperature and salinity (Levitus and Boyer 1994). The grid cells closest to the bottom are fractioned to allow a high-resolution bathymetry. The model has a free surface, and the atmospheric forcing is a dynamic downscaling of the ERA40 data set. Runoff is based on climatological data based on a number of different databases for the Baltic Sea and the North Sea. Validation of the BaltiX shows that the model is able to correctly represent the SSH, both tidally induced and wind driven. The correlation between the model and hourly SSH measurements reach almost 80%. The outflow of Baltic Sea fresh water is predicted with an acceptable accuracy but the variability is somewhat low compared to sampled freshwater outflow (Hordoir et. al 2013). The Lagrangian trajectory model TRACMASS (De Vries and Döös 2001) is a particle-tracking model that calculates transport of water or particles using stored flow field data, and can determine trajectories both forwards and backwards in time between any sections or regions in the ocean. The velocity, temperature and salinity are updated with a regular interval for all grid boxes in the model domain, in this study every three hours, and the trajectory calculations were done with a 15-min time step. To simulate the dispersal of different strategies the vertical position of the trajectories was locked at predetermined depths. If the actual depth of the ocean basin was less than the determined depth the trajectories resided as deep as possible.

Simulations of dispersal were carried out for 4 different dispersal strategies (Table 1), which represent some of the key species in the Baltic Sea: *Fucus* spp., *Idotea* spp., *Mytilus* spp., and the flounder (*Platichthys flesus*). However, the dispersal traits of many Baltic organisms can be approximately represented by these four strategies. A large number of sources covering the Baltic Sea was used where the only habitat restriction was determined by depth intervals (Table 1), because of the general lack of habitat information on the scale of the Baltic Sea (combination of modelled dispersal and more detailed habitat predictions for a few selected taxa is found in work package 3.4). Particles were released from the 28442 model grid cells within the HELCOM area that had a mean depth above 100 m. From each grid cell 49 particles were released (a 7x7 array) each month and for 4 depth intervals (0-2 m, 10-12 m, 24-26 m, 48-50 m), which was repeated for 8 years (1995-2002). Particle positions were

recorded after 5, 10, 20, 30 and 60 days. In total 2.68 billion particle positions were produced.

Data analysis

Dispersal distance and direction

Potential connectivity (Watson et al. 2010), from the 28442 model grid cells, was calculated as the proportion of trajectories starting in grid cell j and ending in grid cell i , and then summarized in 28442 x 28442 connectivity matrices. We further constructed habitat vectors specifying the subsets of the model domain that satisfied the depth intervals 0-10, 0-30, and 30-100 m. By multiplication of the connectivity matrices with the habitat vectors dispersal probabilities could be evaluated for specific habitats.

Based on the connectivity matrices we calculated the mean dispersal distance and direction for each of the 28442 model grid cells, visualized as color-coded maps. The connectivity between 15 sub-basins (defined in HELCOM) in the Baltic Sea was also calculated (Fig. 1).

Source strength

Maps of source strength were produced by summing all columns in the connectivity matrix and plotting the area-specific source strength in color-coded maps. The source strength indicates the proportion of propagules released in grid cell i that settles within the specified habitat, as a proxy for recruitment.

Identification of dispersal barriers

We employed the method by Nilsson Jacobi et al. (2012) to identify partial dispersal barriers from the constructed connectivity matrices. This theoretical framework finds clusters as a signature of partially isolated subpopulations. Identification of subpopulations is formulated as a minimization problem with a tuneable penalty term that makes it possible to generate population subdivisions with varying degree of dispersal restrictions. Areas that has an internal connectivity above the dispersal restriction are color-coded, and the transition of colors thus indicate partial dispersal barriers.

Results

Connectivity with the HELCOM area

Figure 2 shows the geographic differences in dispersal distance for four dispersal strategies and habitat restrictions. The four dispersal strategies are modeled after *Fucus* spp., *Idotea* spp., *Mytilus* spp., and the flounder (*Platichthys flesus*), but also fit a wide range of Baltic Sea organisms. Dispersal directions, aggregated into intervals of the four cardinal directions, are shown in Fig. 3 for the four dispersal strategies. In Table 1 is shown an aggregated connectivity matrix for the 15 sub-basins in the HELCOM area. The average connectivity

should be read as the probability to disperse from a sub-basin in column j to a sub-basin in row i .

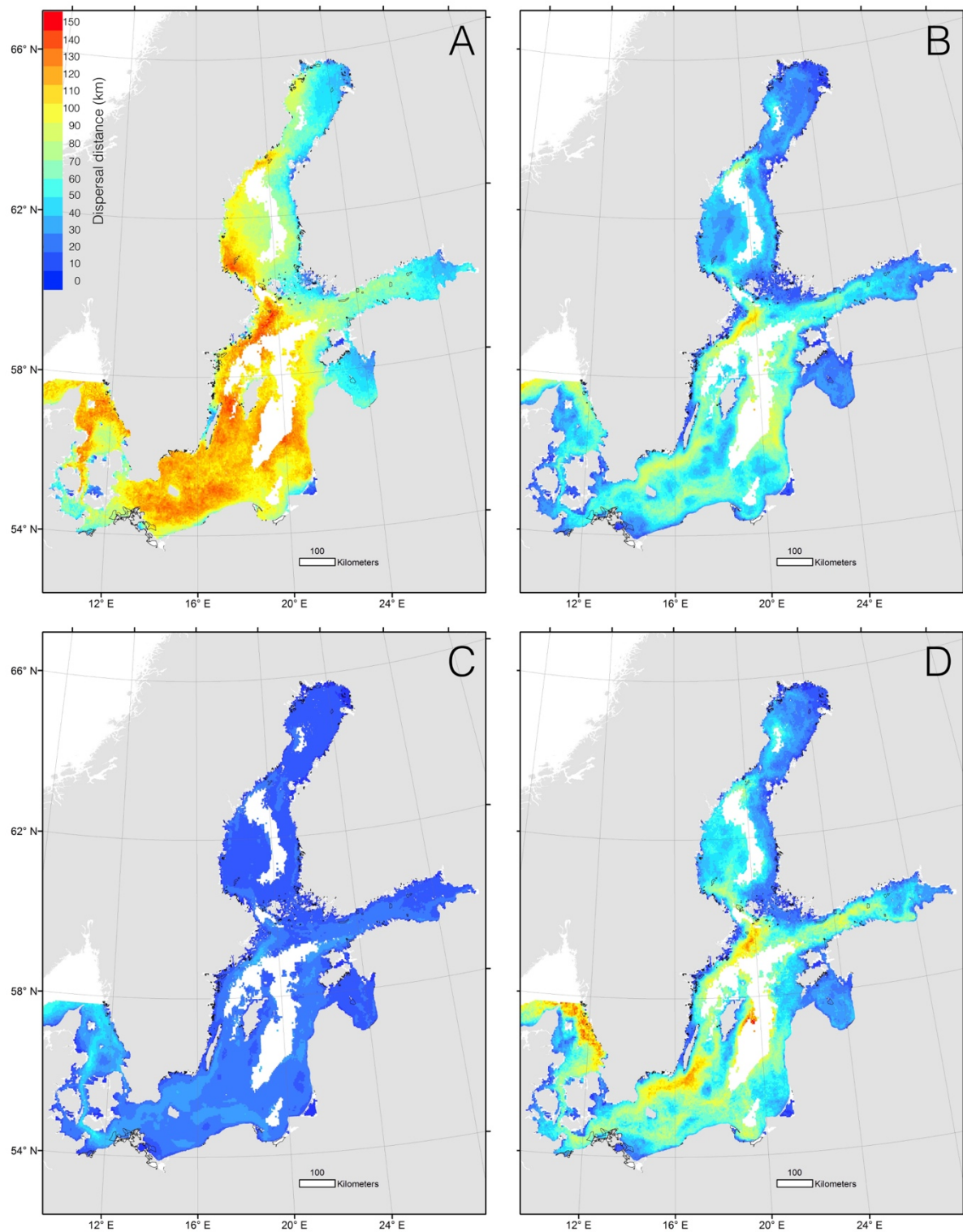


Figure 1. Modelled area-specific dispersal distance for four generic dispersal strategies. **(A)** Spawning time: 25% for each of the months May to August, Pelagic larval duration (PLD): 60 days, Drift depth: 0-2 m. **(B)** Spawning time: 25% June and 75% July, PLD: 30 days, Drift depth: 25% at 0-2 m, 50% at 10-12 m, 25% at 24-26 m. **(C)** Spawning time: 16% for each month between April and September, PLD: 5 days, Drift depth: 100% at 0-2 m.

(D) Spawning time: 50% April and 50% May, PLD: 50% 30 days and 50% 60 days, Drift depth: 25% at 0-2 m and 75% 10-12 m. The white areas indicate where depth is greater than 100 m.

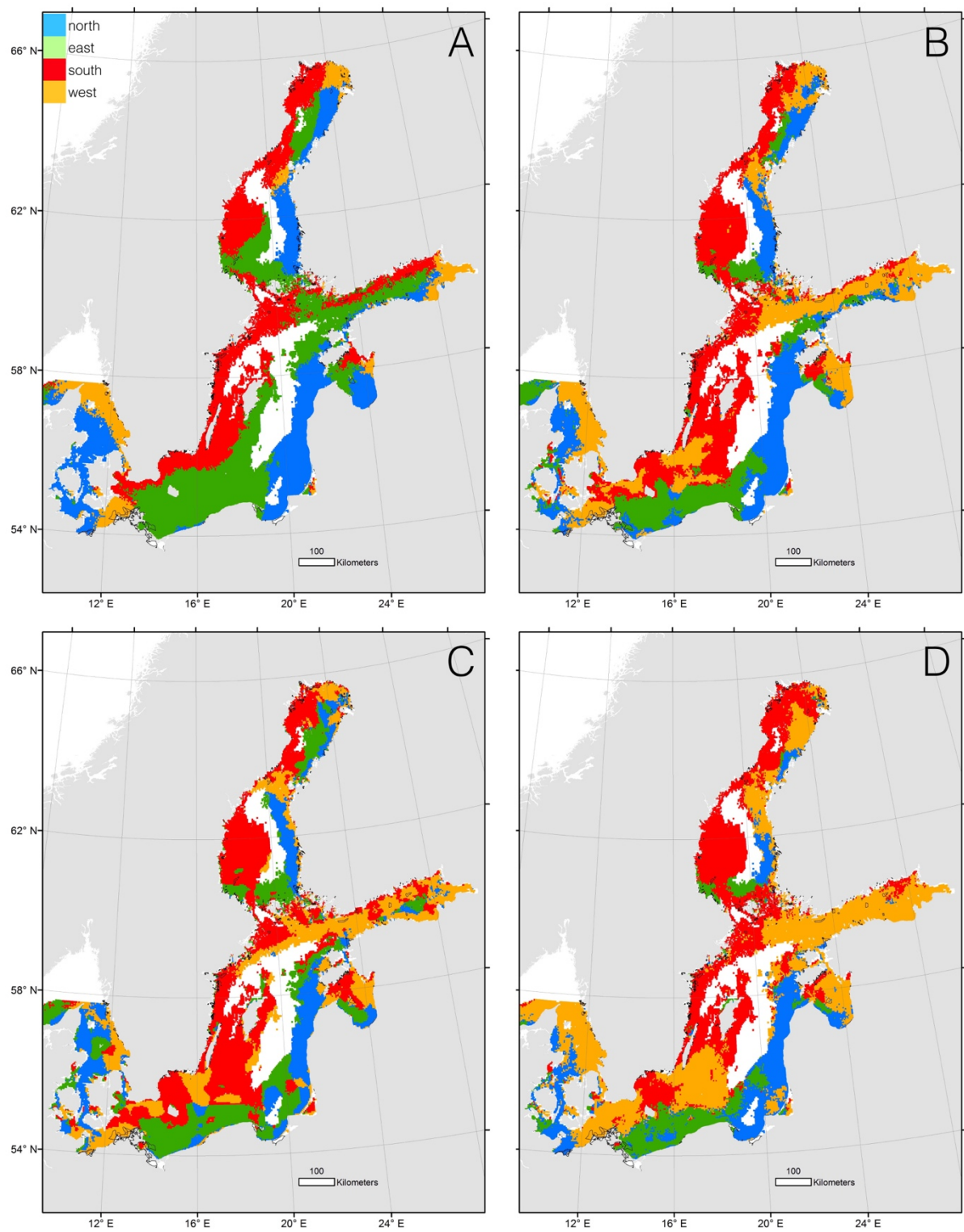


Figure 2. Modelled area-specific dispersal direction for the four generic dispersal strategies described in the legend of Fig. 1. Dispersal directions are aggregated into intervals of the cardinal directions.

Table 1. Aggregated modelled connectivity between 15 Baltic Sea sub-basins. The measures are the probability for a released propagule to disperse from column j to row i . Data are shown for the four dispersal strategies (A-D) described in the legend of Fig. 1. The HELCOM definition of sub-basins is used where some basins have been aggregated: Kattegat, the Belt Sea, the Öresund straight, the Kiel and Mecklenburger Bay, the South Baltic Sea and Gdansk Bay, East Gotland, West Gotland, the Gulf of Riga, the North Baltic, the Gulf of Finland, the Åland Sea, the Archipelago Sea, the Bothnian Sea, the Quark, the Bothnian Bay.

A	Kiel & S Baltic & Archipelago														
	Kattegat	The Belts	Öresund	Mecklenburg	Gdansk	E Gotland	W Gotland	Gulf of Riga	N Baltic	Gulf of Finland	Åland Sea	Sea	Bothnian Sea	Quark	Bothnian Bay
Kattegat	2.82E-02	3.38E-02	4.59E-02	2.70E-03	2.00E-04	0	0	0	0	0	0	0	0	0	0
The Belts	7.00E-04	1.76E-01	6.90E-03	4.33E-02	2.00E-03	0	0	0	0	0	0	0	0	0	0
Öresund	1.10E-03	2.00E-03	4.42E-02	4.00E-04	4.00E-04	0	0	0	0	0	0	0	0	0	0
Kiel & Mecklenburg	0	6.50E-03	1.48E-02	9.64E-02	2.50E-03	0	0	0	0	0	0	0	0	0	0
S Baltic & Gdansk	0	5.00E-04	1.97E-02	4.40E-03	2.80E-02	0	4.40E-03	0	0	0	0	0	0	0	0
E Gotland	0	0	0	0	1.20E-03	1.04E-02	1.80E-03	7.00E-03	2.20E-03	0	3.00E-04	0	0	0	0
W Gotland	0	0	0	0	1.00E-04	1.90E-03	3.84E-02	0	8.60E-03	0	2.30E-03	1.00E-04	1.00E-04	0	0
Gulf of Riga	0	0	0	0	1.00E-04	6.10E-03	0	1.04E-01	5.80E-03	1.20E-03	1.00E-04	2.60E-03	0	0	0
N Baltic	0	0	0	0	0	6.60E-03	1.00E-04	4.50E-03	2.49E-02	8.00E-04	1.73E-02	5.80E-03	1.80E-03	0	0
Gulf of Finland	0	0	0	0	0	9.00E-04	0	1.47E-02	7.40E-03	9.26E-02	2.00E-04	6.70E-03	0	0	0
Åland Sea	0	0	0	0	0	0	0	0	1.00E-04	0	1.76E-02	4.40E-03	2.90E-03	0	0
Archipelago Sea	0	0	0	0	0	0	0	7.00E-04	2.60E-03	4.50E-03	2.24E-02	2.06E-01	2.70E-03	0	0
Bothnian Sea	0	0	0	0	0	0	0	1.00E-04	0	1.10E-03	3.26E-02	2.74E-02	3.10E-02	7.00E-04	0
Quark	0	0	0	0	0	0	0	0	0	0	0	0	2.30E-03	7.48E-02	3.60E-03
Bothnian Bay	0	0	0	0	0	0	0	0	0	0	0	0	2.00E-04	4.37E-02	6.99E-02

B

B	Kiel & S Baltic & Archipelago														
	Kattegat	The Belts	Öresund	Mecklenburg	Gdansk	E Gotland	W Gotland	Gulf of Riga	N Baltic	Gulf of Finland	Åland Sea	Sea	Bothnian Sea	Quark	Bothnian Bay
Kattegat	4.54E-01	5.49E-02	7.31E-02	3.70E-03	1.00E-04	0	0	0	0	0	0	0	0	0	0
The Belts	4.54E-02	6.15E-01	1.47E-02	1.05E-01	2.90E-03	0	0	0	0	0	0	0	0	0	0
Öresund	8.40E-03	1.50E-03	5.57E-01	0	3.10E-03	0	0	0	0	0	0	0	0	0	0
Kiel & Mecklenburg	6.00E-04	5.83E-02	7.10E-03	6.51E-01	1.27E-02	0	0	0	0	0	0	0	0	0	0
S Baltic & Gdansk	0	7.20E-03	1.10E-01	5.18E-02	1.96E-01	2.80E-03	1.70E-02	0	0	0	0	0	0	0	0
E Gotland	0	0	0	0	5.40E-03	1.52E-01	1.70E-03	1.24E-02	9.00E-04	0	0	0	0	0	0
W Gotland	0	0	0	0	1.00E-03	6.30E-03	1.47E-01	0	7.10E-03	0	1.90E-03	0	0	0	0
Gulf of Riga	0	0	0	0	0	1.24E-02	0	5.18E-01	5.90E-03	5.00E-04	0	1.00E-04	0	0	0
N Baltic	0	0	0	0	0	1.16E-02	8.00E-04	6.90E-03	1.23E-01	5.20E-03	3.84E-02	2.19E-02	1.60E-03	0	0
Gulf of Finland	0	0	0	0	0	0	0	4.90E-03	2.90E-03	2.75E-01	0	1.10E-03	0	0	0
Åland Sea	0	0	0	0	0	0	0	0	9.00E-04	0	5.90E-02	9.80E-03	2.10E-03	0	0
Archipelago Sea	0	0	0	0	0	0	0	2.00E-04	1.02E-02	3.10E-03	2.16E-02	5.39E-01	4.10E-03	0	0
Bothnian Sea	0	0	0	0	0	0	0	0	0	0	9.30E-03	3.30E-02	1.14E-01	5.78E-02	2.00E-04
Quark	0	0	0	0	0	0	0	0	0	0	0	0	4.00E-03	4.34E-01	7.40E-03
Bothnian Bay	0	0	0	0	0	0	0	0	0	0	0	0	1.00E-04	3.74E-02	3.20E-01

C

C	Kiel & S Baltic & Archipelago														
	Kattegat	The Belts	Öresund	Mecklenburg	Gdansk	E Gotland	W Gotland	Gulf of Riga	N Baltic	Gulf of Finland	Åland Sea	Sea	Bothnian Sea	Quark	Bothnian Bay
Kattegat	4.96E-01	9.22E-02	9.64E-02	0	0	0	0	0	0	0	0	0	0	0	0
The Belts	8.70E-03	6.59E-01	3.00E-04	9.61E-02	5.00E-04	0	0	0	0	0	0	0	0	0	0
Öresund	1.09E-02	2.00E-04	5.88E-01	0	3.20E-03	0	0	0	0	0	0	0	0	0	0
Kiel & Mecklenburg	0	2.72E-02	0	6.97E-01	1.03E-02	0	0	0	0	0	0	0	0	0	0
S Baltic & Gdansk	0	0	1.04E-01	3.13E-02	2.21E-01	1.60E-03	6.70E-03	0	0	0	0	0	0	0	0
E Gotland	0	0	0	0	3.30E-03	1.89E-01	2.40E-03	1.86E-02	1.10E-03	0	0	0	0	0	0
W Gotland	0	0	0	0	1.00E-03	3.20E-03	1.62E-01	0	3.30E-03	0	0	0	0	0	0
Gulf of Riga	0	0	0	0	0	7.10E-03	0	5.33E-01	7.70E-03	5.00E-04	0	0	0	0	0
N Baltic	0	0	0	0	0	8.00E-03	9.00E-04	5.90E-03	1.42E-01	1.00E-03	2.34E-02	2.80E-02	0	0	0
Gulf of Finland	0	0	0	0	0	0	0	4.90E-03	1.30E-03	2.98E-01	0	1.80E-03	0	0	0
Åland Sea	0	0	0	0	0	0	0	0	6.00E-04	0	9.65E-02	1.07E-02	2.00E-03	0	0
Archipelago Sea	0	0	0	0	0	0	0	0	9.30E-03	2.40E-03	2.24E-02	6.43E-01	5.10E-03	0	0
Bothnian Sea	0	0	0	0	0	0	0	0	0	0	8.40E-03	2.43E-02	1.26E-01	6.63E-02	0
Quark	0	0	0	0	0	0	0	0	0	0	0	0	3.50E-03	5.06E-01	3.70E-03
Bothnian Bay	0	0	0	0	0	0	0	0	0	0	0	0	0	2.48E-02	3.60E-01

D

D	Kiel & S Baltic & Archipelago														
	Kattegat	The Belts	Öresund	Mecklenburg	Gdansk	E Gotland	W Gotland	Gulf of Riga	N Baltic	Gulf of Finland	Åland Sea	Archipelago Sea	Bothnian Sea	Quark	Bothnian Bay
Kattegat	3.68E-01	7.87E-02	8.04E-02	1.27E-02	6.00E-04	0	0	0	0	0	0	0	0	0	0
The Belts	2.96E-02	4.98E-01	1.48E-02	1.74E-01	6.60E-03	0	0	0	0	0	0	0	0	0	0
Öresund	4.90E-03	2.30E-03	5.63E-01	3.00E-04	6.90E-03	0	0	0	0	0	0	0	0	0	0
Kiel & Mecklenburg	1.30E-03	4.23E-02	4.00E-03	5.11E-01	1.66E-02	0	0	0	0	0	0	0	0	0	0
S Baltic & Gdansk	1.00E-04	4.90E-03	7.05E-02	3.86E-02	1.81E-01	2.00E-03	2.05E-02	0	0	0	0	0	0	0	0
E Gotland	0	0	0	0	5.20E-03	1.40E-01	2.00E-03	1.64E-02	9.00E-04	0	2.00E-04	0	0	0	0
W Gotland	0	0	0	0	8.00E-04	5.60E-03	1.49E-01	0	8.20E-03	0	2.70E-03	3.00E-04	0	0	0
Gulf of Riga	0	0	0	0	1.00E-04	1.59E-02	0	5.05E-01	4.50E-03	8.00E-04	0	5.00E-04	0	0	0
N Baltic	0	0	0	0	0	1.45E-02	9.00E-04	9.90E-03	1.23E-01	8.60E-03	5.59E-02	3.54E-02	2.80E-03	0	0
Gulf of Finland	0	0	0	0	0	0	0	3.10E-03	1.10E-03	2.47E-01	0	1.10E-03	0	0	0
Åland Sea	0	0	0	0	0	0	0	0	8.00E-04	0	5.16E-02	1.15E-02	4.60E-03	0	0
Archipelago Sea	0	0	0	0	0	0	0	4.00E-04	9.70E-03	3.40E-03	9.50E-03	5.23E-01	6.00E-03	0	0
Bothnian Sea	0	0	0	0	0	0	0	0	0	0	5.00E-04	1.91E-02	9.63E-02	9.14E-02	5.00E-04
Quark	0	0	0	0	0	0	0	0	0	0	0	0	1.10E-03	4.08E-01	1.16E-02
Bothnian Bay	0	0	0	0	0	0	0	0	0	0	0	0	0	2.27E-02	3.05E-01

Source strength

The maps in Fig. 4 shows the geographic distribution of source strength. Stronger sources contribute more successful dispersal trajectories as the end within the specified habitat (defined as a depth interval).

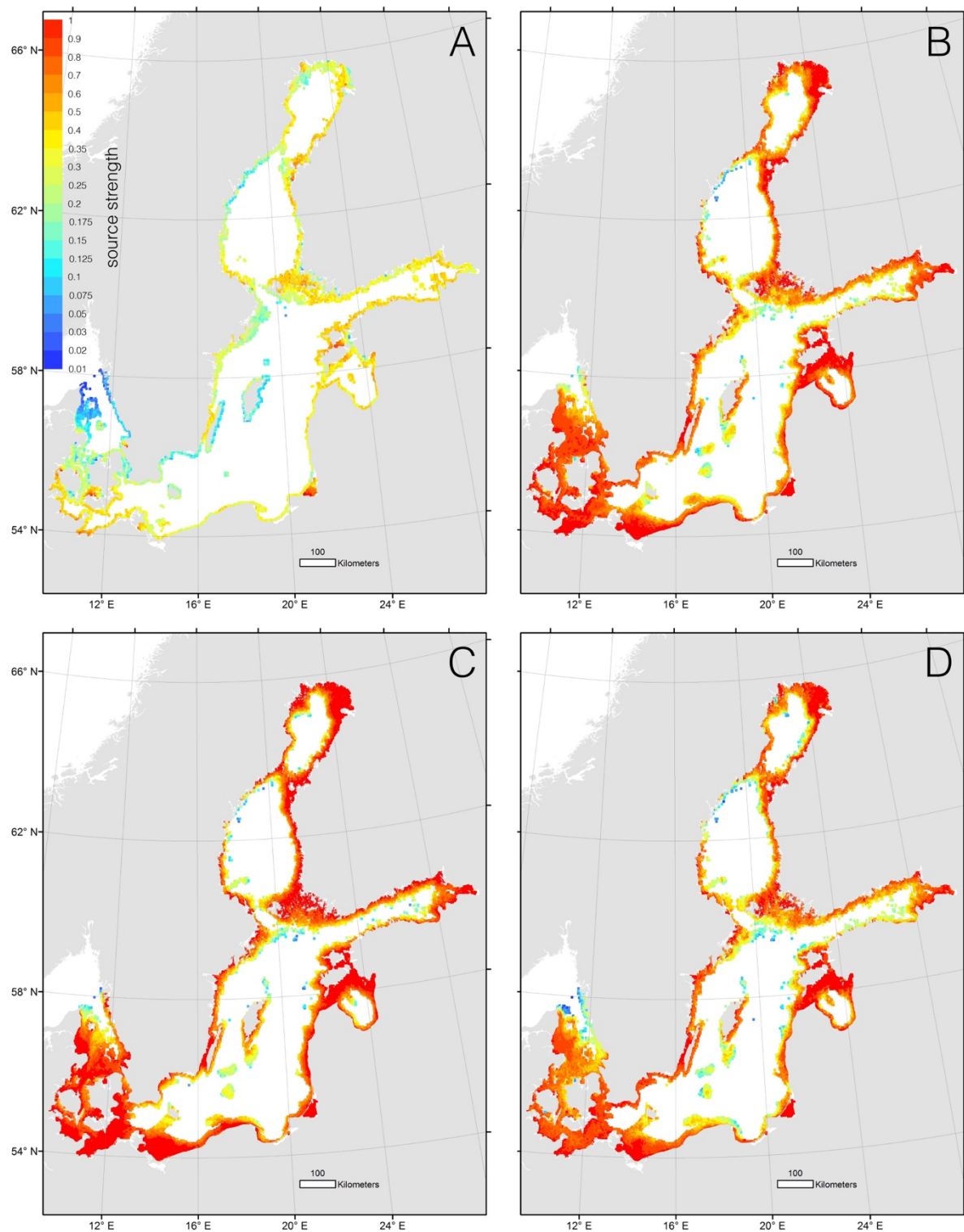


Figure 4. Source strength for the four dispersal strategies (A-D) described in the legend to Fig. 1. High source strength for a given area indicates that there is high probability that release from that area disperse to other areas within the defined habitat. The habitat is defined as a depth interval: (A) 0-10 m, (B-D) 0-30 m.

Identification of dispersal barriers

Based on the connectivity matrices and habitat restrictions of the four modelled dispersal strategies we identified clusters of areas that have high internal connectivity. Figures 5-8

show color-coded maps where color transitions indicate partial dispersal barriers. Each figure shows three examples where the level of the dispersal restriction was varied to produce an increasing number of clusters as the allowed dispersal was increased.

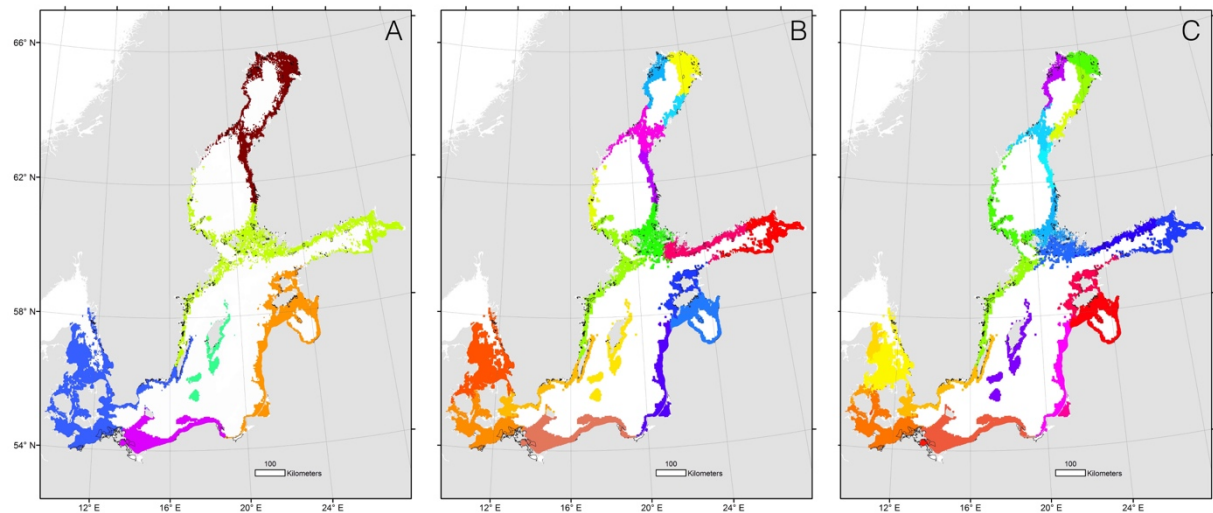


Figure 5. Identification of dispersal barriers for the dispersal strategy A in Fig. 2 and a habitat specified by the depth interval 0-10 m. (A) Low allowed dispersal between areas producing 6 clusters. (B) Medium allowed dispersal between areas producing 20 clusters. (C) High allowed dispersal between areas producing 28 clusters.

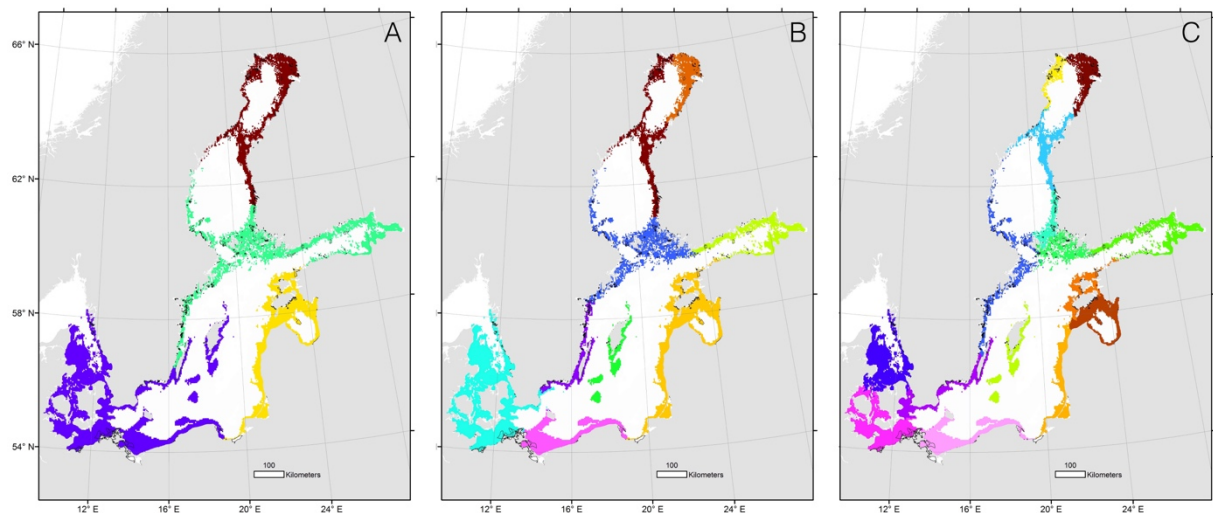


Figure 6. Identification of dispersal barriers for the dispersal strategy B in Fig. 2 and a habitat specified by the depth interval 0-30 m. (A) Low allowed dispersal between areas producing 4 clusters. (B) Medium allowed dispersal between areas producing 9 clusters. (C) High allowed dispersal between areas producing 15 clusters.

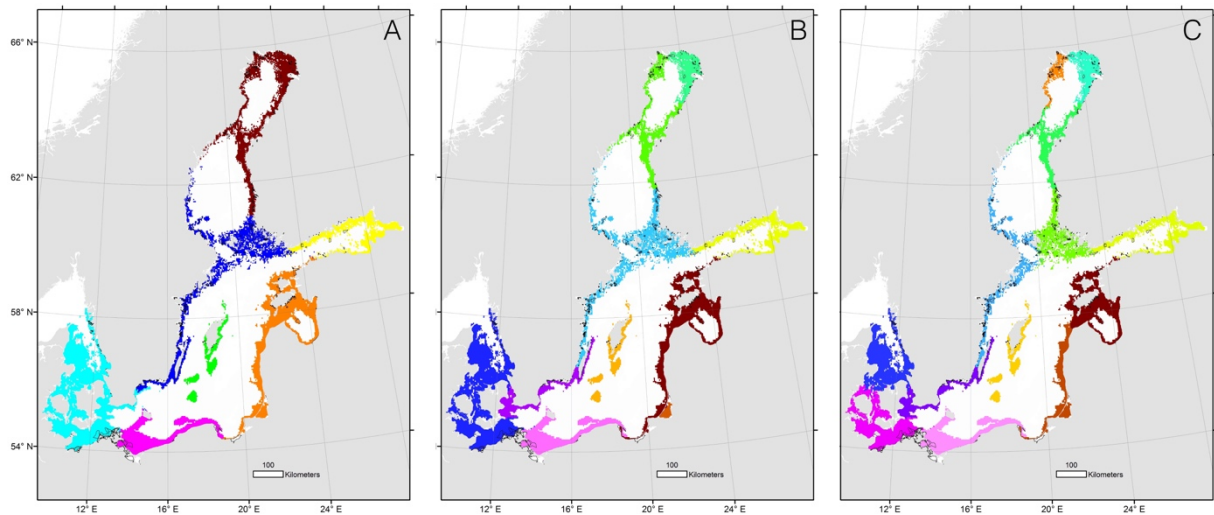


Figure 7. Identification of dispersal barriers for the dispersal strategy C in Fig. 2 and a habitat specified by the depth interval 0-30 m. (A) Low allowed dispersal between areas producing 7 clusters. (B) Medium allowed dispersal between areas producing 10 clusters. (C) High allowed dispersal between areas producing 13 clusters.

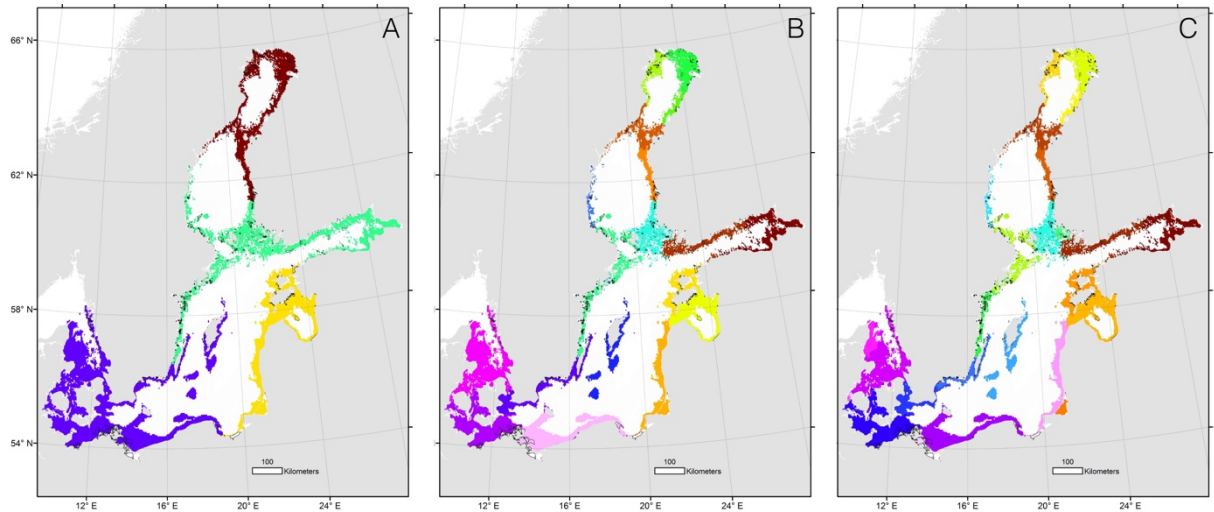


Figure 8. Identification of dispersal barriers for the dispersal strategy D in Fig. 2 and a habitat specified by the depth interval 0-30 m. (A) Low allowed dispersal between areas producing 4 clusters. (B) Medium allowed dispersal between areas producing 20 clusters. (C) High allowed dispersal between areas producing 29 clusters.

Discussion

Modelled dispersal distance shows great differences depending on geographic area. Mean dispersal distances are generally lower in the northern part especially along the Finnish coast. As expected dispersal distances are lower close to the coast compared to off-shore waters especially for deeper drift depths. An exception is the rapid dispersal along the eastern coast of Kattegat where dispersal is fast above the pycnocline because of the Baltic surface current. Dispersal distance is also very dependent on dispersal trait combinations represented by the four strategies. Pelagic larval duration has a strong effect as shown in Fig. 1A, but also the drift depth may be important with shorter dispersal in deeper water, e.g. as

in Fig. 1B. Dispersal direction largely follows the circulation patterns within the sub-basins in the Baltic Sea, and is rather similar for the four dispersal strategies.

Most of the sub-basins show strong local retention, except for the long-distance dispersal strategy (strategy A with 60-days PLD). For strategy A there is particularly low local retention for the area east of Gotland, the north Baltic Sea and the Åland Sea. There is generally moderate connectivity between adjacent sub-basins. Kattegat connects poorly to the Baltic Sea and Bothnian Bay also has limited connectivity with other basins. When dispersal also occurs in deeper layers (strategies B and D) dispersal from Kattegat into the Baltic Sea increases. Note that in the model simulations the detection level of connectivity is partly dependent on the number of particles released which differ among the sub-basins based on size. The detection limit of the probability of dispersal between sub-basins was approximately $1 \cdot 10^{-6}$. In summary, there is no sub-basin that is totally isolated although most dispersal occurs within sub-basins, indicating that basin-scale is of the same magnitude as the tail of the dispersal distance distribution in most cases.

The maps of the source strength show that for most dispersal strategies most released propagules will recruit with the adult habitat, here defined in terms of depth intervals. This is clearly an overestimate since only a subset of each depth interval harbors suitable habitats, e.g. rocky reefs. In the case of the dispersal strategy with a 60-day PLD (strategy A in Fig. 4) there are areas that function poorly as sources, e.g. the Hanö Bay, the east coasts of Öland and Gotland, and the Swedish coast south of the Quark. The Swedish coast south of the Quark generally performed poorly as a source also for the other dispersal strategies.

It is difficult to visualize potential dispersal barriers with only mapped distances, directions or tables of connectivity. A new approach is to use a clustering method that groups well-connected areas in a way to minimize the total dispersal (leakage) among such groups, subjected to some penalty of aggregating groups (see Nilsson Jacobi et al. 2012). This cluster approach indicates that there are some partial dispersal barriers within the HELCOM area. The number of barriers depend on a user-defined critical threshold of allowed dispersal between clusters and may reflect if the relevant separation of sub-populations is viewed from a demographic perspective, e.g. stock management and resilience, or from an evolutionary perspective, e.g. differentiation and local adaptation. The barriers in Figs 5-8 indicate that there may be a few barriers with evolutionary significance (panels A in Figs. 5-8), and several management units relevant on ecological time scales (panels B-C in Figs 5-8). Interestingly, many barriers were similar for the four rather contrasting dispersal strategies indicating some generality. Examples of general barriers are between Kattegat/Belt Sea and the Baltic Sea, the Gdansk Bay, the Finnish Bothnian Bay coast, south of Öland, and the Swedish coast south of the Quark. Two recent reviews (Johannesson and André 2006, Wennerström et al. 2013) discuss the genetic structure and possible barriers to gene flow for several populations in the Baltic Sea and the bordering Kattegat/Skagerrak. It is interesting to note that the scale of population subdivision and in some cases even the inferred geographic location of barriers well corresponds to the clusters and dispersal barriers in Figs-5-8. These barriers may generally indicate the presence of unique local adaptations to different regions in the strong Baltic Sea environmental gradients. Barriers may also slow down recolonization and reduce resilience to regional disturbances, and barriers may impede range shifts as a response to future climate.

Acknowledgements

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References

- Almany GR, Connolly SR, Heath DD, Hogan JD, Jones GP, McCook LJ, Mills M, Pressey RL, Williamson DH (2009) Connectivity, biodiversity conservation and the design of marine reserve networks for coral reefs. *Coral Reefs* 28:339-351
- Botsford LW, White JW, Coffroth MA, Paris CB, Planes S, Shearer TL, Thorrold SR, Jones GP (2009) Connectivity and resilience of coral reef metapopulations in marine protected areas: matching empirical efforts to predictive needs. *Coral Reefs* 28:327-337
- Corell H, Moksnes PO, Engqvist A, Döös K, Jonsson PR (2012) Depth distribution of larvae critically affects their dispersal and the efficiency of marine protected areas. *Marine Ecology Progress Series* 467:29-46
- Cowen RK, Paris CB, Srinivasan A (2006) Scaling of connectivity in marine populations. *Science* 311:522-527
- Cowen RK, Sponaugle S (2009) Larval dispersal and marine connectivity. *Annual Review of Marine Science* 1:443-466
- De Vries P, Döös K (2001) Calculating Lagrangian trajectories using time-dependent velocity fields. *Journal of the Atmospheric Sciences* 18:1092-1101
- Giménez L (2010) Relationships between habitat conditions, larval traits, and juvenile performance in a marine invertebrate. *Ecology* 91:1401-1413
- Hanski I (1999) *Metapopulation Ecology*. Oxford University Press, New York
- Hastings A, Botsford LW (2006) Persistence of spatial populations depends on returning home. *Proceedings of the National Academy of Sciences* 103:6067-6072
- Hellberg ME (2009) Gene flow and isolation among populations of marine animals. *Annual Review of Ecology, Evolution, and Systematics* 40:291-310
- Hinrichsen HH, Lehman A, Petereit C, Nissling A, Ustups D, Bergström U, Hüsey K (2016) Spawning areas of eastern Baltic cod revisited: Using hydrodynamic modelling to reveal spawning habitat suitability, egg survival probability, and connectivity patterns. *Progress in Oceanography* 143:13-25
- Hordoir R, Dieterich C, Basu B, Dietze H, Meier HEM (2013) Freshwater outflow of the Baltic Sea and transport in the Norwegian current: A statistical correlation analysis based on a numerical experiment. *Continental Shelf Research* 64:1-9
- Johannesson K, André C (2006) Life on the margin: genetic isolation and diversity loss in a peripheral marine ecosystem, the Baltic Sea. *Molecular Ecology* 15:2013-2029
- Jones GP, Almany GR, Russ GR, Sale PF, Steneck RS, van Oppen MJH, Willis BL (2009) Larval retention and connectivity among populations of corals and reef fishes: history, advances and challenges. *Coral Reefs* 28:307-325
- Kritzer JP, Sale PF (2004) Metapopulation ecology in the sea: from Levins' model to marine ecology and fisheries science. *Fish and Fisheries* 5:131-140
- Levitus S, Boyer TP (1994) *World ocean atlas, vol 5, salinity*. NOAA atlas

- Madec G (2010) Nemo ocean engine, version 3.3, Tech. rep., IPSL. <<http://www.nemo-ocean.eu/>>
- Moksnes PO, Corell H, Tryman K, Hordoir R, Jonsson PR (2014a) Larval behavior and dispersal mechanisms in shore crab larvae (*Carcinus maenas*): Local adaptations to different tidal environments? *Limnology and Oceanography* 59:588-602
- Nilsson Jacobi M, André C, Döös K, Jonsson PR (2012) Identification of subpopulations from connectivity matrices. *Ecography* 35:1004-1016
- O'Connor MI, Bruno JF, Gaines SD, Halpern BS, Lester SE, Kinlan BP, Weiss JM (2007) Temperature control of larval dispersal and the implications for marine ecology, evolution, and conservation. *Proceedings of the National Academy of Sciences* 104:1266-1271
- Palsbøll PJ, Bérubé M, Allendorf FW (2007) Identification of management units using population genetic data. *Trends in Ecology and Evolution* 22:11-16
- Rumrill SS (1990) Natural mortality of marine invertebrate larvae. *Ophelia* 32:163-198
- Sanford E, Kelly MW (2011) Local adaptation in marine invertebrates. *Annual Review of Marine Science* 3:509-535
- Thorson G (1950) Reproduction and larval ecology of marine bottom invertebrates. *Biological Reviews of the Cambridge Philosophical Society* 25:1-45
- Watson JR, Mitarai S, Siegel DA, Caselle JE, Dong C, McWilliams JC (2010) Realized and potential larval connectivity in the Southern California Bight. *Marine Ecology Progress Series* 401:31-48
- Wennerström L, Laikre L, Ryman N, Utter FM, Ab Ghani NI, André C, DeFaveri J, Johansson D, Kautsky L, Merilä J, Mikhailova N, Pereyra R, Sandström A, Teacher AGF, Wenne R, Vasemägi A, Zbawicka M, Johannesson K, Primmer CR (2013) Genetic biodiversity in the Baltic Sea: species-specific patterns challenge management. *Biodiversity and Conservation* 22:3045-3065

Mapping future connectivity in the whole Baltic seascape

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Introduction

The increasing footprint of human civilisation is rapidly changing ecosystems world-wide, including long-term geological processes even suggesting the beginning of a new era – the Anthropocene (Crutzen 2002, Waters et al. 2016). Although humans have settled in coastal areas and harvested marine organisms for thousands of years it is only the past century that the rapid increase of exploitation of the oceans has begun to cause defaunation on a global scale (McCauley et al. 2015). Important pressures as climate change, eutrophication and industrial fishery combine to cause global habitat and biodiversity loss, as well as altering the functioning of marine ecosystems with their goods and services (Lubchenco et al. 2003, Worm et al. 2006). Today about 40% of the oceans is considered strongly impacted by multiple drivers and the Baltic Sea is considered as one of the most impacted coastal seas (Halpern et al. 2008).

One important consequence of global changes in the environment is that population connectivity may change with effects on metapopulation persistence, range shifts and spread of non-native, invasive species. Multiple factors may change marine connectivity. Patterns of ocean circulation may change caused by changes in temperature, salinity and the wind velocity field (Cowen and Sponaugle 2009). Deterioration of habitats, e.g. caused by land development and eutrophication, may further lead to increased habitat fragmentation reducing connectivity (Gerber et al. 2014). Biological traits affecting dispersal may also change, e.g. the phenology of spawning time (Parmesan 2006, Lett et al. 2010), and increasing temperature will accelerate larval development and reduce the pelagic duration (O'Connor et al. 2007, Munday et al. 2009). The net effect on future connectivity is very difficult to predict, and to our knowledge there is yet no explicit spatial modelling of future connectivity based on scenario simulations of ocean circulation. In this study we aimed at the first attempt to model the future connectivity in the HELCOM area.

We performed particle tracking simulations using projected ocean velocity fields from scenario models based on the emission scenarios A1b and A2 (IPCC 2007). The dispersal distance for a range of pelagic larval durations was estimated for reference and future scenarios to assess potential changes in connectivity. We also estimated effects of the predicted increase in surface water temperature on dispersal distance caused by the accelerated larval development.

Methods

Bio-physical model of future dispersal and connectivity

The dispersal of organisms (eggs, spores, larvae or rafting algae) was modelled with a Lagrangian particle-tracking model driven off-line with flow fields from an ocean circulation model. The stored ocean transport data were produced with the Rossby Centre Ocean model (RCO) (Meier et al. 2011, 2012). Briefly, RCO is a Bryan-Cox-Semtner primitive equation circulation model with a free surface and open boundary conditions in the northern Kattegat. For the simulations in the present study, RCO was used with a horizontal resolution of 3.7 km (2 NM) and with 83 vertical levels with layer thicknesses of 3 m. The modeled velocity fields in this study were produced with a dynamical downscaling approach using the regional climate model RCAO (Rossby Centre Atmosphere Ocean model, see Döscher et al. (2002)) with lateral boundary data from the GCM ECHAM5 (Roeckner et al.

2006). Simulations of ECHAM5 were forced with either the A1b or the A2 emission scenarios (ICCP 2007). Future projections with seasonal resolution refer to a period at the end of this century (2069–2098). As reference we used the mean fields from hindcast simulations of 1978–2007. In the particle tracking simulations only mean velocity fields representing summer (June, July and August) were used. We also used the predicted sea-surface temperature from the scenario models.

Particle tracking simulations were run with the Lagrangian trajectory model TRACMASS (De Vries and Döös 2001). In this study we only had access to a static velocity field representing the summer season averaged for 1978–2007, and two future scenario fields (A1b and A2). This implies that particle streamlines do not conserve mass and momentum since the velocity fields are not conservative (they contain sources and sinks of mass), which calls for great caution when interpreting the results for future dispersal distance and connectivity. TRACMASS interpolates the water velocity in space with a 15-min time step. The model domain contains 24722 grid cells and these were each seeded with 49 particles in a 7x7 array. All simulations were run in the surface layer (0–3 m) and positions were recorded for a Pelagic Larval Duration (PLD) of 5, 10, 20, 30 and 60 days. In total more than 18 million positions were included in the analysis.

Analysis of trajectory data

For each PLD and scenario a connectivity matrix (24722 x 24722) was constructed from the start and end positions of each particle trajectory. Based on the connectivity matrices we calculated the mean dispersal distance and direction for each of the 24722 model grid cells, visualized as color-coded maps. The connectivity between 15 sub-basins (defined in HELCOM) in the Baltic Sea was also calculated (Fig. 1) for reference and scenario simulations.



Figure. 1. Map of the Baltic Sea and the sub-basins according to HELCOM. Note that Kiel and Mecklenburger Bay, and South Baltic and Gdansk Bay were aggregated.

Effect of future temperature on Pelagic Larval Duration and dispersal

The sea-surface temperature in the Baltic sea is expected to increase strongly within this century (Fig. 5). A temperature increase will lead to accelerated larval development and a reduction in PLD (O'Connor et al. 2007), which likely decreases the dispersal distance (Gerber et al. 2014). To assess the net effect on dispersal distance caused by changes in circulation and in sea-surface temperature we formulated a simple model of larval development. O'Connor et al. (2007) reviewed larval metabolic responses to temperature for a range of taxa. We used a metabolic model for PLD as:

$$PLD = e^{3.17} (T/T_c)^{(-1.4-0.27 \cdot \ln(T/T_c))} \quad (\text{eq. 1})$$

where T is the sea-surface temperature and T_c is a reference temperature (here 15° C). Reference and future scenario (A1b and A2) fields of sea-surface temperature during summer was used to estimate the expected change in PLD according to eq. 1. We then plotted dispersal distance against PLD for the reference case where the best fit was ($R^2=0.99$, Fig. 2):

$$\text{dispersal distance} = 2.838 \cdot PLD^{0.863} \quad (\text{eq. 2})$$

The metabolic change in PLD could then be transformed to a change in dispersal distance according to eq. 2.

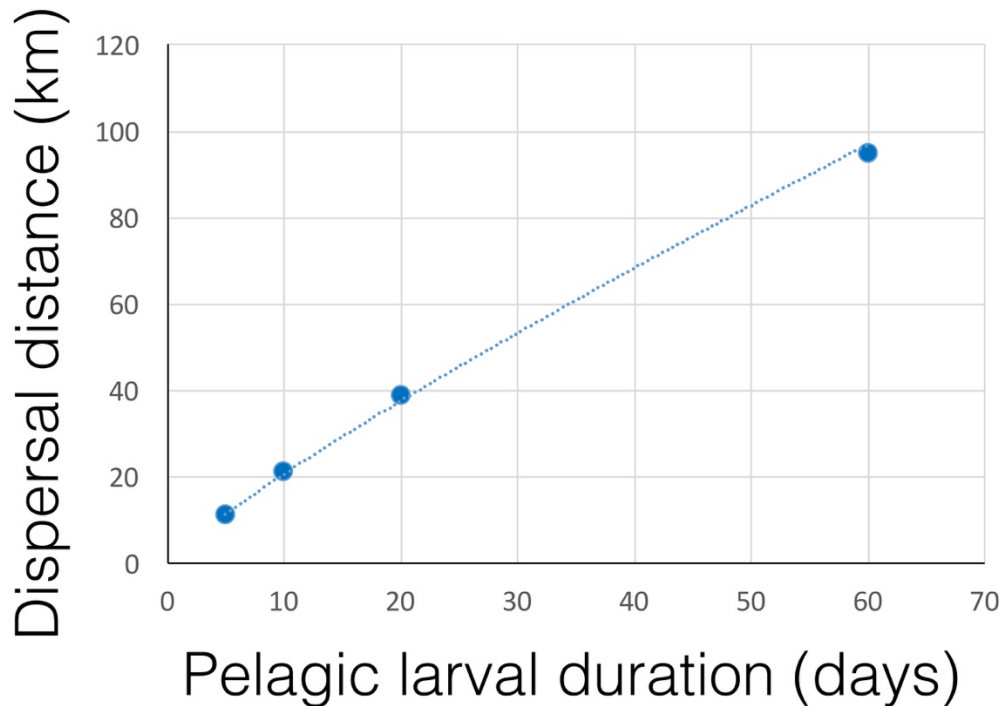


Figure 2. Relationship between pelagic larval duration and average dispersal distance for modelled dispersal based on the reference (1978-2007) velocity fields. The curve is a power fit ($R^2=0.99$) and the equation is given as eq. 1.

Model of future habitat distribution combined with connectivity

A preliminary study was performed where we used habitat prediction models from BIO-C3 task 3.4 in combination with modelled connectivity to assess the effect of habitat fragmentation/extension on metapopulation dynamics. Here we applied this approach for

the bivalve *Mytilus trossulus/edulis*. The species distribution model (SDM, boosted regression-tree) was based on abundance data along the Estonian coastal waters. The regional RCO climate model provided the environmental layers (see above) for the SDM for predictions of distribution change between reference (1978-2007) and with A1b climate scenario (2069-2098). With a simplistic metapopulation model we simulated population redistribution through larval dispersal using a connectivity matrix produced with the Lagrangian trajectory routine TRACMASS and the BaltiX velocity fields (see above). In this model reproduction within predicted habitats was assumed to be constant and no mortality was included apart from larvae being dispersed outside the predicted habitat.

Results

Future dispersal distance

The particle trajectory simulations using reference (1978-2007) and scenario (2069-2098) velocity fields showed that the predicted mean dispersal distance for the scenario cases increased significantly with approximately 35% for A1b and 25% for A2 (Table 1). However, the variation around the means is very big as seen from the distributions of change in dispersal distance shown in Fig. 3. From the mapped changes in dispersal distance in Fig. 4 it is evident that the change in dispersal distance is very dependent on geographic location. Dispersal distance in the Baltic proper is largely expected to increase most while only moderate increase or even decrease of dispersal distance is expected for the Gulf of Bothnia. Especially, the Finnish coast along the Bothnian Sea may see shorter dispersal distances (Fig. 4). Generally, dispersal distance is expected to increase more in off-shore areas compared to coastal.

Table 1. Change in dispersal distances in the Baltic Sea caused by the predicted change in circulation pattern. Data were produced with a model of dispersal trajectories based on reference (1978-2007) and scenario (2069-2098) velocity fields. Averages and standard deviations (SD) of absolute difference are shown for the two emission scenarios A1b and A2 for five pelagic larval durations (PLD). Also shown are the proportional difference (%) in relation to the dispersal distance of the reference cases.

PLD (days)	Absolute change (km)		SD (A1b)	SD (A2)	% change	
	A1b	A2			A1b	A2
5	3.8	2.4	6.4	6.0	34.2	21.8
10	7.4	4.8	12.2	11.5	34.8	22.8
20	14.3	9.9	23.6	22.5	36.8	25.6
30	20.0	14.6	34.6	33.7	36.6	26.7
60	33.8	27.1	65.1	65.0	35.6	28.5

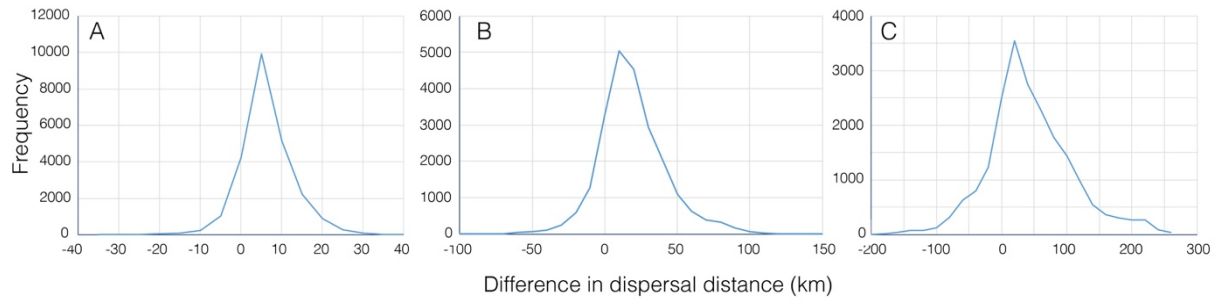


Figure 3. Frequency distributions across model grid cells of changes in dispersal distance in the Baltic Sea for three pelagic larval durations (PLD). (A) PLD of 5 days, (B) PLD of 20 days, (C) PLD of 60 days.

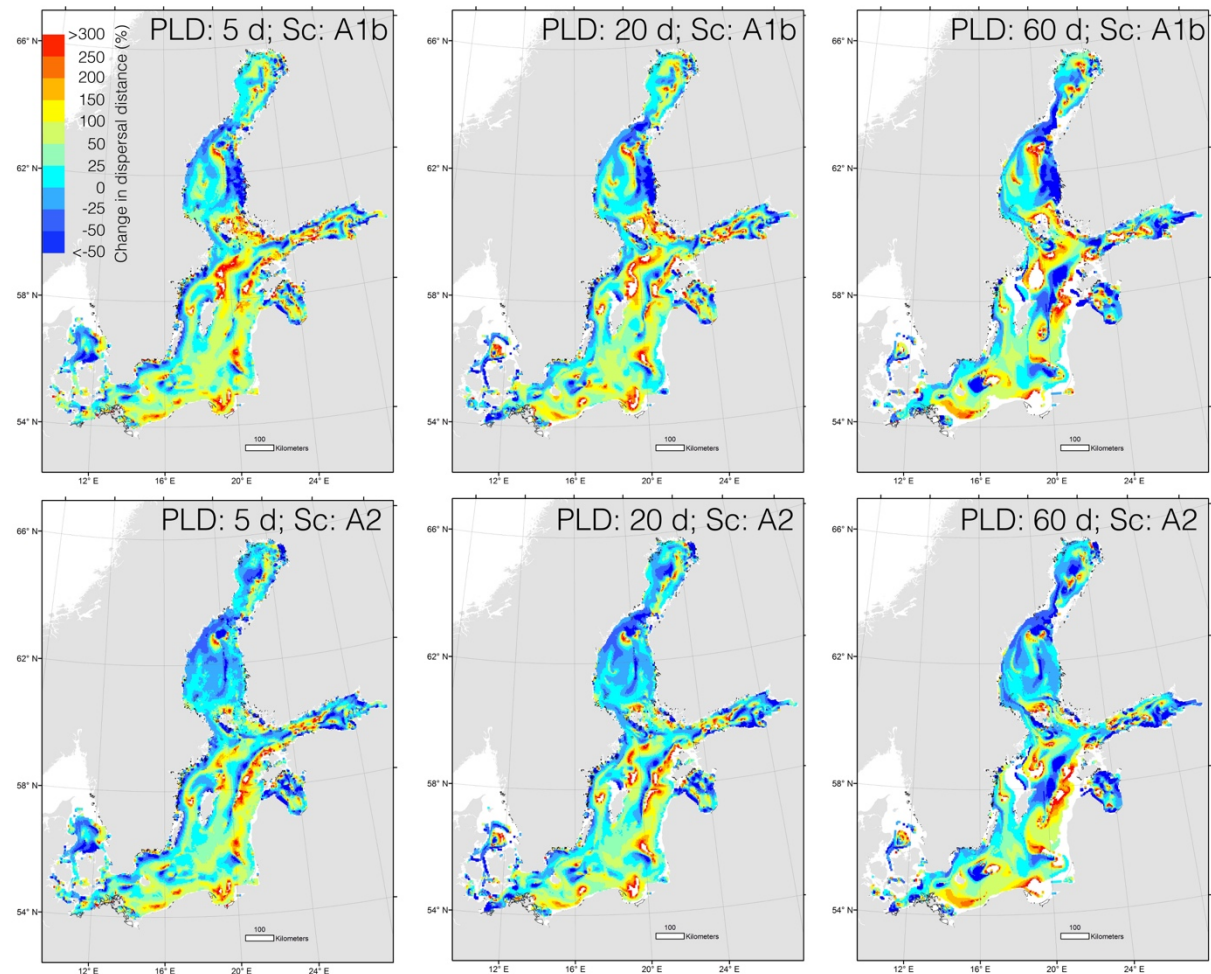


Figure 4. Proportional change (%) in dispersal distance in the Baltic Sea caused by the predicted change in circulation pattern. Data are shown for three pelagic larval durations (PLD) 5, 20 and 60 days, and two emission scenarios (Sc) A1b and A2.

Future sub-basin connectivity

When dispersal probabilities are aggregated to the scale of sub-basins the predicted increase in dispersal distance (see above) translates to lower local retention and an increase in connectivity between sub-basins (Table 2). Paralleling the results on dispersal distance the effect on connectivity is somewhat greater for the A1b than for the A2 scenario.

[illegible][illegible]

C	Kattegat	The Belts	Öresund	Mecklenburg	Gdansk	E Gotland	W Gotland	Gulf of Riga	N Baltic	Gulf of Finland	Åland Sea	Archipelago Sea	Bothnian Sea	Quark	Bothnian Bay
Kattegat	-0.0843	0.1223	-0.0099	0.0242											
The Belts		-0.0197		0.0101	-0.0001										
Öresund			0.0278		0.0001										
Kiel & Mecklenburg			0.0315	0.0995	-0.0031										
S Baltic & Gdansk			-0.0031	0.0120	-0.1747	-0.0039	0.0581								
E Gotland					-0.0019	-0.2928	0.0581	0.0164	0.1982		0.0648				
W Gotland						0.0006	-0.2590		-0.1340		0.0242				
Gulf of Riga						0.0069		0.0317	0.0012	-0.0023		0.0002			
N Baltic					0.0164	0.1094		-0.1045	-0.2534	-0.1306	0.0691	0.4489	0.0314		
Gulf of Finland						0.0166		0.0056	0.0902	0.1646		0.0018			
Åland Sea									-0.0015		-0.2168	-0.0064	0.0136		
Archipelago Sea									-0.0006		-0.0167	-0.4085	0.0433		
Bothnian Sea											-0.0015	-0.0145	-0.0879	0.1123	0.0459
Quark														0.0176	0.0204
Bothnian Bay														-0.0017	-0.0091

[illegible][illegible][illegible]

Effect of future temperature on dispersal distance

Increasing temperature will lead to accelerating development for most larvae and a shorter PLD (e.g. O'Connor et al. 2007). In Fig. 5 shows the change in sea-surface temperature during summer from the reference case to scenario A1b. The predicted average change across the whole Baltic Sea is 3.1°C but in some areas up to 5°C. With the metabolic model in eq. 1 and the regression model in eq. 2 we calculated that the increasing temperature may reduce mean PLD, e.g. from 20 days to 14.4 and 16.8 days assuming emission scenarios A1b and A2, respectively. This translates to a proportional reduction in dispersal distance by 25 and 14% for A1b and A2, respectively. There are, however, large geographic differences in this temperature effect where the reduction in PLD ranges from 10 to 50%.

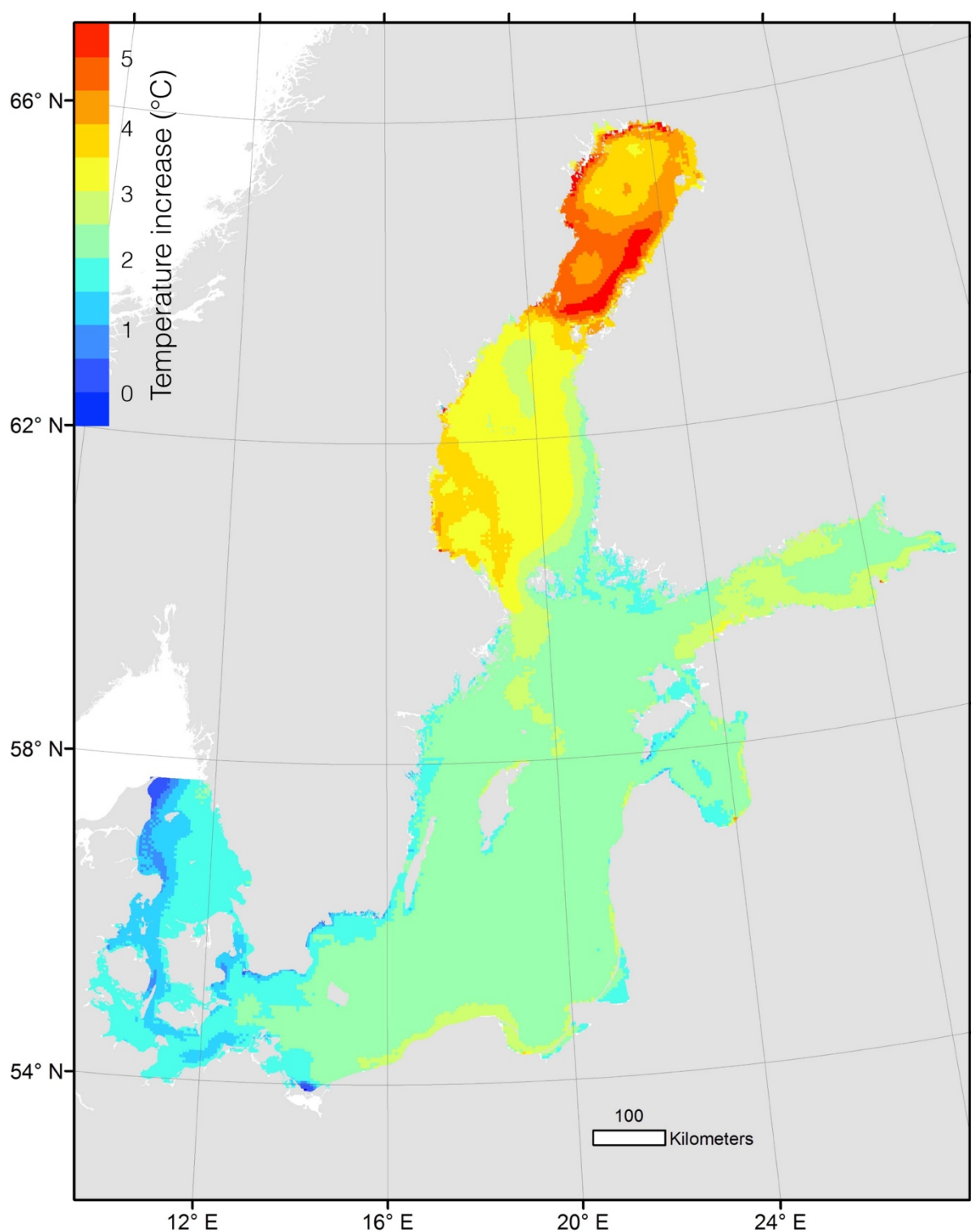


Figure 5. Increase in sea-surface temperature in the Baltic Sea during summer (June, July, August) measured as the difference between the A1b emission scenario (2069-2098) and the reference (1978-2007) as predicted by the RCO model (ECHAM5 downscaling).

Habitat distribution combined with connectivity

The preliminary study of combining habitat prediction models in task 3.4 with modelled connectivity is shown for *Mytilus trossulus/edulis* for Estonian waters in Fig. 6.

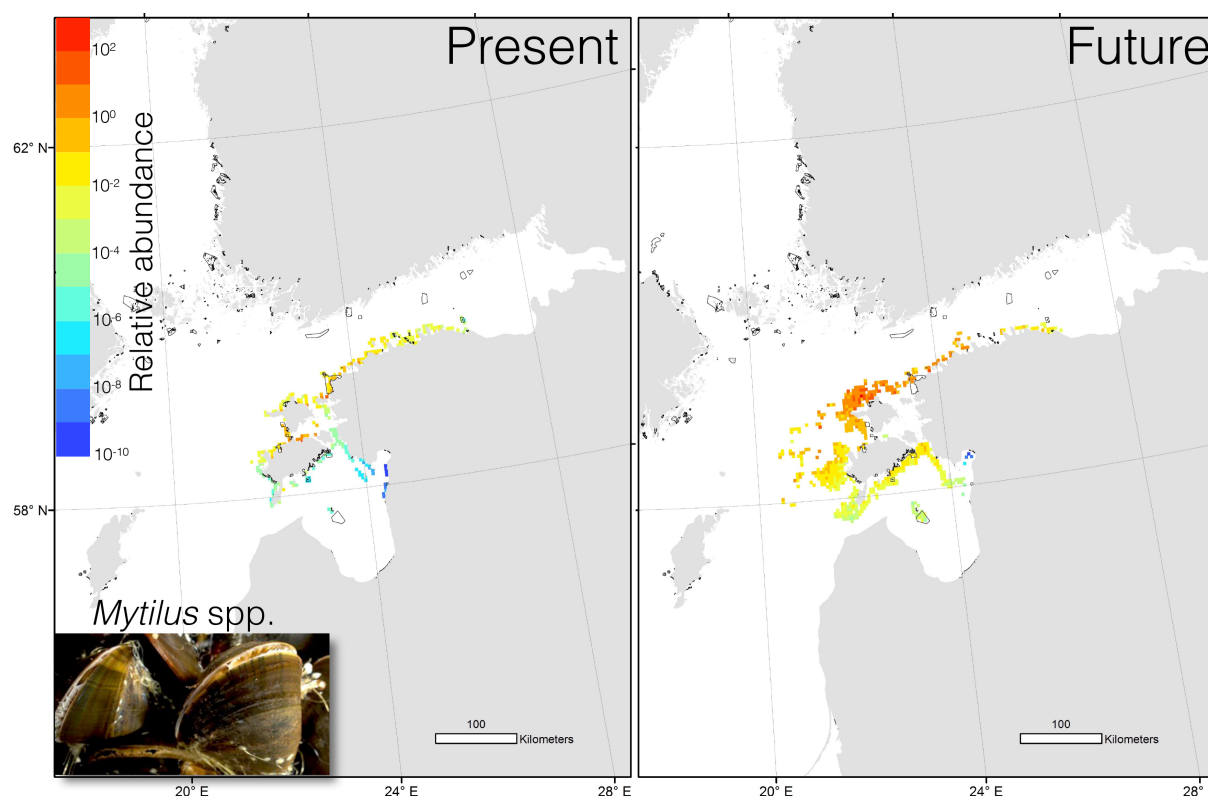


Figure 6. A model of present and future habitat distribution for *Mytilus trossulus/edulis* combined with a metapopulation model using modelled connectivity between habitat patches. The habitat model predicts an increase in the areal cover of habitat, mainly caused by increasing nutrient loading. The future habitat is less fragmented and the population model predicts that this leads to larger population size.

The future increase in habitat cover predicted by the species distribution model resulted in a less fragmented metapopulation, and a larger population size in the population model.

Discussion

The modelling of future dispersal distance in the Baltic sea caused by changes in circulation patterns predicts an average increase in dispersal distance although there are large regional variations. The two emission scenarios resulted in rather similar results. The increase in sea-surface temperature caused by changes in circulation may be partly counteracted by an increase in temperature, which will accelerate larval development and reduce PLD and dispersal distance. However, the pattern of temperature increase (Fig. 5) indicates that the strongest decrease in temperature-dependent dispersal occurring in the northern part of the Baltic Sea is also the area that is expected to experience decreasing dispersal distance caused by changes in circulation. And on the other hand, in the southern Baltic Sea the temperature-dependent change in dispersal is expected to be less compared to the increased dispersal caused by changes in circulation.

The future mean increase in dispersal distance, mainly in the southern Baltic Sea will affect local retention and connectivity between sub-basins in the Baltic Sea. Generally, the local retention is expected to decrease while export to other sub-basins may increase, e.g. in Öresund, East and West Gotland, North Baltic Sea, Åland Sea and Archipelago Sea. This may increase stock mixing and also the spread of non-native species.

A preliminary study where connectivity was combined with predictions of future habitat change also indicates that there may be important interactive effects between changes in habitat distribution and connectivity.

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References

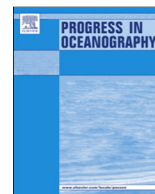
- Cowen RK, Sponaugle S (2009) Larval dispersal and marine connectivity. *Annual Review of Marine Science* 1:443-466
- Crutzen PJ (2002) Geology of mankind. *Nature* 415:23
- De Vries P, Döös K (2001) Calculating Lagrangian trajectories using time-dependent velocity fields. *Journal of the Atmospheric Sciences* 18:1092-1101
- Döscher R, Willén U, Jones C, Rutgersson A, Meier HEM, Hansson U, Pihl Graham L (2002) The development of the regional coupled ocean-atmosphere model RCAO. *Boreal Env Res* 7:183-192
- Gerber LR, Mancha-Cisneros MDM, O'Connor MI, Selig ER (2014) Climate change impacts on connectivity in the ocean: Implications for conservation. *Ecosphere* 5:33
- Halpern BS, Walbridge S, Selkoe KA, Kappel CV, Micheli F, D'Agrosa C, Bruno JF, Casey KS, Ebert C, Fox HE, Fujita R, Heinemann D, Lenihan HS, Madin EMP, Perry MT, Selig ER, Spalding M, Steneck R, Watson R (2008) A global map of human impact on marine ecosystems. *Science* 319:948-952
- IPCC (2007) Climate Change 2007: The Physical Science Basis, Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. In: Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M, Miller HL (eds) IPCC AR4 WG1, Cambridge
- Lett C, Ayata SD, Huret M, Irisson JO (2010) Biophysical modelling to investigate the effects of climate change on marine population dispersal and connectivity. *Progress in Oceanography* 87:106-113
- Lubchenco J, Palumbi SR, Gaines SD, Andelman S (2003) Plugging a hole in the ocean: the emerging science of marine reserves. *Ecological Applications* 13:S3-S7
- McCauley DJ, Pinsky ML, Palumbi SR, Estes JA, Joyce FH, Warner RR (2015) Marine defaunation: Animal loss in the global ocean. *Science* 347:247-254
- McLeod E, Salm R, Green A, Almany J (2009) Designing marine protected area networks to address the impacts of climate change. *Frontiers in Ecology and the Environment* 7:362-370
- Meier HEM, Eilola K, Almroth E (2011) Climate-related changes in marine ecosystems simulated with a 3-dimensional coupled physical-biogeochemical model of the Baltic Sea. *Climate Research* 48:31-55
- Meier HEM, Hordoir R, Andersson HC, Dieterich C, Eilola K, Gustafsson BG, Höglund A, Schimanke S (2012) Modeling the combined impact of changing climate and changing nutrient loads on the Baltic Sea environment in an ensemble of transient simulations for 1961–2099. *Climate Dynamics* 39:2421-2441
- Munday PL, Leis JM, Lough JM, Paris CB, Kingsford MJ, Berumen ML, Lambrechts J (2009) Climate

- change and coral reef connectivity. *Coral Reefs* 28:379-395
- O'Connor MI, Bruno JF, Gaines SD, Halpern BS, Lester SE, Kinlan BP, Weiss JM (2007) Temperature control of larval dispersal and the implications for marine ecology, evolution, and conservation. *Proceedings of the National Academy of Sciences* 104:1266-1271
- Parmesan C (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution and Systematics* 37:637-669
- Roeckner E, Brokopf R, Esch M, Giorgetta M, Hagemann S, Kornblueh L, Manzini E, Schlese U, Schulzweida U (2006) Sensitivity of simulated climate to horizontal and vertical resolution in the ECHAM5 atmosphere model. *Journal of Climate* 19:3771–3791
- Waters CN, Zalasiewicz J, Summerhayes C, Barnosky AD, Poirier C, Gałuszka A, Cearreta A, Edgeworth ME, E.C., Ellis M, Jeandel C, Leinfelder R, McNeill JR, deB. Richter D, Steffen W, Syvitski J, Vidas D, Waple M, Williams M, Zhisheng A, Grinevald J, Odada E, Oreskes N, Wolfe AP (2016) The Anthropocene is functionally and stratigraphically distinct from the Holocene. *Science* 351:137-147
- Worm B, Barbier EB, Beaumont N, Duffy JE, Folke C, Halpern BS, Jackson JBC, Lotze HK, Micheli F, Palumbi SR, Sala E, Selkoe KA, Stachowicz JJ, Watson R (2006) Impacts of biodiversity loss on ocean ecosystem services. *Science* 314:787-790



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Spawning areas of eastern Baltic cod revisited: Using hydrodynamic modelling to reveal spawning habitat suitability, egg survival probability, and connectivity patterns

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ABSTRACT

In the highly variable environment of the Baltic Sea two genetically distinct cod stocks exist, one west of the island of Bornholm, which is referred to as the western stock, and one to the east of Bornholm, the eastern stock. A hydrodynamic model combined with a Lagrangian particle tracking technique was utilised to provide spatially and temporally resolved long-term information on environmentally-related (i) spawning habitat size, (ii) egg/yolk-sac larval survival, (iii) separation of causes of mortality, and (iv) connectivity between spawning areas of eastern Baltic cod. Simulations were performed to quantify processes generating heterogeneity in spatial distribution of cod eggs and yolk sac larvae up to the first-feeding stage. The spatial extent of cod eggs represented as virtual drifters is primarily determined by oxygen and salinity conditions at spawning, which define the habitat requirement to which cod's physiology is suited for egg development. The highest habitat suitability occurred in the Bornholm Basin, followed by the Gdansk Deep, while relatively low habitat suitability was obtained for the Arkona and the Gotland Basin. During drift egg and yolk sac larval survival is to a large extent affected by sedimentation. Eggs initially released in the western spawning grounds (Arkona and Bornholm Basin) were more affected by sedimentation than those released in the eastern spawning grounds (Gdansk Deep and Gotland Basin). Highest relative survival of eastern Baltic cod eggs occurred in the Bornholm Basin, with a pronounced decrease towards the Gdansk Deep and the Gotland Basin. Relatively low survival rates in the Gdansk Deep and in the Gotland Basin were attributable to oxygen-dependent mortality. Low oxygen content had almost no impact on survival in the Arkona Basin. For all spawning areas temperature dependent mortality was only evident after severe winters. Egg buoyancy in relation to topographic features like bottom sills and strong bottom slopes could appear as a barrier for the transport of Baltic cod eggs and yolk sac larvae and could potentially limit the connectivity of Baltic cod early life stages between the different basins in the western and eastern Baltic Sea. The possibility of an eastward directed transport up to the first-feeding larval stage exists only for eggs and yolk sac larvae at high buoyancy levels, suggesting that dispersal of early life stages between these spawning areas is limited.

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1. Introduction

In the highly variable environment of the Baltic Sea two genetically distinct cod stocks exist, one west of the island of Bornholm, which is referred to as the western stock, and one to the east of Bornholm, the eastern stock (Fig. 1). Being a marine species, the Baltic cod stocks are living at the boundary of the species' distribu-

tion range with respect to salinity. While adult cod in this area are adapted to a life in water with low salinities (Neuenfeldt et al., 2009; Berg et al., 2015), the early life stages are more susceptible to variations in hydrographic conditions (Köster et al., 2005).

In contrast to cod stocks outside the Baltic, eggs from eastern Baltic cod do not float in surface waters due to the lower density of the brackish water. Adaptation to lower salinity conditions by larger volume allows eastern Baltic cod eggs to obtain neutral buoyancy at 14.2 ± 1.1 psu (Vallin and Nissling, 2000). Oxygen depletion is a common phenomenon over large areas in the deep

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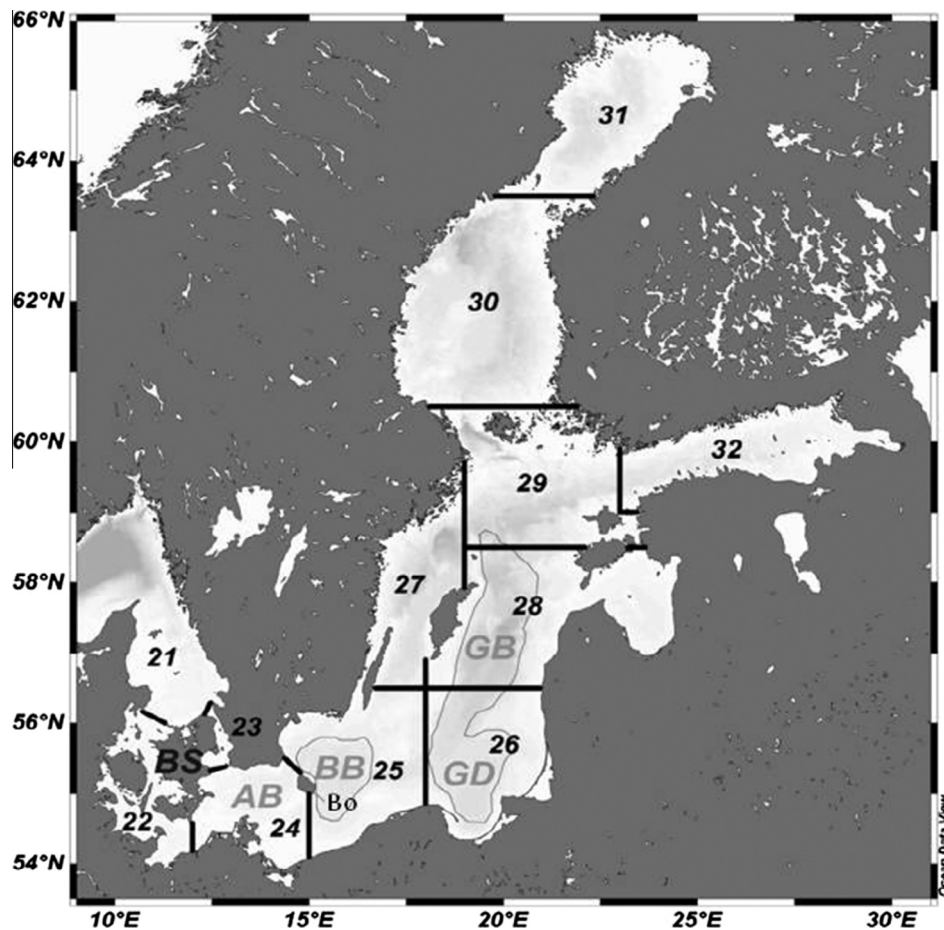


Fig. 1. ICES subdivisions in the Baltic Sea and Baltic cod spawning areas: BS – Belt Sea, AB – Arkona Basin, BB – Bornholm Basin, GD – Gdansk Deep, GB – Gotland Basin, Bo – island of Bornholm.

basins, which has a large impact on the reproduction of eastern Baltic cod by limiting the survival of eggs (Nissling et al., 1994; Wieland et al., 1994). Stagnation of inflow of saline water, coupled with increased oxygen demand due to eutrophication, limited the volume of water where eggs remain buoyant and above the hypoxic bottom layer (Plikshs et al., 1993; MacKenzie et al., 1996). Experimental studies of egg survival confirmed the strong link between environmental salinity, oxygen and egg survival (Wieland et al., 1994; Nissling et al., 1994; Rohlf, 1999). Generally, successful spawning and subsequent egg survival of the eastern stock is restricted to only a few discrete deep water areas (Bornholm Basins, Gdansk Deep, Gotland Basin). In addition also the Arkona Basin, which is shared by both cod stocks, reveals successful spawning and subsequent egg survival of the eastern stock (Hüssy, 2011). The vertical distribution of cod eggs is influenced by egg size, with larger more buoyant eggs occurring higher in the water column at more favourable oxygen conditions, hence having a higher probability of survival. Egg size itself is related to female spawner size, with larger, older females producing larger eggs (Vallin and Nissling, 2000) and batch number (Kjesbu et al., 1991). However, a limited correlation between egg production and larval abundance suggests that not only egg survival but also processes occurring during the late egg and early larval stage regulate recruitment (Köster et al., 2003).

The distribution of cod in the Baltic Sea is not only the result of their environmental selection, but is also influenced by dispersal of early life stages. Passively drifting fish eggs are particularly vulner-

able as they are not capable of avoiding water masses with less favourable environmental conditions for development and survival. The strong thermohaline stratification of this brackish water system in combination with eutrophication results in frequent hypoxia and even anoxia in near bottom layers, which creates an especially harsh environment for passively drifting organisms. Drift modelling studies have been used for eastern Baltic cod spawned in the Bornholm Basin to investigate the dispersal dynamics of early life stages (Voss et al., 1999; Hinrichsen et al., 2003a), the impact on the survival of larvae (Hinrichsen et al., 2001, 2003b), and the influence of copepod species composition on the growth and survival of larvae (Hinrichsen et al., 2002). Another study also suggested the potential for considerable connectivity between areas through dispersal of early life stages (Hinrichsen et al., 2001, 2009).

A spatially and temporally highly-resolved biophysical model of the Baltic Sea was already utilised to describe mortalities and survival success of western Baltic cod eggs and yolk-sac larvae (Hinrichsen et al., 2012; Hüssy et al., 2012). Mortality of western Baltic cod eggs was mainly caused by sedimentation (bottom contact) and/or lethal temperatures, while oxygen contents in the cod spawning environment was generally high and had no significant impact on egg survival. The simulation of deep water dissolved oxygen distribution with its seasonal and quasi-permanent extended areas of oxygen deficiency, one of today's major challenges for the eastern Baltic Sea, has been successfully performed by Lehmann et al. (2014). This improved simulation of oxygen

conditions forms the basis for running another type of biophysical Baltic cod early life stage model. For the first time, the resulting model output allowed the consideration of oxygen content and oxygen-related early life stage processes (e.g. egg survival, larval activity, settlement) as important contributors for the eastern Baltic cod stock recruitment variability.

The objectives of this paper are to provide new knowledge on environmentally-driven survival and drift of eastern Baltic cod eggs and yolk-sac larvae and to quantify processes generating heterogeneity in the spatial distribution of Baltic cod early life stages. We estimate spatio-temporal differences in survival rates within the main spawning areas of eastern Baltic cod in relation to season and year and use drift modelling to test whether the environmental conditions in the different spawning grounds (i) are suitable for spawning, (ii) are suitable for egg survival, and (iii) could be separated quantitatively for the causes of mortality. Finally (iv), we estimate the population connectivity of eastern Baltic cod eggs and yolk-sac larvae between the different spawning grounds.

2. Materials and methods

2.1. Hydrodynamic modelling

The basis of the Lagrangian particle tracking is the hydrodynamic Kiel Baltic Sea Ice-Ocean Model (BSIOM, [Lehmann and Hinrichsen, 2000a,b](#); [Lehmann et al., 2002](#)). The horizontal resolution of the coupled sea-ice ocean model is at present 2.5 km, and in the vertical 60 levels are specified, which enables the upper 100 m to be resolved into levels of 3 m thickness. The model domain comprises the Baltic Sea, Kattegat and Skagerrak. The oxygen conditions in the entire Baltic Sea are described by an oxygen consumption sub-model coupled to BSIOM ([Lehmann et al., 2014](#)). Pelagic and benthic oxygen consumption is modelled as a function of temperature and oxygen concentration ([Hansen and Bendtsen, 2009, 2013](#); [Jonasson et al., 2012](#)), which takes into account increased oxygen consumption rates at high temperatures as well as decreased consumption at low oxygen levels. At the western boundary, a simplified North Sea is connected to the model domain to represent North Sea water masses in terms of characteristic temperature and salinity profiles resulting from the different forcing conditions. The model is forced by low frequency sea level variations in the North Sea/Skagerrak calculated from the BSI (Baltic Sea Index, [Lehmann et al., 2002](#); [Novotny et al., 2006](#)). The coupled sea ice-ocean model is forced by realistic atmospheric conditions taken from the Swedish Meteorological and Hydrological Institute (SMHI Norrköping, Sweden) meteorological database (Lars Meuller, pers. comm.) which covers the whole Baltic drainage basin on a regular grid of $1 \times 1^\circ$ with a temporal increment of 3 h. The database consists of synoptic measurements that were interpolated on the regular grid with a two-dimensional optimum interpolation scheme. This database, which for modelling purposes was further interpolated onto the model grid, includes surface pressure, precipitation, cloudiness, air temperature and water vapour mixing ratio at 2 m height and geostrophic wind. Wind speed and direction at 10 m height were calculated from geostrophic winds with respect to different degrees of roughness on the open sea and off the coast ([Bumke et al., 1998](#)). BSIOM forcing functions, such as wind stress, radiation and heat fluxes were calculated according to [Rudolph and Lehmann \(2006\)](#). Additionally, river runoff was derived from a monthly mean runoff data set ([Kronsell and Andersson, 2012](#)). The numerical model BSIOM has been run for the period 1971–2010. This time series was used for the subsequent analysis of habitat suitability and early life stage survival in the Baltic.

2.2. Environmental threshold levels

Environmental threshold levels for egg survival were based on published literature on minimum values for salinity, temperature and oxygen. The critical threshold levels used in this study were 11 psu for salinity, 1.5°C for temperature and $2\text{ ml O}_2\cdot\text{l}^{-1}$ for oxygen, where survival was only possible at values above these levels. [Wieland et al. \(1994\)](#) showed that survival of eggs is higher at lower temperatures when oxygen levels are poor. However, the existence of low temperatures was only of minor importance in the Arkona and Bornholm Basin due to cold water temperatures after severe winters and were totally negligible in the Gdansk Deep and the Gotland Basin, thus this effect of temperature on egg survival was not considered in our study. An oxygen-egg survival relationship revealed that oxygen concentrations above the threshold level of 2 ml l^{-1} have a pronounced impact on egg survival ([Köster et al., 2005](#)). This relationship ($r^2 = 0.94$) describes a sigmoid curve with almost total mortality at 2 ml l^{-1} oxygen content, $\sim 50\%$ mortality at 4 ml l^{-1} , and $<10\%$ mortality at 7 ml l^{-1} ([Wieland et al., 1994](#); [Rohlf, 1999](#)). Eggs being buoyant at salinity levels exceeding those at the bottom presumably die due to sedimentation, while eggs displaying neutral buoyancy at lower salinities float in the water column ([Nissling et al., 1994](#)), with largest eggs being buoyant at 11 psu. A salinity of $>11\text{ psu}$ is also necessary for spermatozoa activation and egg fertilisation ([Nissling and Westin, 1997](#)). Egg development is strongly temperature dependent, with development times decreasing exponentially from 18 to 7 days with increasing temperature ([Petereit, 2004](#)). Both high and low temperatures become increasingly detrimental to egg development. In the water masses below the halocline, temperatures never rise to upper lethal temperature levels ($>11^\circ\text{C}$; [Nissling, 2004](#)), hence only the lower limit of 1.5°C was relevant for this study.

2.3. Particle tracking and drift model

Simulated three-dimensional velocity fields were extracted (at 3 h intervals) from the hydrodynamic model in order to develop a database for particle tracking. This data set offers the possibility to derive Lagrangian drift routes by calculating the advection of “marked” water particles. Based on ambient temperature and salinity values at egg release derived from hydrodynamic modelling, neutral egg buoyancy was calculated. Buoyancy was assumed to remain unchanged for the entire drift periods. Simulated drift routes were obtained from Eulerian flow fields by utilisation of a Lagrangian particle-tracking technique. The three-dimensional trajectories of the simulated drifters were computed using a 4th order Runge–Kutta scheme ([Hinrichsen et al., 1997](#)).

Each release of drifters consisted of particles distributed within the main spawning areas of the central Baltic Sea with a horizontal resolution of $\sim 4.5\text{ km}$. To quantitatively account for intra- and interannual variability of the cod spawning habitat size, the drifters (successfully spawned cod eggs at developmental stage Ia) were released at 3 m depth intervals in the reproduction volume ($>11\text{ psu}$ for salinity, $>1.5^\circ\text{C}$ for temperature and $>2\text{ ml O}_2\cdot\text{l}^{-1}$ for oxygen). For the drifters representing successfully spawned Baltic cod eggs, their initial neutral buoyancy (water density) levels were calculated based on the ambient hydrographic conditions (temperature and salinity). Thus, the number of drifters varied between release events corresponding to the habitat suitability conditions. The drifters were released every 10 days from 1st February to 10th November. According to the ambient hydrographic conditions required for successful spawning (initial egg survival at stage Ia) these drifters represent a measure of spawning habitat suitability. The particles representing cod eggs at developmental egg stage Ia

were released into the simulated flow fields and tracked through the different egg stages until the end of the yolk-sac larval stage (i.e. mouth opening/first-feeding). However, this exercise will only provide probabilities of different processes and parameters, and does not take into account how many eggs are actually spawned, e.g. factors affecting spatial distribution of spawners, female fecundity and egg quality. During their drift, eggs and yolk-sac larvae floated at the initially assigned density levels. If their initially assigned density level was found to be higher than those available at the bottom along the positions of the drift route the eggs were assumed to die due to sedimentation. Similarly, the eggs also died if exposed to lethal temperature ($<1.5^{\circ}\text{C}$) or oxygen ($<2\text{ ml/l}$) conditions. For individuals that died during the simulations, the positions where the death occurred were recorded. For the surviving individuals the final positions reached at the end of the yolk-sac stage were recorded. For each release event, the different mortalities (sedimentation, lethal temperature and/or oxygen concentration) are represented relative to the spawning habitat suitability (number of successfully spawned eggs released as drifting particles).

2.4. Estimation of survival and mortality and model experiment design

Duration of the egg and yolk-sac larval drift period depended on temperatures and were provided by the hydrodynamic model. Temperature-dependent development from stage Ia eggs to first feeding larvae (Thompson and Riley, 1981) was calculated along the drift paths of individual egg/larva. The simulations were stopped when yolk-sac larvae reached the first feeding larval stage (mouth opening).

2.5. Spawning time and spawning areas

The focus of this study is on the eastern Baltic cod's general reproduction potential for the whole spawning season. This stock is known to spawn from February to November, with the main spawning season in May–August with considerable inter-annual variability in peak spawning (Wieland et al., 2000; Bleil et al., 2009). The locations of the spawning grounds of the eastern Baltic cod stock (Bornholm Basin, Gdansk Deep, Gotland Basin) were taken from Bagge et al. (1994), while a potential spawning ground

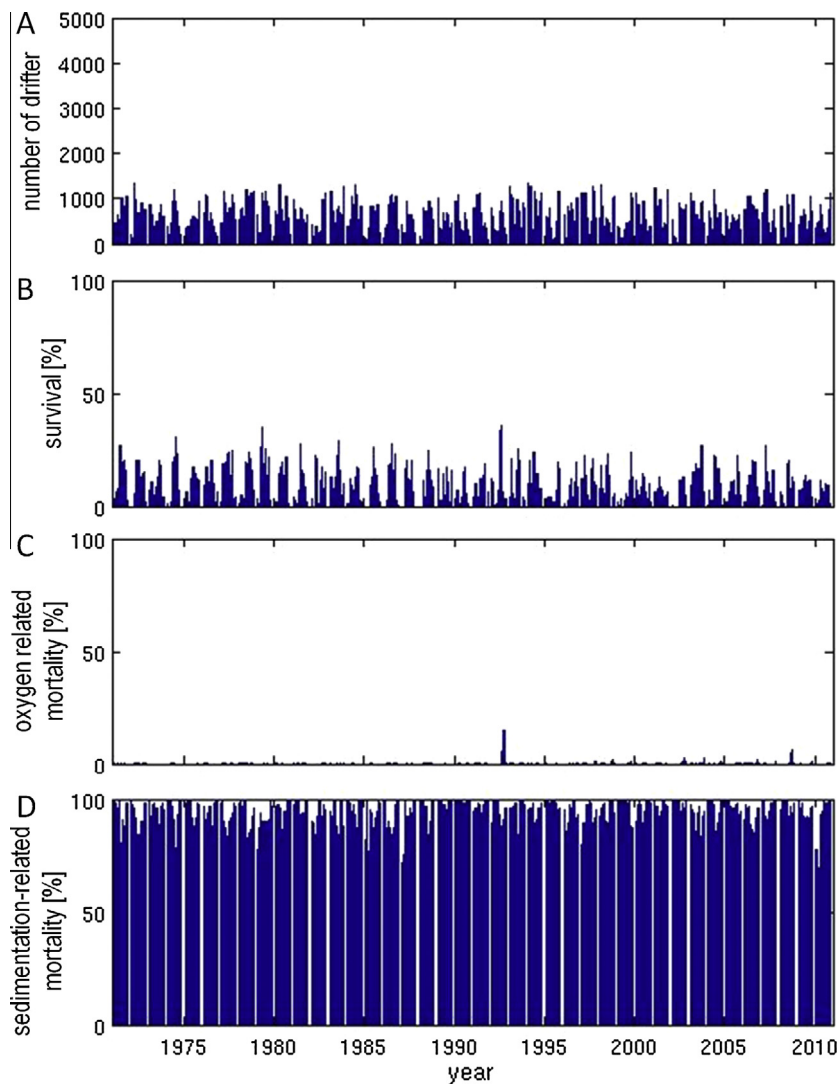


Fig. 2. Number of drifter representing Arkona Basin (ICES SD 24) Eastern Baltic cod spawning ground (a) habitat suitability (released as initially successfully spawned cod eggs), (b) relative survival of cod eggs until the first-feeding yolk-sac larval stage, (c) relative oxygen-related mortality of cod eggs during drift, and (d) relative mortality of cod eggs caused by sedimentation during drift. Bars represent the range of single release events.

of the eastern Baltic cod stock in the Arkona Basin was selected based on already existing information provided by Nissling and Westin (1997) and Hüssy et al. (2015).

3. Results

3.1. Spatially disaggregated patterns of habitat suitability, mortality and survival probability

The habitat suitability (drifter released as initially successfully spawned cod eggs), their relative survival rates as well as oxygen-related mortality and mortality caused by sedimentation during drift to the different spawning areas are displayed in Figs. 2–5. The highest long-term mean of habitat suitability occurred in the Bornholm Basin (Fig. 3a), followed by the Gdansk Deep (Fig. 4a). On average lower habitat suitability was obtained for the Arkona and the Gotland Basin (Figs. 2a and 5a). Generally, the relative survival probability in the westernmost cod spawning area was also low (Fig. 2b; mean ~7%), mainly due to high sedimentation rates (Fig. 2d; mean ~90%), while oxygen-related mortality was of only minor importance (Fig. 2c). Highest relative survival of eastern Baltic cod eggs up to the first feeding yolk-sac larval stage occurred in

the Bornholm Basin (Fig. 3b; mean ~40%), with a pronounced decrease towards the Gdansk Deep and the Gotland Basin (Figs. 4b and 5b). Relatively low survival rates in the Gdansk Deep (mean ~14%) and in the Gotland Basin (mean ~2%) were attributable to oxygen-dependent mortality (Figs. 4c and 5c; means ~30 and 55%). Low oxygen content had almost no impact on survival in the Arkona Basin (Fig. 2c), while in the Bornholm Basin it became evident since the beginning of the 1990s (Fig. 3c; mean ~5%). In the Arkona and in the Bornholm Basin the majority of eggs (means 90 and 54% respectively) died due to sedimentation (Figs. 2d and 3d). Relative mortality due to sedimentation was also pronounced (Fig. 4d; mean ~49%) in the Gdansk Deep, but was of less importance in the Gotland Basin (Fig. 5d; mean ~6%). Temperature-related mortality was only of minor importance in the Arkona and Bornholm Basin due to cold water temperatures after severe winters (not shown) and totally negligible in the Gdansk Deep and in the Gotland Basin. Generally, for all spawning grounds our analyses revealed strong spatiotemporal variation in habitat suitability and survival up to the first feeding yolk-sac larval stage, but also revealed strong positive correlations between model based habitat suitability and survival ($r^2 = 0.50$, $p < 0.05$) as well as between habitat suitability and sedimentation ($r^2 = 0.63$, $p < 0.05$).

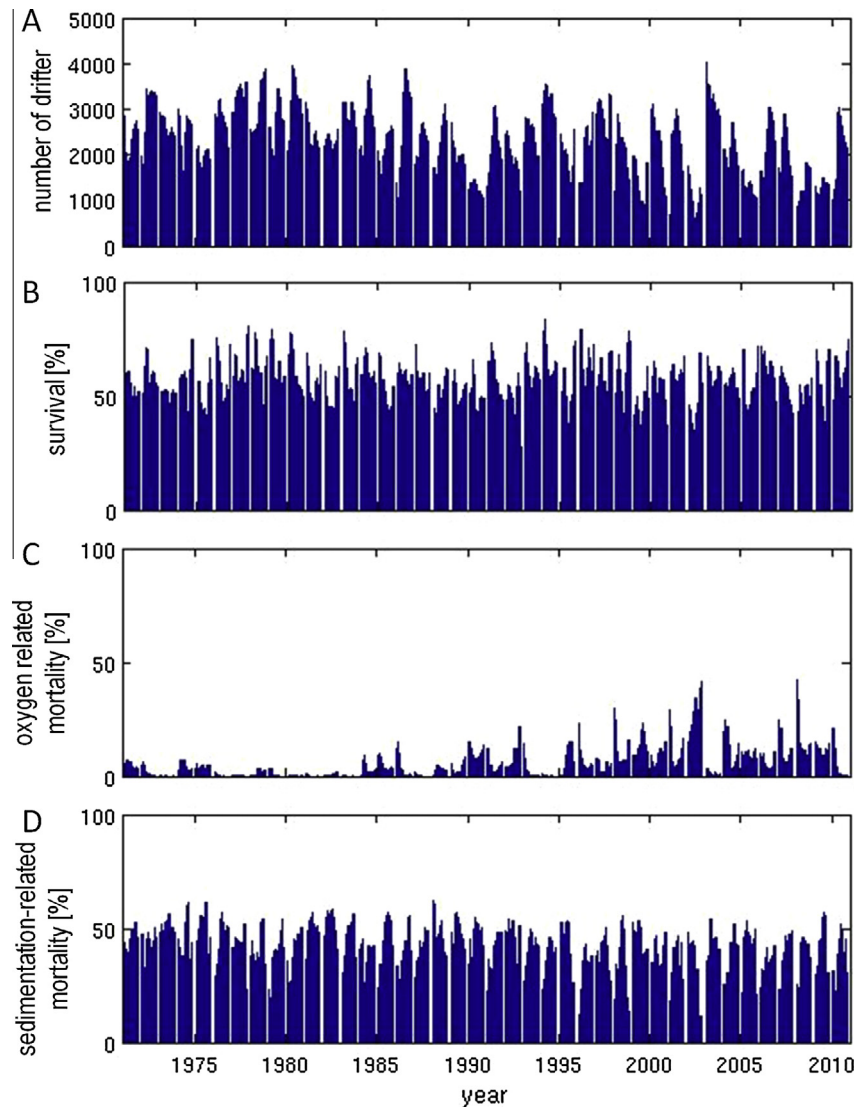


Fig. 3. Number of drifter representing Bornholm Basin (ICES SD 25) Eastern Baltic cod spawning ground (a) habitat suitability (released as initially successfully spawned cod eggs), (b) relative survival of cod eggs until the first-feeding yolk-sac larval stage, (c) relative oxygen-related mortality of cod eggs during drift, and (d) relative mortality of cod eggs caused by sedimentation during drift. Bars represent the range of single release events.

3.2. Seasonal patterns of habitat suitability and survival probability

The seasonality of habitat suitability and survival probability was generally weak and statistically not significant, but some patterns were discernible (Figs. 6 and 7). For the spawning grounds in the Arkona and Bornholm Basins (Fig. 6a and b) the most favourable but highly variable spawning conditions predominantly occurred in late spring/early summer, while in the Gdansk Deep and the Gotland Basin better conditions were observed during summer months (Fig. 6c and d). In the Arkona and the Bornholm Basin survival probability was highest in May–August (Fig. 7a and b). Similar peaks were observed approximately one month later in the Gdansk Deep and the Gotland Basin (Fig. 7c and d). Peak survival mainly occurred during time periods of relatively high ambient water temperatures, resulting in short egg developmental times.

3.3. Geographic patterns of egg survival probability

The long-term spatial distribution (1971–2010) of survivors up to the first feeding yolk sac larval stage originating from the differ-

ent spawning grounds, represented by the drifters (successfully spawned eggs stage Ia) at their initial release positions, is illustrated in Fig. 8. For drifters originating from the Arkona Basin, the Bornholm Basin, and the Gdansk Deep, horizontal distribution maps clearly show highest concentrations of surviving eggs in the central areas. In contrast, surviving eggs of the Gotland Basin were exclusively spawned at the southern edge of the basin. The spatial distribution of the drifter endpoints (Fig. 9) is based on the same egg cohorts. For the Arkona and the Bornholm Basin, areas predicted to have highest concentration of yolk-sac larvae were found in the centre of the Bornholm Basin, although the distribution areas were widely extended to the north and northeast. The final distributions of yolk-sac larvae spawned in the eastern spawning grounds (Gdansk Deep and Gotland Basin) are of a more retentive character: the surviving fractions of eggs mostly ended up in the original spawning areas.

3.4. Connectivity patterns of eggs and yolk-sac larvae

To quantify the connectivity patterns of eastern Baltic cod early life stages, we calculated retention within and advective transport

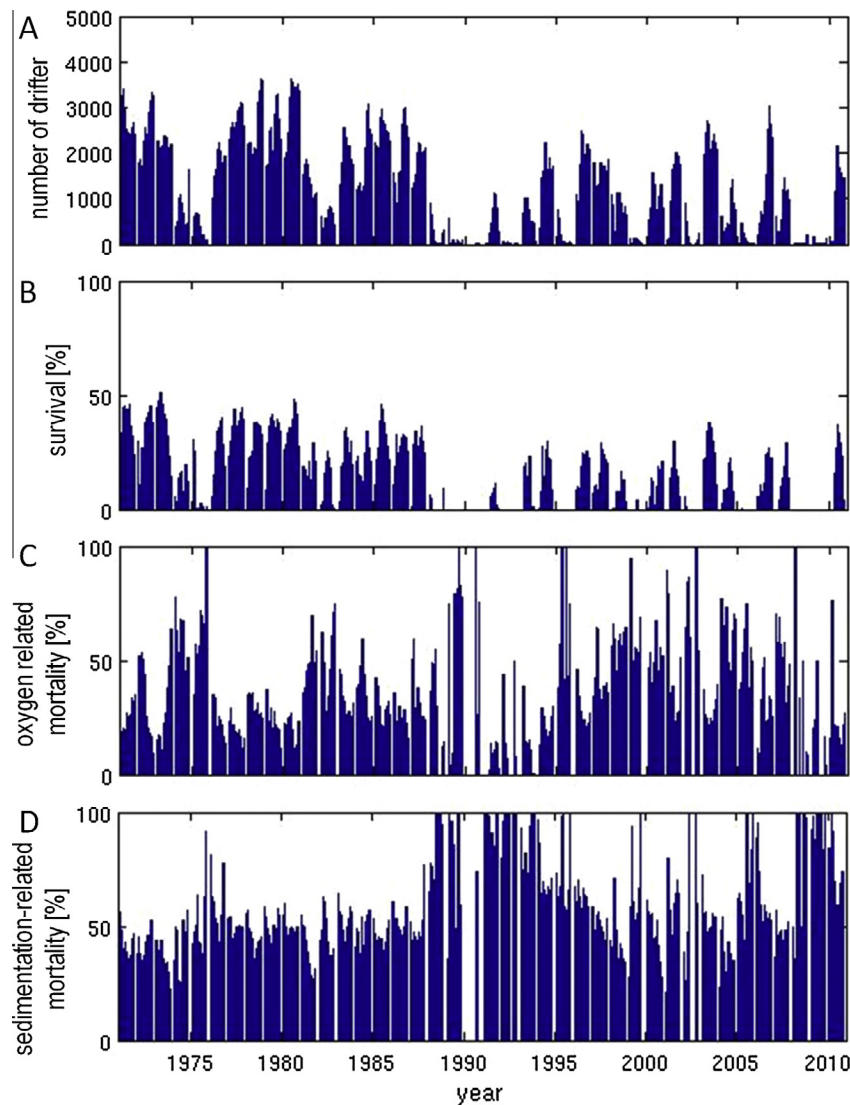


Fig. 4. Number of drifter representing Gdansk Deep (ICES SD 26) Eastern Baltic cod spawning ground (a) habitat suitability (released as initially successfully spawned cod eggs), (b) relative survival of cod eggs until the first-feeding yolk-sac larval stage, (c) relative oxygen-related mortality of cod eggs during drift, and (d) relative mortality of cod eggs caused by sedimentation during drift. Bars represent the range of single release events.

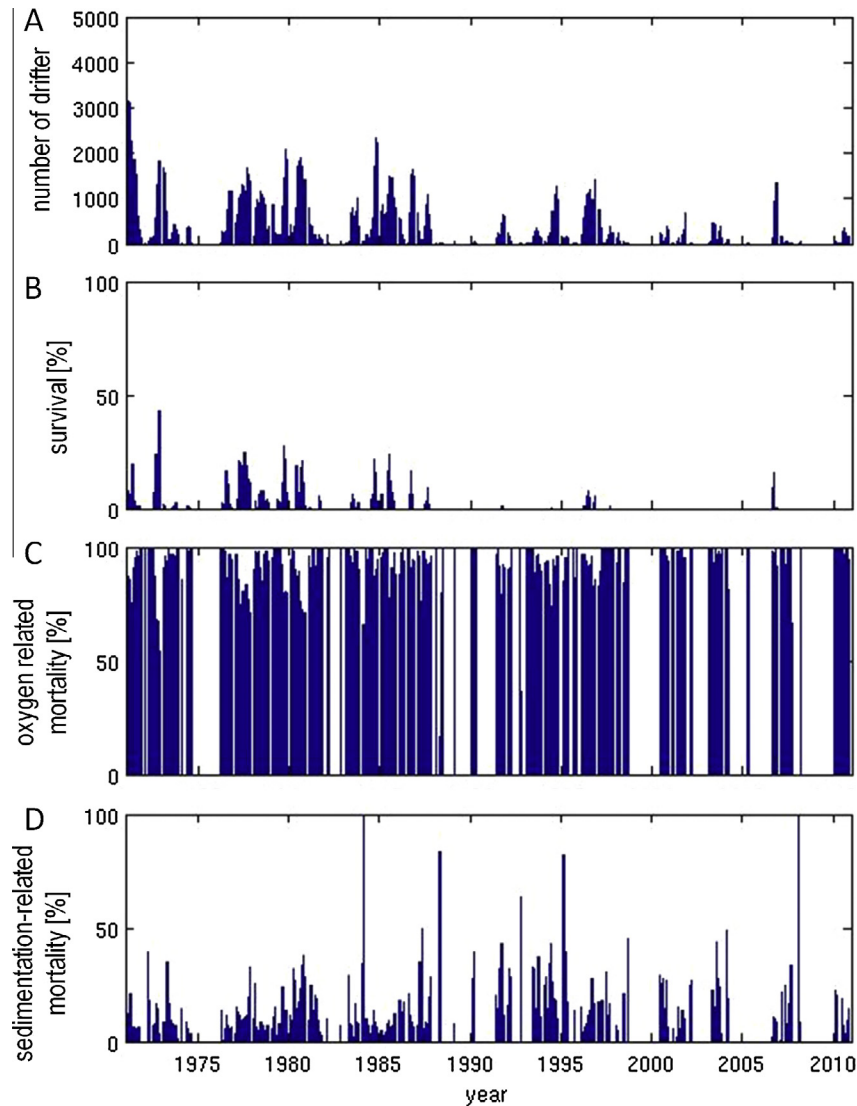


Fig. 5. Number of drifter representing Gotland Basin (ICES SD 28) Eastern Baltic cod spawning ground (a) habitat suitability (released as initially successfully spawned cod eggs), (b) relative survival of cod eggs until the first-feeding yolk-sac larval stage, (c) relative oxygen-related mortality of cod eggs during drift, and (d) relative mortality of cod eggs caused by sedimentation during drift. Bars represent the range of single release events.

rates between spawning grounds (Table 1). In a long-term perspective, survival probability patterns of eggs and yolk-sac larvae were dominated by retention of drifters in the Bornholm Basin, the Gdansk Deep, and in the Gotland Basin. The Bornholm Basin contributed more than 70% and the Gdansk Deep around 20% of survivors to the overall production of larvae. For drifters initially released in the Arkona Basin a high probability of transport towards the Bornholm Basin was estimated. However, the numerical simulations also showed remarkable inter- and intra-annual differences in numbers of surviving yolk-sac larvae retained in the Bornholm Basin (not shown). Only low eastward directed transport of eggs and yolk-sac larvae was obtained from the simulations (Fig. 10). On average around 2% of the surviving individuals were transported from the Arkona towards the Bornholm Basin, while the transport between the Bornholm Basin and the Gdansk Deep was limited to less than 1% due to a relatively shallow sill depth. Somewhat higher advective transport from the Gdansk Deep to the Gotland Basin (mean 3%) was only obtained for the first part of the time series (1971–1987).

4. Discussion and conclusions

Coupled biophysical models have proved useful in fisheries management. Their applicability includes estimation of connectivity in fish stocks through transport of egg, larval and early juvenile stages, and spatio-temporal differences in potential survival (Hinrichsen et al., 2011). This manuscript presents results of the first numerical drift modelling exercise on eastern Baltic Sea cod eggs originating from different spawning areas. Habitat suitability, mortality, survival and transport patterns of eastern Baltic cod eggs and yolk-sac larvae were quantified by detailed model simulations for the years 1971–2010. The data were derived from highly spatially and temporally resolved hydrographic Eulerian property fields obtained from hydrodynamic model runs (Lehmann et al., 2014). Here we examined the transport of virtual drifters initially released into these simulated flow fields as successfully spawned and fertilised eggs. However, this exercise only provides probabilities of different processes and parameters, and does not take into account how many eggs are actually spawned, e.g. factors affecting

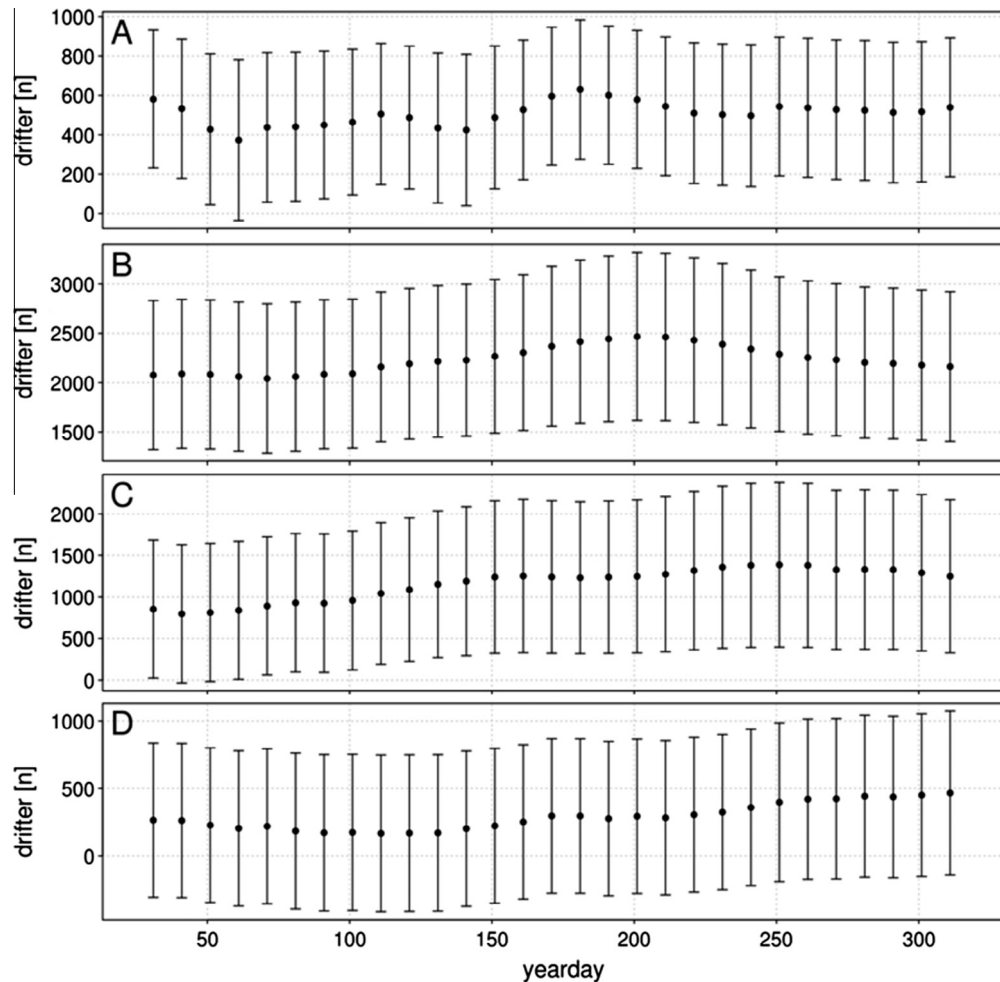


Fig. 6. Seasonal variability in eastern Baltic cod spawning habitat size (number of successfully spawned eggs) for spawning grounds in (a) Arkona Basin, (b) Bornholm Basin, (c) Gdansk Deep, and (d) Gotland Basin. Please note the different scales of the y-axis.

spatial distribution of spawners, female fecundity and egg quality. The estimation of habitat suitability as well as mortality and survival probabilities during drift are based on abiotic tolerance levels in terms of threshold values and egg specific gravity measurements (Vallin and Nissling, 2000), selected for egg survival at the spawning location as well as during drift duration. These threshold values were obtained from both laboratory experiments and field studies (Wieland et al., 1994; Nissling, 2004). However, low cod egg occurrence in the Gotland Basin observed at salinities and oxygen concentrations below these threshold values (Plikshs et al., 2015), suggests either local adaptation to less favourable environmental conditions or eggs with extremely high neutral buoyancy, usually related to large, old females (Vallin and Nissling, 2000).

The extent of species distributions in the Baltic Sea during spawning is, as for many species inhabiting water masses below the halocline, determined by their physiological requirements for minimum oxygen concentrations. The high resolution 3D circulation model of the Baltic Sea was coupled to an innovative oxygen sub-model (Lehmann et al., 2014) for realistic estimation of habitat suitability across space and time. The oxygen content in the spawning environment of pelagic fish species in the Baltic Sea as the major driver of egg survival is based on relatively simple empirically derived respiratory relationships of oxygen consumption in the water column and a boundary condition of oxygen production at the sea surface. However, there is a close agreement between hydrographic property fields obtained from long-term

hydrodynamic model runs and observations suggesting the model to be applicable for detailed analyses of ecological and environmental interactions (Lehmann et al., 2014), such as the estimation of hypoxia and anoxia on egg survival as applied in this study.

The high correlations between the size of the spawning habitat and both, survival and sedimentation of eggs is based on the inflow of oxygen-enriched water masses from the North Sea as the basic hydrographic process affecting the environmental conditions for egg survival (Hinrichsen et al., 2002). An increase in the size of the suitable habitat, i.e. larger volumes of water with salinity, temperature and oxygen content above threshold levels as well as an increase of eggs floating higher in the water column, results in an initial increase in egg survival probability at spawning, but also in higher mortality due to sedimentation of eggs during their drift. The latter, however, suggests that despite an improvement in environmental conditions at the bottom or in near-bottom water layers, many of the eggs were located in suitable spawning habitat conditions closer to the bottom or closer to the edges of the basins. For those individuals sedimentation-related mortality might increase, because the probability that eggs or yolk-sac larvae hit the bottom during their drift might also increase. This is supported by the strong decrease in sedimentation from the western to the eastern spawning grounds. The volume of water in the Arkona and the Bornholm Basin where successful spawning is possible are much smaller compared to those in the Gdansk Deep and in the Gotland Basin. Consequently, also the drift distances of the

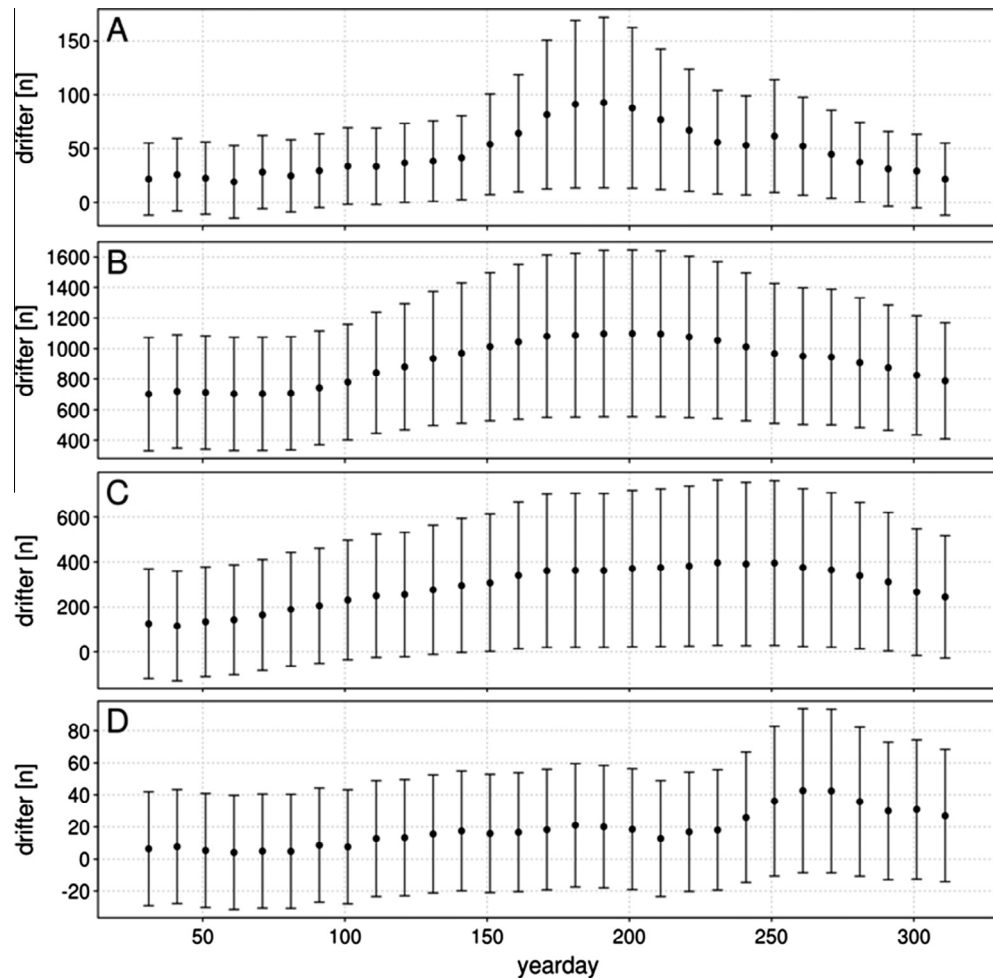


Fig. 7. Seasonal variability in eastern Baltic cod egg survival probability (number of successfully spawned eggs surviving until the first-feeding yolk-sac larval stage) spawned in (a) Arkona Basin, (b) Bornholm Basin, (c) Gdansk Deep, and (d) Gotland Basin. Please note the different scales of the y-axis.

eggs towards shallower areas of the basins are much lower. This sedimentation-related increase in mortality may contribute significantly to the observed decoupling between egg production and larval abundance (Köster et al., 2003). However, compared to previous research on early life stage processes on eastern Baltic cod, the finding of sedimentation derived mortality is rather new. In earlier studies on this topic, simple CTD-derived oxygen profiles from measurements were the only opportunity to measure bottom-close oxygen content. Now oxygen fields in the Baltic Sea can be taken from hydrodynamic modelling. The duration, in which eggs are subject to potential oxygen depletion, is of course relevant. For any field-based validation of sedimentation-related mortality, there are currently no functional sampling gears which sample reliably the boundary layer between substrate and water column and would allow the necessary and secure determination of the condition of the egg. It remains a real challenge to collect eggs from soft bottom, which constitutes by far the largest area of substrate where cod eggs are lost due to sedimentation. Horizontally towed Multinet (open/closure nets) sampling would of course be an option to sample the last 2 m of the water column. However, weather conditions and wave action often prevent operations so close to the bottom. Benthos sledges would be another option, however, the chances to provide clear evidence that potentially detected eggs come exactly from the bottom and not from the water layer above are very low. All other vertically resolved plankton nets usually have the disadvantage that they have to keep

a certain distance from the bottom to avoid the direct disruption of the net. Uncontrolled mud collection immediately destroys the remaining sample, and entangling of the net in the structures on the sea floor result in the loss of gear. Consequently, it would be a very desirable step forward to develop an appropriate method demonstrating directly the occurrence of eggs on the bottom under field conditions. To the authors' knowledge direct evidence (either derived by observations or experiments) of our assumption that eggs do not survive if hitting the bottom (sedimentation) has not yet been published in the literature. The likelihood for fragile pelagic cod eggs to survive e.g. potential predation pressure or exposure to benthic fungi, maybe expected to be largely reduced. That survival of bottom lying eggs is not impossible in general is evident from the two different ecotypes of spawning strategies of Baltic flounder populations (one spawning small benthic eggs in coastal waters – the other, like cod, spawning large pelagic eggs in the deep basins). However, no cod populations with benthic spawning stock components are known. The circumstance that other species have evolutionary adapted by e.g. thickening their egg shell to be able to spawn demersal instead of pelagic eggs, make it highly unlikely that the survival of purely pelagic cod eggs is not severely reduced by bottom contact. A large body of recently published studies shared this assumption (Hinrichsen et al., 2012; Hüsey et al., 2012; Pacariz et al., 2013; Petereit et al., 2014).

Propagation of eastern Baltic cod eggs and yolk-sac larvae has been calculated by simulating the advective transport of passively

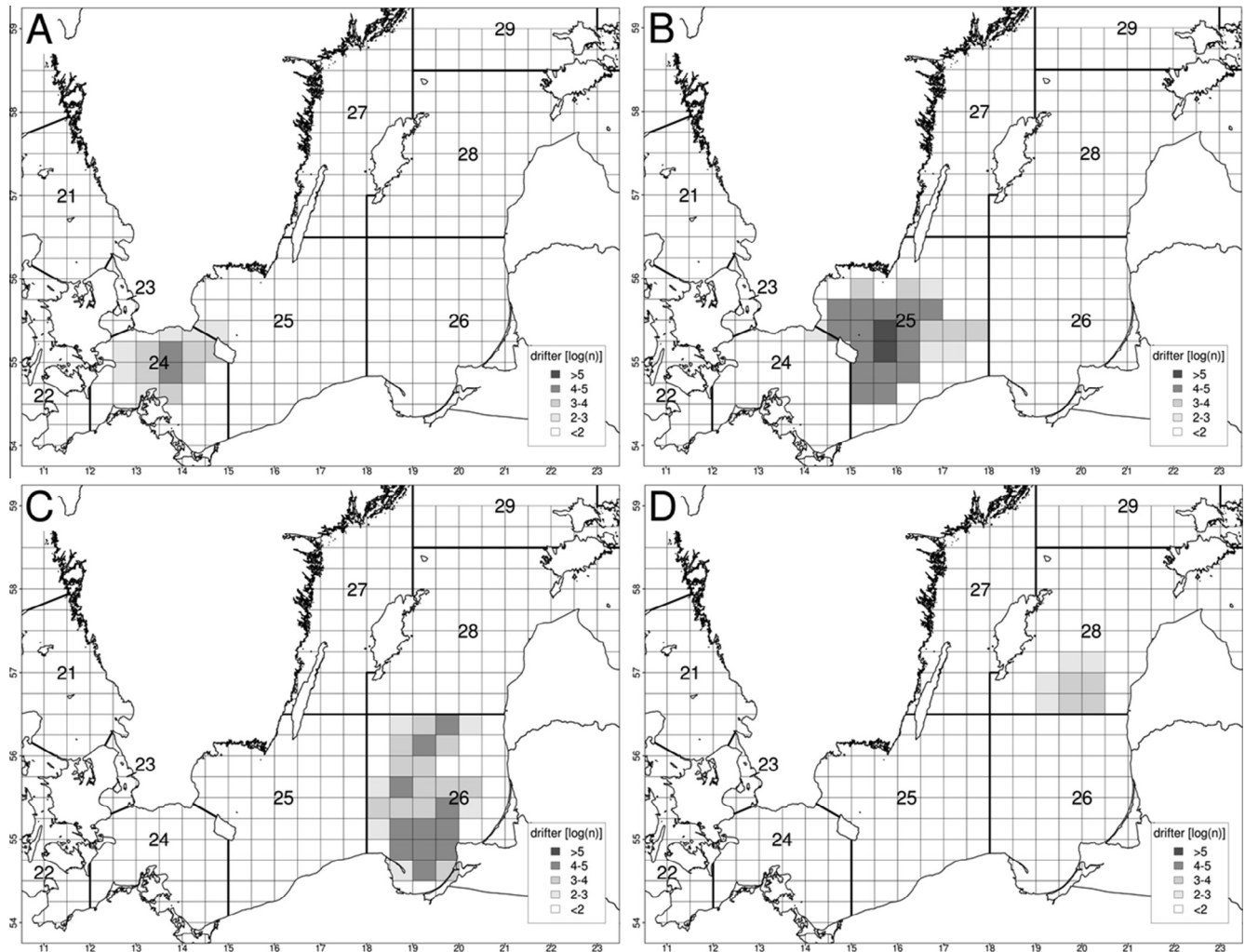


Fig. 8. Initial horizontal distribution of virtual drifters (1971–2010) representing surviving eastern Baltic cod first-feeding yolk-sac larvae (\log_{10} -transformed) successfully spawned in different spawning grounds in the central Baltic Sea (a) Arkona Basin, (b) Bornholm Basin, (c) in Gdansk Deep, and (d) in Gotland Basin.

drifting particles together with the temporally and spatially resolved abiotic environmental conditions along the trajectories. A major task of our study was to improve knowledge on the connectivity of eastern Baltic cod eggs and yolk-sac larval stages and their survival probabilities in relation to abiotic environmental conditions by including information on the vertical egg distribution. The eggs are released homogeneously on regular grids, i.e. our model study does not account for any spatial variability in egg production. This might be a task of future studies, coupled with spatio-temporal information on female abundance and age/size distributions to account for spatial heterogeneity in spawning aggregations and maternal effects on egg buoyancy.

For this study no information on changes in buoyancy during egg development was available. As observed for western Baltic cod eggs (Petereit et al., 2014), it could be expected that an egg buoyancy decrease during the last quarter of egg development would result in reduced egg survival probability, mainly caused by an increase in sedimentation or further exposure of eggs to detrimental oxygen concentrations.

This modelling study has clearly identified the role of different biophysical processes as drivers for mortality of Baltic cod egg and yolk-sac larvae. The results improve particularly the understanding of the impact of sedimentation as well as of oxygen deficiency and low temperatures on egg survival probability at small spatial scales. The model results indicate that traditional sampling

methodology is unable to resolve spatial egg distributions adequately without considering flow dynamics (Voss and Hinrichsen, 2003) in combination with the impact of abiotic conditions on egg survival. Furthermore, the model results on spatial distribution of Baltic cod egg survival probability could serve as drifter release locations representing the start of the first feeding larval stage, while the degree of survival probability could provide a reasonable measure of initial virtual larval abundance. Regardless of the specific information obtained for eastern Baltic cod, this study shows that hydrodynamic models and Lagrangian particle tracking methods provide an efficient tool to analyse the passive movements of fish early life stages and that the models may provide essential information to respond dynamically to the establishment of spatially varying fishing closures in relation to changes in transport patterns (Hinrichsen et al., 2009). According to advice given by ICES (2004) for eastern Baltic cod, closed areas could be set up dynamically in zones and at times corresponding to specific features like spatially and temporally varying spawning habitat suitability and cod egg survival probability (Hinrichsen et al., 2007). However, to dynamically implement closed areas is not an easy task to do, but our model results show the existence of areas with consistently higher survival probabilities, suggesting that these should be priority areas in marine spatial planning. Furthermore, our model exercise confirms results published by Huwer et al. (2014), where the location of an area closed to fishing in the Born-

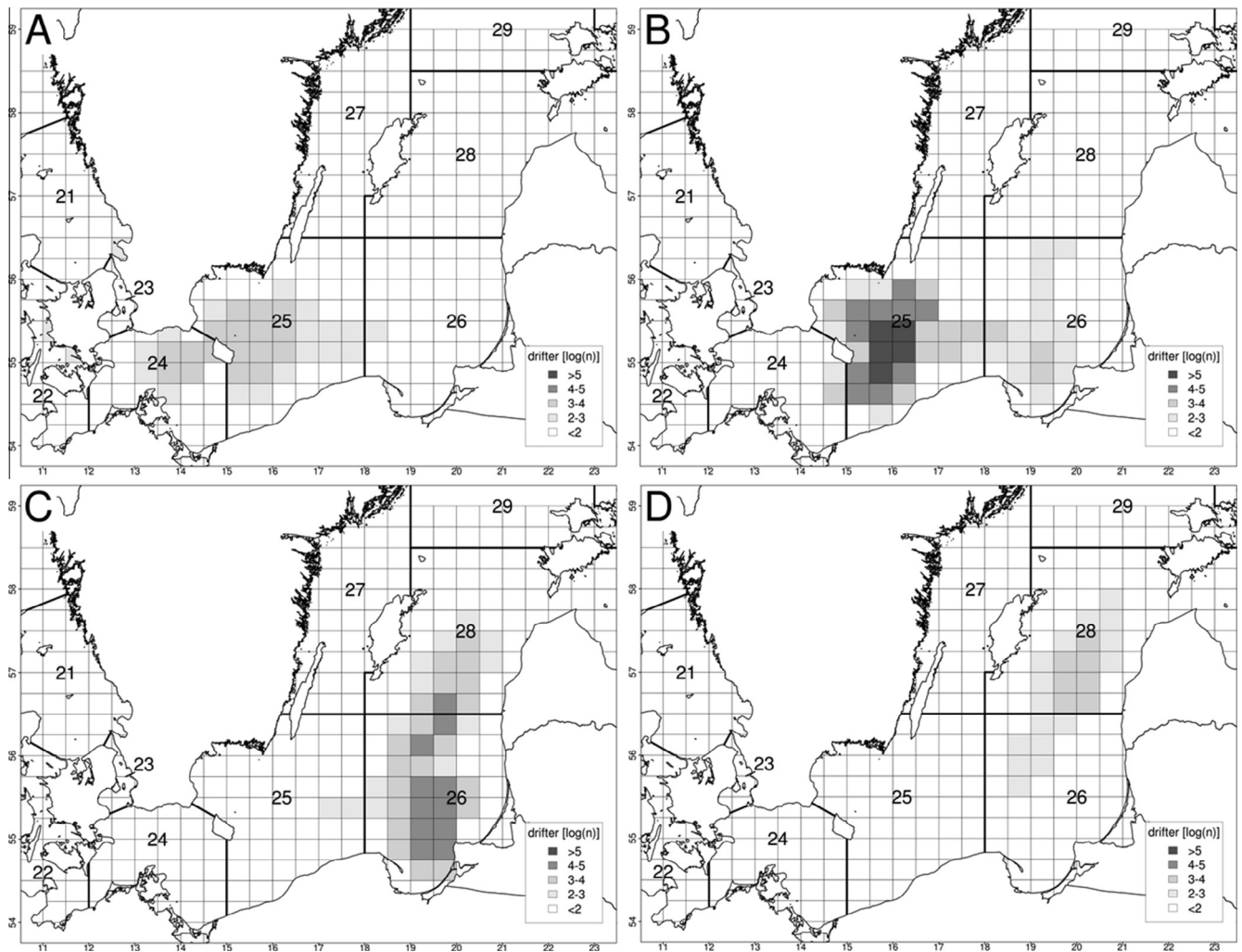


Fig. 9. Final horizontal distributions of virtual drifters (1971–2010) representing surviving eastern Baltic cod first-feeding yolk-sac larvae (\log_{10} -transformed) successfully spawned in different spawning grounds in the central Baltic Sea (a) Arkona Basin, (b) Bornholm Basin, (c) in Gdansk Deep, and (d) in Gotland Basin.

Table 1

Overall means and standard deviations of dispersal/retention patterns (percentages) of virtual drifters representing surviving eastern Baltic cod eggs until the yolk-sac larval stage. Bold numbers represent retention patterns within spawning grounds. West means further west than the Arkona Basin.

Spawning area	Drifter location at end of yolk-sac stage				
	West	Arkona	Bornholm	Gdansk	Gotland
Arkona	0.2 ± 0.8	1.0 ± 0.4	2.4 ± 3.2	0.0	0.0
Bornholm	0.0	0.1 ± 0.4	70.5 ± 29.6	0.6 ± 1.1	0.0
Gdansk	0.0	0.0	0.0	19.8 ± 24.7	3.1 ± 6.9
Gotland	0.0	0.0	0.0	0.3 ± 1.5	1.9 ± 10.5

holm Basin had only a low potential of effectively contributing to the enhancement of the Baltic cod stock, as the majority of offspring with a high survival probability were not spawned in the closed area.

Connectivity between spawning areas may also be due to passive dispersal of feeding larvae or pelagic juveniles, as shown by Hinrichsen et al. (2009) and migration of adults (Aro, 1989). This finding is interesting also from a homing behaviour perspective. If site imprinting appears already at the egg or yolk-sac larval stage, it would be important for these early stages not to spread from the spawning area during this period, for the adult cod to be able to find its way back to the spawning location of its ancestors.

Natal homing behaviour may be imprinted at earlier life stages, as they seem to be in herring in the North Sea region (Ruzzante et al., 2006). The kind of high-resolution hydrodynamic modelling presented in this study could together with novel genetic methods improve our understanding of the mechanisms regulating such stock separation.

Generally, the findings of our study underscore the potential role of environmental conditions for the recruitment success of this stock. Similar conclusions were derived previously by Köster et al. (2005), although their conclusions were based on the “reproduction volume concept”, where only simple indicators, e.g. based on single station observations, were used to describe overall integrated measures of spatially varying environmental process information (MacKenzie et al., 2000; Hinrichsen et al., 2007). In contrast to this previous approach, we are now able to disentangle spatio-temporally resolved distribution patterns of spawning habitat, environmental-related mortality and egg survival potential.

The main conclusion from our study is that topographic features in combination with hydrographic conditions can act as a barrier and potentially limit the transport of Baltic cod eggs and yolk-sac larvae between basins in the central Baltic. Egg buoyancy is positively correlated to female spawner age/size. The possibility of an advective exchange between the western and eastern spawning areas exists only for eggs at high buoyancy levels, suggesting that dispersal is limited to eggs spawned by older, larger females.

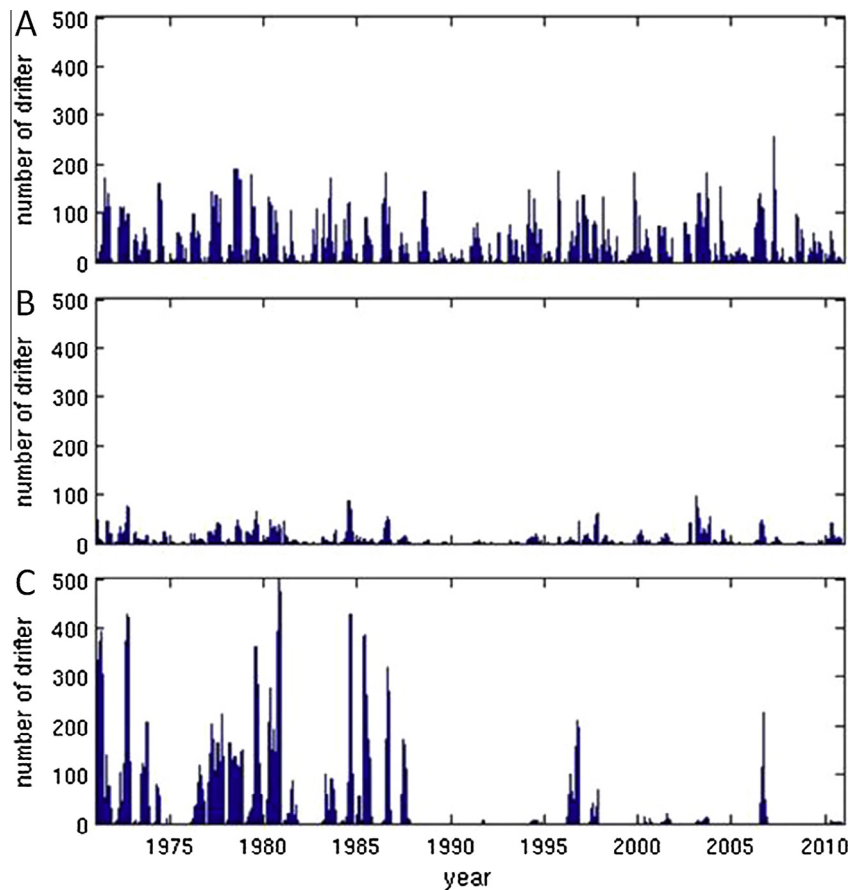


Fig. 10. Number of drifter representing intra- and interannual transport variations of surviving cod first-feeding yolk-sac larvae (a) from the Arkona to the Bornholm Basin, (b) from the Bornholm Basin to the Gdansk Deep, and (c) from the Gdansk Deep to the Gotland Basin. Bars represent the range of single release events.

However, potentially higher connectivity might have occurred in former times when the age structure of the stock was less truncated, the abundance of large old females was higher, and the oxygen conditions were more beneficial (see Fig. 10c). During the most recent decades, there was only a narrow salinity range available (11–13 psu), so that most of the eggs spawned in the most reproductively successful spawning ground (Bornholm Basin) would not meet the required neutral buoyancy levels for survival if they were transported eastwards. Hence, transport of eastern Baltic cod eggs and yolk-sac larvae from west to east will only be possible for offspring of older females. As the majority of the stock consists of young females, the stock components in the different geographical areas might not currently be connected via dispersal of eggs and yolk-sac larvae.

Generally, habitat suitability and cod egg and yolk-sac larval survival correspond to Baltic cod recruitment and abundance during the last decades by only a weak positive but significant relationship, suggesting that what happens after the yolk sac larval stage has an significant impact on recruitment and thus stock development. Earlier studies identified other factors to be related to reduction in salinity and oxygen as well as variations on prey availability for first-feeding larvae, egg predation by sprat and herring as well as cannibalism, all related to the prevailing hydrographic conditions (Köster et al., 2005).

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References

- 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*, vol. 190, pp. 72–96.
- Bagge, O., Thurow, F., Steffensen, E., Bay, J., 1994. The Baltic cod. *Dana* 10, 1–28.
- Berg, P.R., Jentoft, S., Star, B., Ring, K.H., Knutsen, H., Lien, S., Jakobsen, K.S., Andre, C., 2015. Adaptation to low salinity promotes genomic divergence in Atlantic cod (*Gadus morhua* L.). *Genome Biology and Evolution*. <http://dx.doi.org/10.1093/gbe/evv093>.
- 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.
- Bumke, K., Karger, U., Hasse, L., Niekamp, K., 1998. Evaporation over the Baltic Sea as an example of a semi-enclosed sea. *Contributions to Atmospheric Physics* 71 (2), 249–261.
- Hansen, J.L.S., Bendtsen, J., 2009. Effects of climate change on hypoxia in the North Sea–Baltic transition zone. *IOP. C. Ser. Earth Environ. Sci.*, 6, Copenhagen, Denmark, 10–12 March 2009, p. 302016.
- Hansen, J.L.S., Bendtsen, J., 2013. Parameterisation of oxygen dynamics in the bottom water of the Baltic Sea–North Sea transition zone. *Marine Ecology Progress Series* 481, 25–39.
- Hinrichsen, H.-H., Lehmann, A., St John, M.A., Brugge, B., 1997. Modeling the cod larvae drift in the Bornholm Basin in summer 1994. *Continental Shelf Research* 17, 1765–1784.
- 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., Möllmann, C., Köster, F.W., Kornilovs, G., 2002. Biophysical modelling of larval Baltic cod (*Gadus morhua*) growth and survival. Canadian Journal of Fisheries and Aquatic Sciences 59, 1858–1873.
- Hinrichsen, H.-H., Böttcher, U., Köster, F.W., Lehmann, A., St. John, M.A., 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., Möllmann, C., Schmidt, J.O., 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., Voss, R., Wieland, K., Köster, 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., Böttcher, U., Köster, 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.
- Hinrichsen, H.-H., Dickey-Collas, M., Huret, M., Peck, M.A., Vikebo, F.B., 2011. Evaluating the suitability of coupled biophysical models for fishery management. ICES Journal of Marine Science 68, 1478–1487.
- Hinrichsen, H.-H., Hüsey, K., Huwer, B., 2012. Spatio-temporal variability in western Baltic cod early life stage survival mediated by egg buoyancy, hydrography and hydrodynamics. ICES Journal of Marine Science 69, 1744–1752.
- Hüsey, K., 2011. Review of western Baltic cod (*Gadus morhua*) recruitment dynamics. ICES Journal of Marine Science 68, 1459–1471.
- Hüsey, K., Hinrichsen, H.-H., Huwer, B., 2012. Hydrographic influence on the spawning habitat suitability of western Baltic cod (*Gadus morhua*). ICES Journal of Marine Science 69, 1736–1743.
- Hüsey, K., Hinrichsen, H.-H., Mosegaard, H., Eero, M., Hemmer Hansen, J., Lehmann, A., Scherffenberg Lundgaard, L., 2015. Spatio-temporal trends in stock mixing of eastern and western Baltic cod in the Arkona Basin and the implications for recruitment. ICES Journal of Marine Science. <http://dx.doi.org/10.1093/icesjms/fsv227>.
- Huwer, B., Hinrichsen, H.-H., Böttcher, U., Voss, R., Köster, F.W., 2014. Characteristics of juvenile survivors reveal spatio-temporal differences in early life stage survival of Baltic cod. Marine Ecology Progress Series 511, 165–180.
- ICES, 2004. Report of the Study Group on Closed Spawning Areas of Eastern Baltic Cod (SGCSA). ICES Council Meetings Documents, ICES CM 2004/ACFM:17, pp. 1–98.
- Jonasson, L., Hansen, J.L., Wan, Z., She, J., 2012. The impacts of physical processes on oxygen variations in the North Sea–Baltic transition zone. Ocean Science 8, 37–48.
- Kjesbu, O.S., Klungsoyr, J., Kryvi, H., Witthames, P.R., Greer Walker, M., 1991. Fecundity, atresia, and egg size of captive Atlantic cod (*Gadus morhua*) in relation to proximate body composition. Canadian Journal of Fisheries and Aquatic Sciences 48, 2333–2343.
- Köster, F.W., Hinrichsen, H.-H., Schnack, D., St. John, M.A., MacKenzie, B.R., Tomkiewicz, J., Möllmann, 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 (Suppl. 1), 129–154.
- Köster, F.W., Möllmann, C., Hinrichsen, H.-H., Wieland, K., Tomkiewicz, J., Kraus, G., Voss, R., 2005. Baltic cod recruitment – the impact of climate variability on key processes. ICES Journal of Marine Science 62, 1408–1425.
- Kronsell, J., Andersson, P., 2012. Total regional runoff to the Baltic Sea. HELCOM Indicator Fact Sheets 2011. <<http://www.helcom.fi/environment2/ifs>>.
- Lehmann, A., Hinrichsen, H.-H., 2000a. On the thermohaline variability of the Baltic Sea. Journal of Marine Systems 25, 333–357.
- Lehmann, A., Hinrichsen, H.-H., 2000b. On the wind driven and thermohaline circulation of the Baltic Sea. Physics and Chemistry of the Earth (B) 25, 183–189.
- 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.
- Lehmann, A., Hinrichsen, H.-H., Getzlaff, K., Myrberg, K., 2014. Quantifying the heterogeneity of hypoxic and anoxic areas in the Baltic Sea by a simplified coupled hydrodynamic-oxygen consumption model approach. Journal of Marine Systems 134, 20–28.
- MacKenzie, B.R., Hinrichsen, H.-H., Plikshs, M., Wieland, K., Zezera, A.S., 2000. Quantifying environmental heterogeneity: estimating the size of habitat for successful cod egg development in the Baltic Sea. Marine Ecology Progress Series 193, 143–156.
- MacKenzie, B.R., 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.
- Neuenfeldt, S., Hinrichsen, H.-H., Andersen, K.H., 2009. Some Atlantic cod *Gadus morhua* visit hypoxic water briefly but often. Journal of Fish Biology 75 (1), 290–294.
- Nissling, A., 2004. Effects of temperature on egg and larval survival of cod (*Gadus morhua*) and sprat (*Sprattus sprattus*) in the Baltic Sea – implications for stock development. Hydrobiologia 514, 115–123.
- Nissling, A., Westin, L., 1997. Salinity requirements for successful spawning of Baltic and Belt Sea cod and the potential for cod stock interactions in the Baltic Sea. Marine Ecology Progress Series 152, 261–271.
- 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.
- Novotny, K., Liebsch, G., Lehmann, A., Dietrich, R., 2006. Variability of sea surface heights in the Baltic Sea: an intercomparison of observations and model simulations. Marine Geodesy 29, 113–134.
- Pacariz, S., Björk, G., Jonsson, P., Börjesson, P., Svedäng, H., 2013. A model study of the large scale transportation of fish eggs in the Kattegat in relation to egg density. ICES Journal of Marine Science 71, 345–355.
- Petereit, C., 2004. Experimente zum Temperatureinfluss auf frühe Entwicklungsstadien des Ostseesardines *Gadus morhua*. Dipl. thesis, University Kiel, 46pp.
- Petereit, C., Hinrichsen, H.-H., Franke, A., Köster, F.W., 2014. Floating along buoyancy levels: dispersal and survival in western Baltic fish eggs. Progress in Oceanography 122, 131–152.
- 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 Document CM 1993/J:22.
- Plikshs, M., Hinrichsen, H.-H., Elferts, D., Sics, D., Kornilovs, G., Köster, F.W., 2015. Baltic cod reproduction in the Gotland Basin: causes of annual variability. Acta Ichthyologica et Piscatoria 45 (3), 247–258.
- Rohlf, N., 1999. Aktivität und Vertikalwanderung der Larven des Ostseesardines (*Gadus morhua callarias*) während der Dottersackphase PhD thesis, Institute of Marine Sciences, Kiel. Berichte Institut für Meereskunde Kiel, Nr. 312, 60pp.
- Rudolph, C., Lehmann, A., 2006. A model-measurements comparison of atmospheric forcing and surface fluxes of the Baltic Sea. Oceanologia 48 (3), 333–380.
- Ruzzante, D.E., Mariani, S., Bekkevold, D., Andre, C., Mosegaard, H., Clausen, L.A.W., Dahlgren, T.G., Hutchinson, W.F., Hatfield, E.M.C., Torstensen, E., Brigham, J., Simmonds, E.J., Laikre, L., Larsson, L., Stet, R.J.M., Ryman, N., Carvalho, G.R., 2006. Biocomplexity in a highly migratory pelagic marine fish, Atlantic herring. Proceedings of the Royal Society B: Biological Sciences 273 (1593), 1459–1464.
- 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, vol. 178, pp. 553–559.
- 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., StJohn, 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., 2003. Sources of uncertainty in ichthyoplankton surveys: influence of wind forcing and survey strategy on abundance estimates. Journal of Marine Systems 43, 87–103.
- 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.
- Wieland, K., Waller, U., Schnack, D., 1994. Development of Baltic cod eggs at different levels of temperature and oxygen content. Dana 10, 163–177.



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Survival and dispersal variability of pelagic eggs and yolk-sac larvae of central and eastern baltic flounder (*Platichthys flesus*): application of biophysical models

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A hydrodynamic model coupled with a Lagrangian particle tracking technique was utilized to simulate spatially and temporally resolved long-term environmentally related (i) size of habitat suitable for reproduction, (ii) egg/yolk-sac larval survival, (iii) separation of causes of mortality, and (iv) connectivity between spawning areas of Baltic flounder with pelagic eggs. Information on reproduction habitat requirements and mortality sources were obtained from field or laboratory studies. In our modelling study we only quantified physical processes generating heterogeneity in spatial distribution of eggs and yolk-sac larvae, as e.g. predation is not accounted for. The spatial extent of eggs and larvae represented as modelled particles is primarily determined by oxygen and salinity conditions. The reproduction habitat most suitable was determined for the Gdansk Deep, followed by the Bornholm Basin. Relatively low habitat suitability was obtained for the Arkona Basin and the Gotland Basin. The model runs also showed yolk-sac larval survival to be to a large extent affected by sedimentation. Eggs initially released in the Arkona Basin and Bornholm Basin are strongly affected by sedimentation compared with those released in the Gdansk Deep and Gotland Basin. Highest relative survival of eggs occurred in the Gdansk Deep and in the Bornholm Basin. Relatively low survival rates in the Gotland Basin were attributable to oxygen-dependent mortality. Oxygen content had almost no impact on survival in the Arkona Basin. For all spawning areas mortality caused by lethally low temperatures was only evident after severe winters. Buoyancy of eggs and yolk-sac larvae in relation to topographic features appear as a barrier for the transport of eggs and yolk-sac larvae and potentially limits the connectivity of early life stages between the different spawning areas.

Keywords: connectivity, Egg buoyancy, environmental variability, Individual-Based modelling, mortality, retention vs. dispersal.

Introduction

The Baltic Sea is the largest brackish water area in the world, with a restricted water exchange through the Sound and the Belt Sea [ICES Subdivision (SD) 22 and 23, Figure 1], resulting in a gradient in salinity in the surface water from 9 in the western Baltic

Sea (SD 24) to 3 in the far north (SD 31, Voipio, 1981). In the deep basins of the Baltic proper, SD 24–28, there is also a vertical gradient with higher salinity (10–22) below the halocline (Voipio, 1981). Renewal of the bottom water is mainly driven by major inflows of saline, oxygenated water occurring under certain

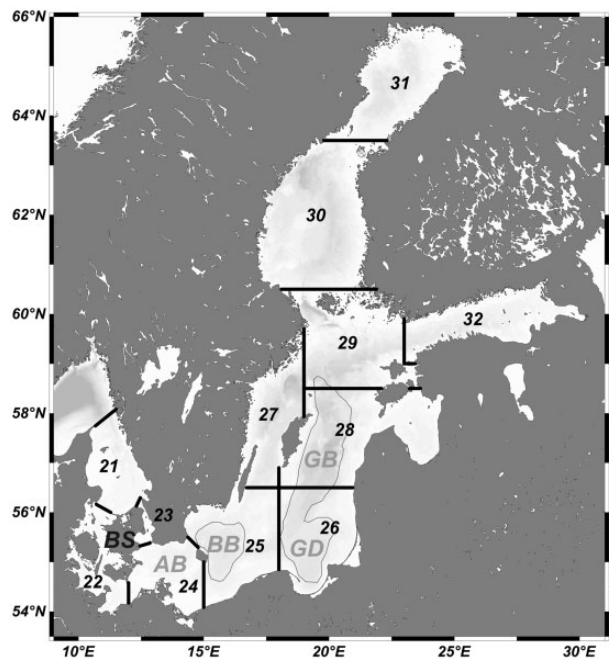


Figure 1. ICES SDs in the Baltic Sea and Baltic flounder spawning areas: BS, Belt Sea; AB, Arkona Basin; BB, Bornholm Basin; GD, Gdansk Deep; lines indicate 60 m depth contour.

meteorological conditions (Schinke and Matthäus, 1998). Stagnant conditions, accompanied by a decrease in salinity and oxygen concentration, may prevail for years (Franck *et al.*, 1987; Matthäus and Lass, 1995). Although major Baltic inflows may not occur for longer time periods, minor inflow events affecting only upper halocline water masses are recorded regularly (Lehmann *et al.*, 2014). The Baltic Sea is heavily affected by human activities including eutrophication which have led to large part of the deeper areas in the Baltic Sea being oxygen depleted (Conley *et al.*, 2002; Diaz and Rosenberg, 2008). This has been further aggravated by less frequent inflow events during the last decades, potentially an effect of climate change (Meier *et al.*, 2014).

The low salinity is a limiting factor for successful reproduction for most marine teleosts, directly by reducing fertilisation success and diminishing egg survival and indirectly by reduced buoyancy of eggs leading to pelagic eggs sinking into oxygen-depleted water or directly to the bottom where successful development is not possible (Nissling *et al.*, 2002; 2006). Thus, due to differences in tolerances and preferences among species, abundance and distribution of fish differ. Further, reproduction/recruitment varies spatially and temporally due to varying conditions affecting egg/larval survival and thus stock abundance and distribution. The system is highly influenced by the irregular inflow events of high salinity and oxygen rich water which to a large extent determines the reproductive success for marine fishes in the Baltic Sea (MacKenzie *et al.*, 2000; Nissling *et al.*, 2002; Casini *et al.*, 2011; Ustups *et al.*, 2013).

In marine ecosystems like the Baltic Sea, distribution variability of upper trophic level species is not only the result of their chosen environmental conditions, but is also influenced by dispersal of early life stages. However, passive drifting individuals (e.g. fish eggs and early larvae) are particularly vulnerable due to their lack of ability to avoid water masses with less favourable

environmental conditions for development and survival. Flounder (*Platichthys flesus*) in the Baltic Sea consists of two different ecotypes, one with pelagic eggs spawning at more saline conditions (10–20), e.g. below the halocline in the deep basins in SD 24–26 and 28, and one with demersal eggs spawning in the less saline water (ca 5–7) in shallow coastal areas at ~20 m depth and on offshore banks in the central, eastern and northern parts of the Baltic Sea (Bagge, 1981; Nissling *et al.*, 2002; Florin and Höglund, 2008; ICES, 2014). Both ecotypes share feeding areas along the coast during summer-autumn and winter in deeper areas, i.e. they are separated only during spawning in March–May. Within the pelagic eggs ecotype local adaptation with larger more buoyant eggs in the less saline eastern and central Baltic Sea compared with the western Baltic Sea has been observed, whereas egg characteristics within the demersal eggs ecotype seem to be the same irrespective of spawning area (Nissling *et al.*, 2002; Peterait *et al.*, 2014). After the larval stage in the pelagic zone above the halocline larvae undergo a metamorphosis, become flat, and settle in suitable nursery areas (<1 m depth sandy beaches) and feed on benthic fauna (Ustups *et al.*, 2007; Florin *et al.*, 2009; Martinsson and Nissling, 2011). Passive drift during the larval stage may affect recruitment by failure to transport larvae to suitable nursery areas (Riley *et al.*, 1981; van der Veer *et al.*, 2000).

The flounder is a commercially exploited species and advice for management is given yearly by ICES (e.g. ICES, 2015). In the last years there has been an extensive debate about stock structure of this species with a current suggestion of one stock with demersal eggs in SD 27, 29–32, and three different stocks of flounder with pelagic eggs: one in SD 22–23, one in SD 24–25 and one in SD 26 and 28 (ICES, 2015). There are major knowledge gaps related to whether connectivity of the flounder stock in the central and eastern Baltic Sea (ICES, 2014) is an important process (e.g. by dispersal of eggs and yolk-sac larvae).

Spatial and temporal distribution patterns of early life stages could be obtained by simulating survival and drift of eggs and yolk-sac larvae. Drift modelling studies have already been used for eastern Baltic cod (*Gadus morhua*) spawning in the Bornholm basin (SD 25) to investigate the dispersal dynamics of early life stages (Hinrichsen *et al.*, 2003a, 2016), the impact of dispersal on the survival of larvae (Hinrichsen *et al.*, 2001a, 2003b), and the influence of copepod species composition on the growth and survival of larvae (Hinrichsen *et al.*, 2002a). These studies also suggested the potential for considerable connectivity between areas through dispersal of early life stages (Hinrichsen *et al.*, 2001b; 2009).

In the western Baltic Sea (SD 22–23), dispersal patterns of flounder eggs and yolk-sac larvae have been recently modelled (Peterait *et al.*, 2014). Generally, the results suggest retention of early life stages as an important process, both under hydrodynamic inflow events and stagnant conditions. However, considerable variation in egg specific gravity among experimentally derived flounder egg batches was obvious, which could mirror a much more complex population structure than currently assumed. Mortality of modelled western Baltic flounder eggs was mainly caused by sedimentation (bottom contact) and/or lethal temperatures, while oxygen content was not expected to be a major cause of egg mortality, because model results suggested that eggs were exposed to a generally high saturation level (Peterait *et al.*, 2014). On the contrary for fish spawning in the central and eastern deep basin oxygen conditions are crucial

(Bagge, 1981; Grauman, 1981; MacKenzie *et al.*, 2000). One of today's major challenges for modelling the central and eastern Baltic Sea ecosystem, i.e. the simulation of deep water dissolved oxygen distribution with its seasonal and quasi-permanent extended areas of oxygen deficiency, has been successfully performed by Lehmann *et al.* (2014). Since mortality of eastern Baltic cod early life stages was shown to be severely affected by oxygen content (Hinrichsen *et al.*, 2016), the oxygen content as a major contributor to egg mortality for the central and eastern Baltic flounder stock should be taken into consideration.

The objectives of this manuscript are to analyse the effects of environmental variability on the spatial and temporal distribution of early life stages of one of the most widely distributed, and commercially important, marine fish species in the Baltic Sea, the European flounder. We aim to reveal egg survival probabilities and drift/dispersal of flounder of the pelagic egg ecotype in the eastern and central Baltic Sea (SD 24–26 and 28) with similar spawning strategy/spawning areas as cod but with somewhat different threshold levels for egg survival due to egg specific gravity and different vertical egg distribution patterns. We simulate spatio-temporal differences in egg survival rates within the main spawning areas of the stock in relation to season and year and use drift modelling to test, whether along the drift routes of simulated eggs and yolk-sac larvae the experienced environmental conditions in the different spawning areas are (i) suitable for reproduction, (ii) suitable for egg and yolk-sac larval survival, and (iii) estimate the population connectivity of central and eastern Baltic flounder early life stages between the different spawning areas.

Material and methods

Hydrodynamic modelling

The basis of the Lagrangian particle tracking is the hydrodynamic Kiel Baltic Sea Ice-Ocean Model (BSIOM, Lehmann and Hinrichsen, 2000; Lehmann *et al.* 2002). The model 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). Prognostic variables are the baroclinic current field, the 3D temperature, salinity and oxygen distributions, the 2D surface elevations and the barotropic transport. The horizontal resolution of the coupled sea-ice ocean model is at present 2.5 km, and in the vertical 60 levels are specified, which enables the upper 100 m to be resolved into levels of 3 m thickness. The model domain comprises the Baltic Sea, Kattegat, and Skagerrak. The oxygen conditions in the entire Baltic Sea are described by an oxygen consumption sub-model coupled to BSIOM (Lehmann *et al.*, 2014). At the western boundary, a simplified North Sea is connected to the model domain to represent characteristic North Sea water masses in terms of characteristic temperature and salinity profiles resulting from the different forcing conditions. The coupled sea ice-ocean model is forced by realistic atmospheric conditions taken from the Swedish Meteorological and Hydrological Institute (SMHI Norrköping, Sweden) meteorological database (Lars Mueller, pers. comm.) which covers the whole Baltic drainage basin on a regular grid of $1 \times 1^\circ$ with a temporal increment of 3 h. The database consists of synoptic measurements (including geostrophic wind, 2-m air temperature, 2-m relative humidity, surface pressure, cloudiness, and precipitation) that were interpolated on the regular grid with a two-dimensional optimum interpolation scheme. This database,

which for modelling purposes was further interpolated onto the model grid, includes surface pressure, precipitation, cloudiness, air temperature and water vapour mixing ratio at 2 m height and geostrophic wind. Wind speed and direction at 10 m height were calculated from geostrophic winds with respect to different degrees of roughness on the open sea and off the coast (Bumke *et al.*, 1998). BSIOM forcing functions, such as wind stress, radiation and heat fluxes were calculated according to Rudolph and Lehmann (2006). Additionally, river runoff was prescribed from a monthly mean runoff data set (Kronsell and Andersson, 2012). The model is also forced by low frequency sea level variations in the North Sea/Skagerrak (Baltic Sea Index, Lehmann *et al.*, 2002; Novotny *et al.*, 2006). The numerical model BSIOM has been run for the period 1971–2010. This time series was used for the subsequent analysis of habitat suitability and early life stage survival in the Baltic.

Environmental threshold levels

Simulated habitat suitable for reproduction is exclusively based on the required environmental threshold limits of particles released as spawned eggs, i.e. the stage Ia. Other additional information which might be of relevance for the determination of habitats such as adult behaviour or fecundity could not be considered due to the lack of stock specific flounder data. The environmental threshold levels for egg survival were based on field and laboratory experiment-based minimum requirements for temperature and oxygen. At oxygen levels $< 1.0 \text{ ml O}_2 \text{ l}^{-1}$, or temperatures $< 2.0^\circ \text{C}$ development fails and the eggs die or result in inferior larvae (Vitinsh, 1980; Grauman, 1981; Bagge 1981). More than 90% survival occurred at $4\text{--}10^\circ \text{C}$ but significantly lower at 2°C with a higher fraction of inferior larvae. Although high temperatures become increasingly detrimental to egg development, this effect could be disregarded, since temperatures $> 10^\circ \text{C}$ are not expected. Moreover, egg development and consumption of yolk sac is strongly temperature dependent, with development times decreasing exponentially from around 45 to 15 days with increasing temperature (Figure 2; data source and method are described in Appendix 1). A salinity of ~ 10 is needed for spermatozoa activation and fertilisation (Nissling *et al.*, 2002). However, based on egg specific gravity measurements, successful reproduction of flounder with pelagic eggs is restricted by the ability to obtain neutral egg buoyancy. Observed minimum egg specific gravity, 1.0079 g/cm^3 (calculated as average egg specific gravity in SD 28, subtracted 2.326 standard deviations, corresponding to the 1 and 99% percentiles of a normal distribution, verified by observations *in situ* in the main spawning areas) corresponds to a salinity of 10.2 (Nissling *et al.*, own data), i.e. 98% of all egg batches are included. Since some discrepancies between areas have been observed (Nissling *et al.*, 2002) we used a salinity of 12.0 for SD 24, 10.8 for SD 25 and 10.2 in SD 26 and 28 as minimum salinity for neutral egg buoyancy in the respective spawning area (Table 1; data source and method are described in Appendix 1). Eggs being neutrally buoyant at salinity levels exceeding those at the bottom presumably die due to sedimentation, while eggs displaying neutral buoyancy at lower salinities ensure them to be buoyant and to float in the water column (e.g. Nissling *et al.*, 1994).

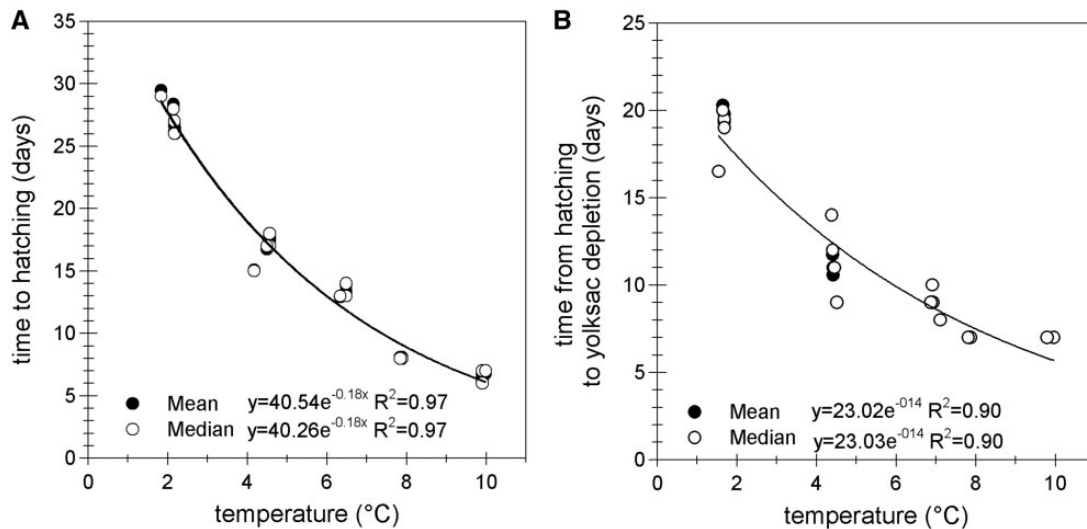


Figure 2. Relationship between (a) time to hatching and (b) time from hatching to yolk-sac depletion, and temperature for Baltic flounder based on incubations of eggs/larvae at different temperatures after stripping and artificial fertilization. Equations of the relationship based on mean and median values, respectively are given.

Table 1. Egg specific gravity/buoyancy of pelagic flounder eggs, based on average \pm 2.326*SD (corresponding to 98% of egg batches).

SD	N	Density g/cm3	Salinity (psu)	Range (psu)
26 + 28	69	1.00791–1.01119	10.2–14.3	4.1
25	29	1.00842–1.01416	10.8–18.1	7.3
24	13	1.00936–1.01504	12.0–19.3	7.3

Particle tracking, drift model and reproduction habitat suitability

Simulated three-dimensional velocity fields were extracted (at 3 h intervals) from the hydrodynamic model in order to develop a database for a particle tracking method. This data set offers the possibility to derive Lagrangian drift routes by calculating the advection of “marked” water particles. Simulated drift routes were obtained from Eulerian flow fields by utilization of a Lagrangian particle-tracking technique. The three-dimensional trajectories of the simulated particles were computed using a fourth order Runge-Kutta scheme (Hinrichsen *et al.*, 1997). Particles representing flounder eggs at developmental egg stage Ia (Thompson and Riley, 1981) were released into the simulated flow fields in each of the respective spawning areas (ICES subdivisions) and were tracked through the different egg stages as well as the yolk-sac larval stage. If the released eggs at spawning survived in response to the required environmental condition, their area and volume extensions determined the habitat suitability for reproduction. As a second step particles were exposed to hydrographic property fields along the drift routes with high temporal and spatial resolution provided by the hydrodynamic model (temperature, salinity and oxygen). The hydrographic information was used to calculate the development time of the eggs/yolk-sac larvae as well as the environmentally-related mortalities. Each release of particles consisted of particles distributed within the main spawning areas of the central Baltic Sea (ICES SD 24, 25, 26, and 28, see Figure 1), with a horizontal resolution of 4.5 km and in the

vertical at 3 m steps. This allows to quantitatively account for intra- and interannual variability of the flounder spawning habitat size in terms of reproduction volumes. Those particles which initially (at release) survived according to the above described spawning area-specific threshold values ($T > 2^{\circ}\text{C}$, $\text{O}_2 > 1\text{ ml/l}$), have been counted as particles representing successfully spawned flounder eggs at developmental stage Ia. For those particles representing successfully spawned Baltic flounder eggs, their initial neutral buoyancy (water density) levels were calculated based on the ambient hydrographic conditions (temperature and salinity). Eggs that were not able to obtain neutral buoyancy at stage Ia (Table 1; see Appendix 1) were not included in the drift modelling, thus, the number of particles varied between release events corresponding to the habitat suitability conditions. In order to provide intra-annual distribution variability of flounder early life stage mortality and survival, the particles were released every 10 days from 1 February to 31 July. During their drift, eggs and yolk-sac larvae floated at the initially spawning area-specific assigned density/buoyancy levels (Table 1; see Appendix 1). If their initially assigned density level was found to be higher than those available at the bottom along the positions of the drift route the eggs were assumed to die due to sedimentation. Similarly, the eggs also died if they were exposed to lethal temperature ($< 2.0^{\circ}\text{C}$), oxygen ($< 1.0\text{ ml/l}$), or salinity (< 10.2 and > 12 resulting in low spermatozoa activation and fertilisation success) conditions. For individual particles that died during the simulations, the positions where death occurred were recorded, while for the surviving particles the final positions reached at the end of the yolk-sac stage were noted.

Estimation of survival and mortality and model experiment design

Duration of the drift period until the end of the yolk-sac larval stage was based on the temperature-dependent developmental time (Figure 2, see Appendix 1) and was provided by the hydrodynamic model, i.e. temperature-dependent development from stage Ia eggs to the yolk-sac larval stage was calculated along the

drift paths of individual particles. The simulations were stopped when yolk-sac larvae reached the first feeding larval stage (mouth opening), because for feeding purposes the larvae migrate into the near surface layers. Drift simulations of the later larval and juvenile stages were not subject of this manuscript, because other processes (e.g. swimming ability, ontogenetic shift and subsequent settlement) have to be taken into account. However, this will be included in future studies on the drift of these later early life stages of Baltic flounder.

Spawning time and spawning areas

The focus of this study is on the central and eastern Baltic flounder's general reproduction potential for the whole spawning season. These stocks are known to generally spawn from March to June, with the main spawning season differing between different parts of the Baltic Sea (SD 24 March–April, SD 25 March–May, SD 26–28 March–June; Bagge 1981).

Results

Spatially disaggregated patterns of habitat suitability for reproduction

The probabilities of successful particle release (habitat suitability for reproduction) of central and eastern Baltic flounder eggs is shown in Figures 3–6 (long-term trends are presented in Appendix 2). Generally, the spatial patterns showed almost constant habitat suitability throughout the time period in the Arkona Basin (ICES SD 24, Figure 3a) while for the Bornholm Basin (ICES SD 25, Figure 4a) stronger inter- and intra-annual variability occurred. Best habitat suitability was revealed for the first half of the time series in the Gdansk Deep (ICES SD 26, Figure 5a) with lower levels and higher intra- and inter-annual variability during the most recent decades. Similar conditions, but with strong inter- and intra-annual variability were observed in the Gotland Basin (ICES SD 28, Figure 6a), however, for some years in the 1990s and 2000s the habitat was not suitable for egg and yolk-sac larval survival.

Spatially disaggregated patterns of mortality

Differences in survival probability are caused by spatial and temporal variations of different mortality sources. Generally, predicted temperature-related mortality was low as released particles were not subject to sub-lethal temperatures and could be noticed only in the Arkona and Bornholm Basin (ICES SDs 24 and 25) due to cold water temperatures after severe winters. On the contrary, an expected relatively high impact on survival rates in the Gdansk Deep (ICES SD 26, Figure 5b) and especially in the Gotland Basin (ICES SD 28, Figure 6b) was attributable to predicted oxygen-dependent mortality. Oxygen-related mortality was more important in the Gdansk Deep, but highest temporal variability of predicted oxygen-dependent mortality was observed in the Gotland Basin. Low oxygen content had almost no impact on survival in the Arkona Basin (ICES SD 24, Figure 3b) and in the Bornholm Basin (ICES SD 25, Figure 4b). In these areas the majority of eggs (on average >50%) died due to sedimentation (Figures 3c and 4c). Bottom contact of the flounder eggs also played a significant role in the Gdansk Deep (Figure 5c), while it was almost negligible in the Gotland Basin (Figure 6c).

Spatially disaggregated patterns of survival probability

When compared with the habitat suitable for reproduction (released particles within the environmental thresholds limits), only relatively low survival of central and eastern Baltic flounder eggs up to the yolk-sac larval period was observed in the Arkona Basin (ICES SD 24, Figure 3d) and in the Gotland Basin (ICES SD 28, Figure 6d), while higher survival was obtained for the Bornholm Basin (ICES SD 25, Figure 4d) and in the Gdansk Deep (ICES SD 26, Figure 5d). For the two analysed westernmost spawning areas (Arkona and Bornholm Basin) relatively constant levels of survival probability occurred. Contrary, for the Gdansk Deep and the Gotland Basin the modelled egg survival was relatively high during the first half of the time series but with lower values for the second half. Especially in the Gotland Basin egg survival was on a low level since the 1990s.

Geographic patterns of egg survival probability

The long-term spatial distribution (1971–2010) of surviving eggs (stage Ia) originating in the spawning areas of the different SDs, represented by the particle release positions, is illustrated in Figure 7. For particles released in the SDs 24, 25, and 28, the horizontal distribution maps clearly show highest concentrations of survivors originating from the central areas. In contrast, survivors of SD 26 originated from a more widely distributed spawning area over almost the entire areas of this SD. The spatial distribution of the particle endpoints (Figure 8) is based on the same egg cohorts. Generally, the particle distributions revealed retention of surviving eggs and yolk-sac larvae in their SDs; however, there indication for dispersal (transport to neighbouring SDs) was shown. Eggs spawned in the SD 24 were mainly transported towards the SD 25 area, while a relatively small fraction of survivors from SD 25 was advected to SD 26. Strongest dispersal was observed from SD 26 towards 28 as well as northward into SD 29. From SD 28 a minor fraction dispersing towards SD 26 as well as northward into SD 29 occurred.

Connectivity patterns of eggs and yolk-sac larvae

To quantify the connectivity patterns of central and eastern Baltic flounder early life stages, we calculated retention within and advective transport rates of eggs and yolk-sac larvae between ICES subdivisions (Table 2). The long-term mean survival probability of eggs and yolk-sac larvae calculated for the whole simulation period (1971–2010) were dominated by retention of particles in the ICES SDs 25, 26, and 28. However, in total SD 25 contributed on average to 39% and SD 26 around 42% of survivors to the overall production of yolk-sac larvae. This can be compared with 16% from SD 28 and merely around a 3% contribution from SD 24. For particles initially released at the spawning ground in SD 26 a relatively high probability of transport towards SD 28 (8%) was estimated and for particles released in SD 24 2% were transported to SD 25. In contrast, westward transport is in general of only minor importance.

Intra- and interannual reproduction potential of central and eastern Baltic flounder spawning grounds

The numerical simulations showed remarkable inter- and intra-annual differences in survival of flounder yolk-sac larvae. Relative survival of flounder yolk-sac larvae in their different spawning grounds are presented in Figure 9. From our modelling exercise it

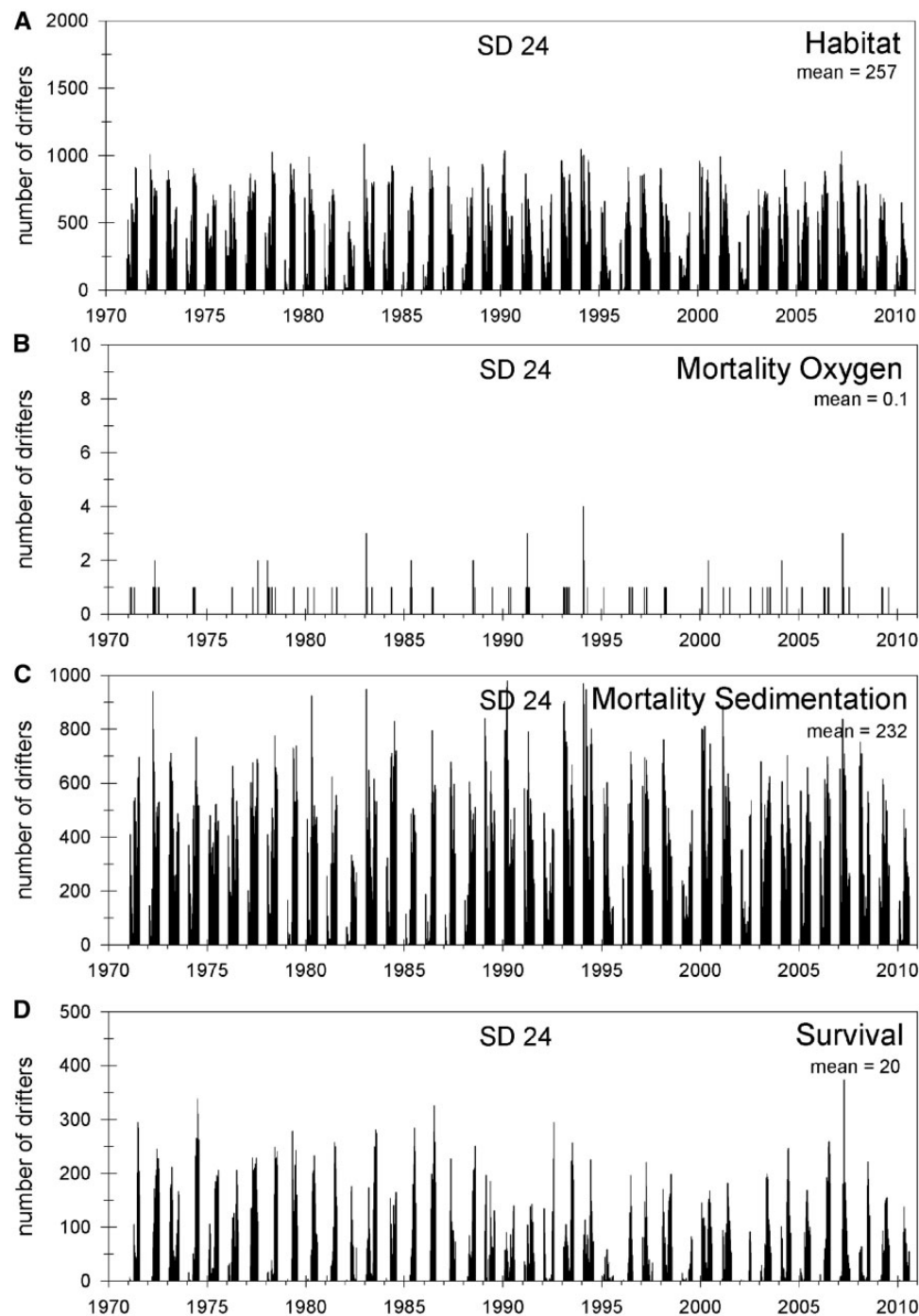


Figure 3. Number of particles representing the Arkona Basin (ICES SD 24) Baltic flounder spawning ground (a) reproduction habitat suitability (released as initially successfully spawned flounder eggs), (b) relative oxygen-related mortality of flounder eggs during drift, (c) relative mortality of flounder eggs caused by sedimentation during drift, and (d) relative survival of flounders eggs until the first-feeding yolk-sac larval stage. Bars represent the range of single release events.

becomes evident that reproduction in terms of survival was highest in the Bornholm Basin. Here, for many years since the end of the late 1980s, relative survival reached a maximum of 75%, while before the late 1980s, the same survival was also obtained for the Gdansk Deep and occasionally on a similar level in the Gotland Basin. Throughout the entire time period relative survival was lowest in the Arkona Basin.

Discussion and conclusions

Survival probabilities related to abiotic factors

For the first time survival probabilities and dispersal of flounder eggs and early larvae in the central and eastern Baltic have been considered and show that survival probabilities vary greatly, both spatially and temporally with causes of mortality differing

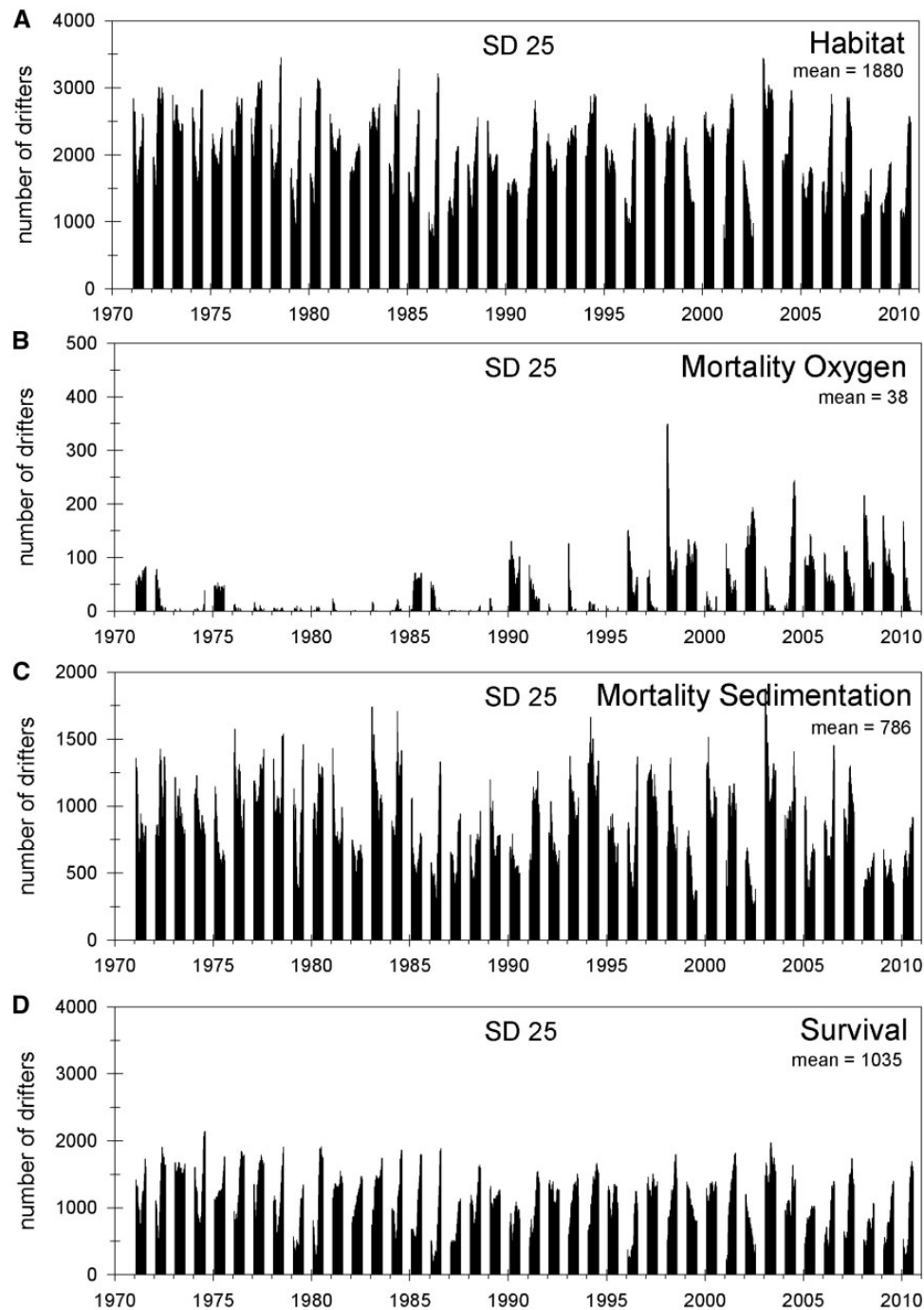


Figure 4. Number of particles representing the Bornholm Basin (ICES SD 25) Baltic flounder spawning ground (a) reproduction habitat suitability (released as initially successfully spawned flounder eggs), (b) relative oxygen-related mortality of flounder eggs during drift, (c) relative mortality of flounder eggs caused by sedimentation during drift, and (d) relative survival of flounders eggs until the first-feeding yolk-sac larval stage. Bars represent the range of single release events.

between basins. The highest survival probabilities occurred in SD 26 (Gdansk Deep) with a decrease since the beginning of the 1990s. Estimated survival probabilities were of the same level in SD 25 compared with SD 26, but with no decreasing trend, low in SD 24 and highly variable in SD 28 with a minor decreasing trend. The importance of favourable salinity and oxygen conditions for the reproductive success (Nissling *et al.* 2002; Casini *et al.*, 2011; Ustups *et al.* 2013) of eastern Baltic flounder is clearly

visible, e.g. the dependency of saline water inflows from the North Sea, but additionally sedimentation is an important source of mortality, especially in SD 24, 25 and 26.

Sedimentation and temperature-related mortality

Similar to previous research on early life stage processes on eastern Baltic cod (Pacariz *et al.*, 2013; Hinrichsen *et al.* 2016), the

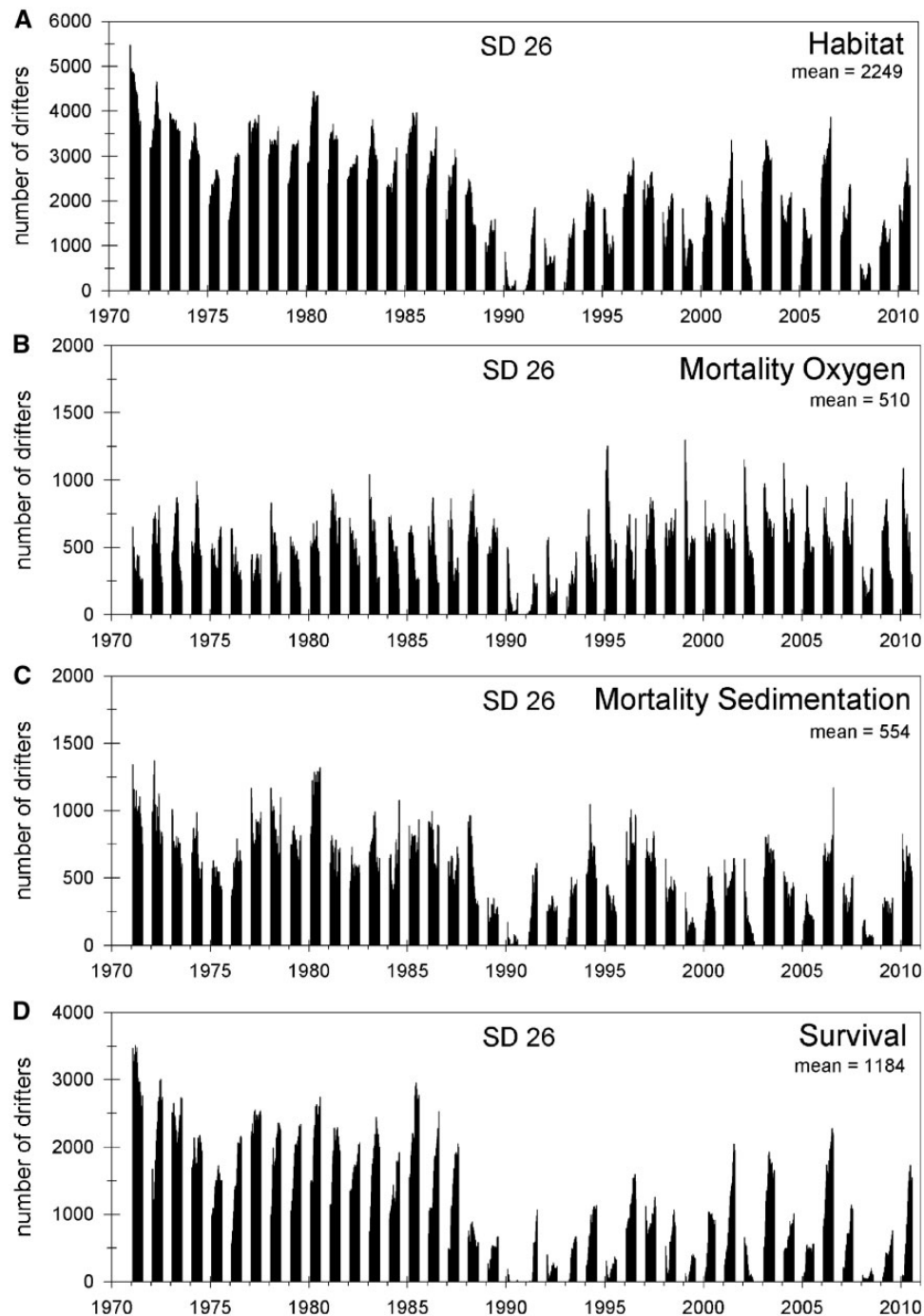


Figure 5. Number of particles representing the Gdansk Deep (ICES SD 26) Baltic flounder spawning ground (a) reproduction habitat suitability (released as initially successfully spawned flounder eggs), (b) relative oxygen-related mortality of flounder eggs during drift, (c) relative mortality of flounder eggs caused by sedimentation during drift, and (d) relative survival of flounders eggs until the first-feeding yolk-sac larval stage. Bars represent the range of single release events.

finding of sedimentation derived mortality is rather new. If the assumption of egg mortality upon bottom contact is true, then this source of mortality is predicted to be relatively high compared with mortality affected by sub-lethal temperature and oxygen conditions. However, for any field-based validation of sedimentation-related mortality, no functional sampling gear which reliably samples the boundary layer between substrate and

water column and would allow the determination of the condition of the egg exists. It remains a challenge to collect eggs from soft bottom, which constitutes by far the largest area of substrate where eggs are lost due to sedimentation. To the author's knowledge the direct evidence (either derived by observations or experiments) of our assumption that eggs do not survive if hitting the bottom (sedimentation) has not yet been published in the

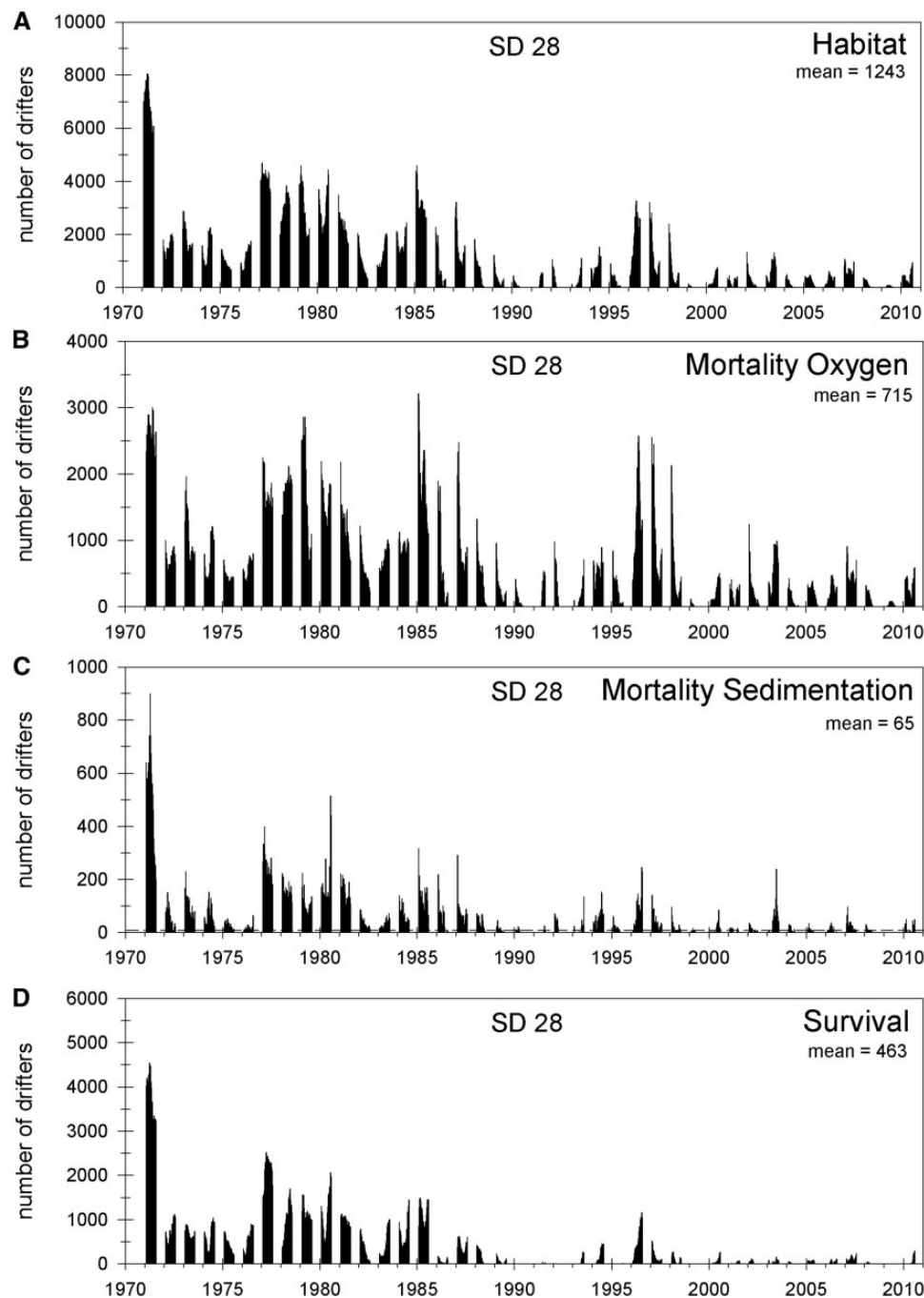


Figure 6. Number of particles representing the Gotland Basin (ICES SD 28) Baltic flounder spawning ground (a) reproduction habitat suitability (released as initially successfully spawned flounder eggs), (b) relative oxygen-related mortality of flounder eggs during drift, (c) relative mortality of flounder eggs caused by sedimentation during drift, and (d) relative survival of flounders eggs until the first-feeding yolk-sac larval stage. Bars represent the range of single release events.

literature. The likelihood for fragile pelagic eggs to survive these conditions, like potential predation pressure or exposure to benthic fungi, is at least largely reduced. A large body of recently published studies shares this assumption (Hinrichsen *et al.*, 2012; Hüsey *et al.*, 2012; Pacariz *et al.*, 2013; Petereit *et al.*, 2014).

Although temperature was shown not to be an important source of mortality, temperature directly affects developmental time and thus the probabilities for sedimentation and dispersal,

e.g. the simulations provided temperature-dependent egg and yolk-sac larval stage durations of 45 days at low and only 15 days at high temperatures. Hence, not only sedimentation mortality can be expected but also strong intra-annual variability of predation mortality (see below), with the highest impact of predation potentially occurring during the early spawning season of Baltic flounder. Furthermore, spatial differences in temperature among spawning grounds (increasing from west to east) as well as

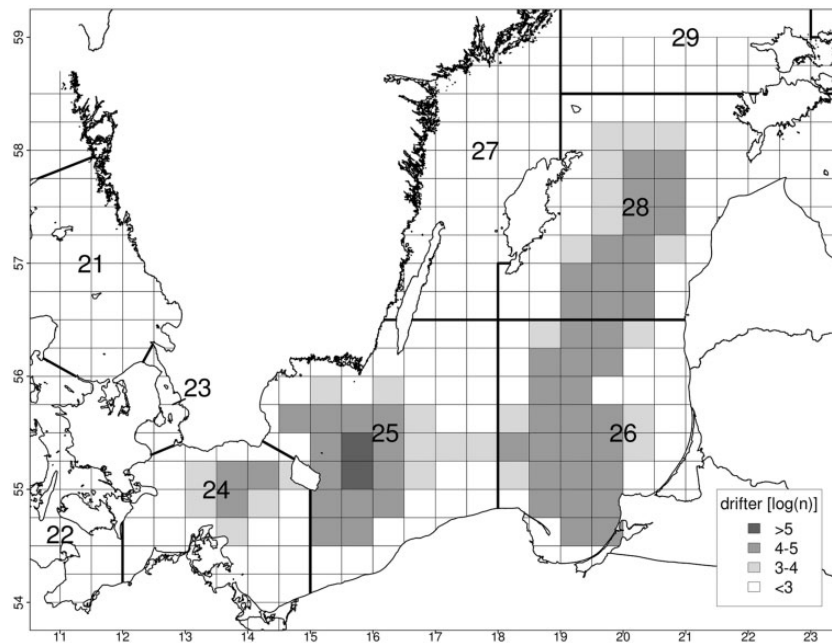


Figure 7. Origin (release areas) of particles (1971–2010) representing Baltic flounder first-feeding yolk-sac larvae (\log_{10} -transformed) successfully spawned in different spawning grounds in the central and eastern Baltic Sea (Arkona Basin, Bornholm Basin, in Gdansk Deep, and in Gotland Basin).

differences in spawning time (early in the west and later in the east), might explain why the SD 24 (Arkona Basin) appears to be a highly used spawning ground despite low egg and yolk-sac larval survival.

Additional mortality sources during drift period

The here presented abiotic environment-dependent mortality sources could only partly contribute to the determination of the overall absolute survival of the flounder early life stages from the egg stage Ia to the end of the yolk-sac stage (mouth opening). First of all, it is presently impossible to specifically quantify these mortality sources, because no field based or laboratory-based experiments describing environmentally driven relationships, as e.g. for eastern Baltic cod (Köster *et al.*, 2005), are available. For example, we lack relationships between oxygen/temperature and egg survival for flounder derived from laboratory experiments or field studies. Due to the lack of field data on the vertical distribution of flounder eggs, as a simplification particles representing successfully spawned eggs were distributed only evenly every 3 m. When compared with *in situ* conditions, vertical egg distributions vary in accordance with variability in egg specific gravity (assuming normal distribution), i.e. most eggs will obtain neutral buoyancy at water densities corresponding to average egg specific gravity and fewer at water densities corresponding to the lower and upper range. Second, mortality attributed to abiotic factors interacts with key biotic factors, such as encounter with predators (Bailey and Houde, 1989). Based on estimates for Baltic cod and sprat (Voss *et al.*, 2011; Neumann *et al.*, 2014), it is evident that our modelled environment-driven abiotic mortality rates accounted for only a part of the total mortality. Usually, estimates of field-based total mortality rates rely on daily egg production of different egg stages (Voss *et al.*, 2011), which could be compared with independent estimates obtained from cohort analyses.

To our knowledge, calculations of any kind of field-based total mortality rates have never been performed for Baltic flounder. Consequently, we have to consider the results of our mortality calculations to be an underestimate of the total mortality.

Drift related dispersal patterns vs. Current ICES stock management units

Concerning dispersal the results revealed dominance for retention (although an east-northward dispersal was observed from SD 26 to 28) apart from SD 24 where the majority of eggs/larvae were transported into SD 25.

The current stock unit of western Baltic flounder (SD24 + 25) seems to be justified by the relatively strong drift from SD 24 into SD 25 and the retention of larvae in SD 25. Furthermore SD 24 by itself has very little contribution of larvae surviving to the end of the yolk-sac stage, hence it could be questioned to what extent it could be a self-sustaining population. Although there is some drift from SD 25 into SD 26 it is minor compared with the number of surviving larvae spawned in SD 26 and retained in SD 26. From SD 26 there is however a contribution to SD 28 and also some larvae in SD 26 originating from SD 28. Hence the stock units of SD 26 and 28 also seem to be justified from an egg and larval connectivity perspective.

Temporal and spatial survival probabilities in relation to other stock measures and critical periods

Looking at the trends in environment-related survival probabilities of eggs and yolk-sac larvae in the respective spawning area (Figures 3–6), an increasing trend is shown for SD 25 while decreasing over time in SD 26 and 28 with a notable change in the late 1980s/early 1990s. Interestingly, despite the stable egg to yolk-sac larval survival of flounder in SD 24 and 25 the stock has

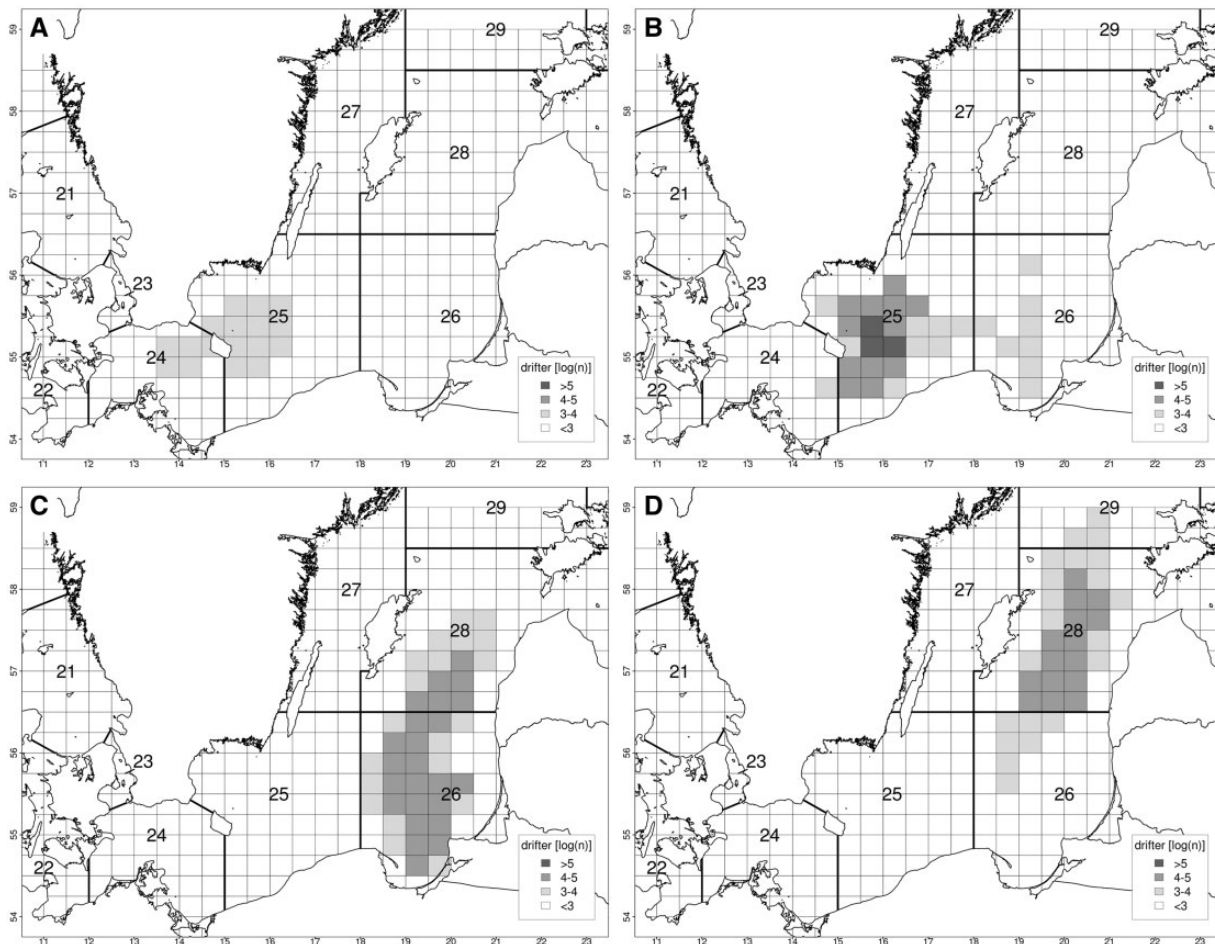


Figure 8. Final horizontal distributions of particles (1971–2010) representing surviving Baltic flounder first-feeding yolk-sac larvae (\log_{10} -transformed) successfully spawned in different spawning grounds in the central and eastern Baltic Sea (a) Arkona Basin, (b) Bornholm Basin, (c) in Gdansk Deep, and (d) in Gotland Basin.

Table 2. Overall means and standard deviations of dispersal/retention patterns (percentages) of particles representing surviving of central and eastern Baltic flounder eggs until the yolk-sac larval stage.

Spawning area	Particle location at end of larval yolk-sac stage					Total contribution
	West	SD 24	SD 25	SD 26	SD28	
SD 24	0.1±0.4	0.8±1.4	1.9±2.1	0.0±0.1	0.0	2.8±1.7
SD 25	0.0	0.1±0.2	37.8±14.	0 1.1±1.3	0.0±0.	39.0±13.6
SD 26	0.0	0.0	0.0±0.1	33.9±24.2	8.2±8.7	42.1±21.1
SD 28	0.0	0.0	0.0	1.3±2.8	14.8±24.2	16.1±22.4

Bold numbers represent retention patterns within ICES subdivisions. West means ICES SDs further west than ICES SD 24.

increased significantly during the last decade as assessed in trawl surveys (ICES, 2015; Figure 10) suggesting that what happens after the yolk-sac larval stage has a significant impact on recruitment and thus stock development. This is evident also for SD 26 and 28 where egg to yolk-sac larval survival decreased significantly, especially in SD 28, while at the same time the adult stock size (flounders above 20 cm in length with a majority of 3–8 years age) increased in the late 1990s and has since then fluctuated up to recently, when it declined in SD 28 (Figure 10). This means that the production of surviving larvae was, at least until 2010,

still high enough to sustain a viable population. However, results of our study are covering a relatively short time period of early life stage of flounder eggs and yolk-sac larvae (ca. 20–40 days depending on temperature) while flounder larval development until metamorphosis is remarkable longer (Grauman, 1981). Interestingly, the survival probabilities of flounder early life stages is highest in SD 25 but the density of flounder is much higher in the eastern Baltic SD 28 compared with the central Baltic (SD 24 and 25) when comparing catch per unit effort in the Baltic International Trawl Survey (Figure 10).

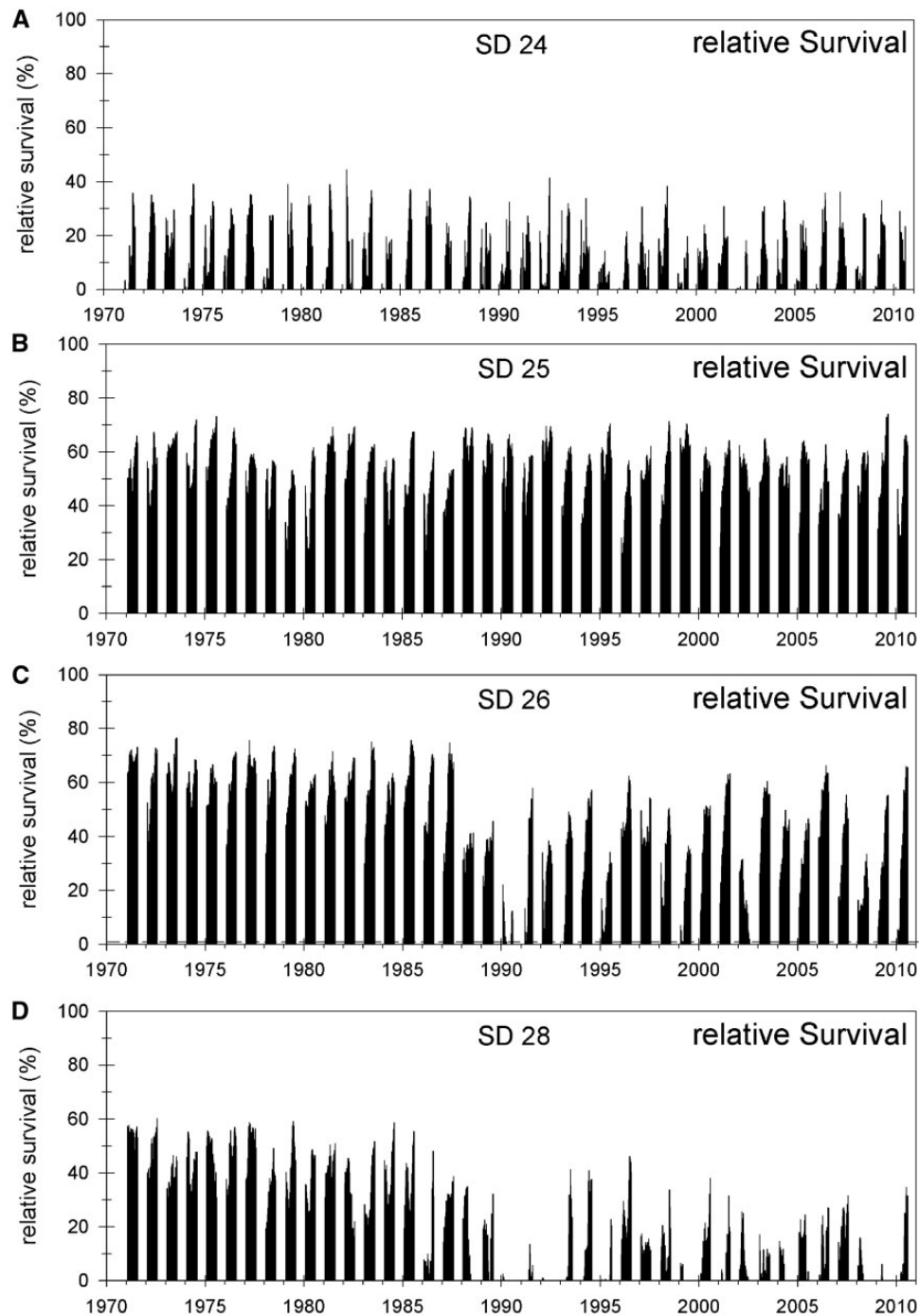


Figure 9. Fraction of particles representing intra- and inter-annual reproduction potential of Baltic flounder spawning grounds, (a) Arkona Basin, (b) Bornholm Basin, (c) Gdansk Deep, and (d) Gotland Basin. Bars represent the range of single release events.

Apparently food availability following the yolk-sac period, predation on eggs, larvae or juveniles (Bailey and Houde, 1989), transportation of early stages to suitable nursery areas along the coast (see van der Veer *et al.*, 2000) or availability/quality of nursery areas (Florin and Lavados 2010; Martinsson, 2011) may be regulating factors. Alternatively, stock development might reflect mortality in the adult stage such as fishing mortality, but unfortunately no estimates of fishing mortality are available for flounder in the Baltic Sea. Moreover, stock development,

especially in SD 26 and 28 may be blurred due to mixing between the ecotypes. Recent findings (EU BONUS project INSPIRE) show that the distribution of the ecotype with demersal eggs is wider than previously assumed. As both ecotypes share the same feeding and wintering areas, and are separated only during spawning in March to May (e.g. Nissling *et al.*, 2014), surveys (BITS carried out by trawling at 10–120 m depth in Q 1 January–March and Q 4 November–December) may target both ecotypes.

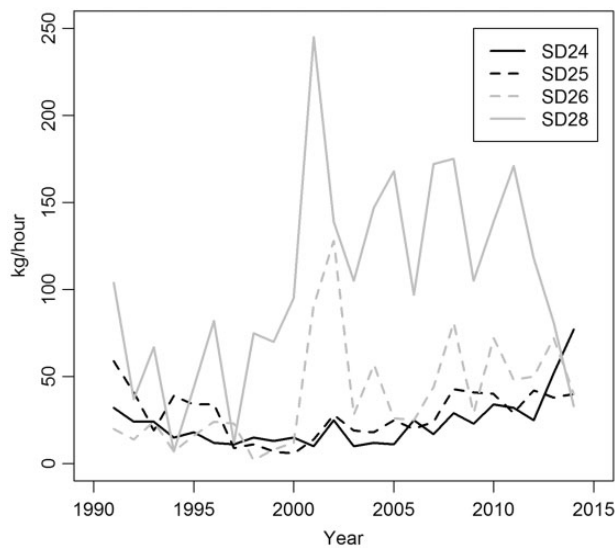


Figure 10. Trends in abundance of flounder stocks in ICES SD 24, 25, 26, and 28, measured as kg per hour in the Baltic International Trawl survey. Geometric mean for Quarter 1 and 4. Data from ICES (2015).

Methodological considerations: probabilities of processes and parameters

This article presents results of a numerical drift modelling exercise on central and eastern Baltic Sea flounder eggs originating from different spawning areas. The applicability of coupled biophysical models in fisheries management includes estimation of connectivity within fish stocks through transport of egg, larval and early juvenile stages, and spatio-temporal differences in potential survival (Hinrichsen *et al.*, 2011). Habitat suitability for reproduction, mortality, survival and transport patterns of central and eastern Baltic flounder eggs and yolk-sac larvae were quantified by detailed model simulations for the years 1971–2010. The data were derived from highly spatially and temporally resolved hydrographic Eulerian property fields obtained from hydrodynamic model runs performed by Lehmann *et al.* (2014).

Here we examined the transport of particles initially released into these simulated flow fields as successfully spawned and fertilised eggs. However, this exercise only provides probabilities of different processes and parameters, and does not take into account how many eggs are actually spawned, e.g. factors affecting female fecundity. The estimation of habitat suitability as well as mortality and survival probabilities during drift are based on abiotic tolerance levels in terms of threshold values and egg specific gravity measurements, selected for egg survival at the spawning location as well as during drift duration.

Recommendations for managers and scientific needs considering environmental change

To reveal the population structure of flounder in the whole Baltic Sea (as a tool in management to obtain a sustainable stock development), connectivity and population mixing in all life stages should be considered. Dispersal may occur during the egg and early larval stage (this study) and during the pelagic larval stage until settlement (different cohorts with settling from early July to early September share the same nursery areas; Martinsson and

Nissling, 2011), and furthermore, the two ecotypes share feeding and wintering areas (e.g. Bagge, 1981; Nissling *et al.*, 2014). Hence, apart from genetic discrepancies (Hemmer-Hansen *et al.*, 2007; Florin and Höglund, 2008) throughout the distribution area, drift patterns during the larval phase (see van der Veer *et al.*, 2000) and migration patterns (Aro, 1989), e.g. occurrence of natal homing (e.g. Svedäng *et al.*, 2007) and changes in distribution due to poor oxygen conditions in deeper areas, remain topics for future studies.

With respect to the ongoing climate change, presumably resulting in less frequent saline water inflows (MacKenzie *et al.*, 2007), with potentially lower oxygen concentrations due to elevated water temperatures (Hinrichsen *et al.*, 2002b), egg and early larval survival of flounder with pelagic eggs can be expected to decrease in the future as salinity and oxygen conditions (major sources of mortality according to the model, particularly in SD 26 and 28) will deteriorate. However, mortality caused by low water temperatures after severe winters (identified as a source of mortality in SD 24 and 25) probably will decrease. Hence, potentially poorer conditions in SD 26 and 28 but less so in SD 24 and 25 may cause a shift in the distribution of flounder with pelagic eggs (especially as drift from SD 24–25 to SD 26 and 28 seem to be insignificant). Egg and early larval survival probabilities and the connectivity between areas may also be affected by the age/size structure of the stock determined by fishing mortality. In several species, larger (older) females have been shown to produce more buoyant eggs (Vallin and Nissling, 2000) affecting the vertical egg distribution (buoyant at lower salinities, i.e. less deep) and thus both survival probabilities and connectivity patterns by drift. Although this has not been studied for Baltic flounder so far, it might be expected to be valid also for the flounder ecotype with pelagic eggs. Thus, an important topic for management may be to counterbalance a truncation of the length/age distribution to maintain a sustainable stock development and increase the resilience of climate change.

Supplementary data

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

Funding

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References

- 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.
- Bagge, O. 1981. Demersal fishes. In *The Baltic Sea*. Elsevier Oceanographic Series No. 30 ED by A. Voipio. Elsevier Scientific Company, Amsterdam, pp. 320–323.
- Bailey, K. M., and Houde, E. 1989. Predation on eggs and larvae of marine fishes and the recruitment problem. *Advances in Marine Biology*, 25: 1–83.
- Bryan, K. 1969. A numerical method for the study of the circulation of the world ocean. *Journal of Physical Oceanography*, 15: 1312–1324.

- Bumke, K., Karger, U., Hasse, L., and Niekamp, K. 1998. Evaporation over the Baltic Sea as an example of a semi-enclosed sea. *Contribution Atmospheric Physics*, 71: 249–261.
- Casini, M., Kornilovs, G., Cardinale, M., Möllmann, C., Grygiel, W., Jonsson, P., Raid, T., Flinkman, J., and Feldman, V. 2011. Spatial and temporal density dependence regulates the condition of central Baltic Sea clupeids: compelling evidence using an extensive international acoustic survey. *Population Ecology*, 53: 511–523.
- Conley, D. J., Humborg, C., Rahm, L., Savchuk, O. P., and Wulff, F. 2002. Hypoxia in the Baltic Sea and Basin-Scale Changes in Phosphorus Biogeochemistry. *Environmental Science and Technology*, 36: 5315–5320.
- Cox, M. D. 1984. A primitive equation 3-dimensional model of the ocean. GFDL Ocean Group Technical Report No. 1, Geophysical Fluid Dynamics Laboratory, Princeton, NJ, 75 pp.
- Diaz, R. J., and Rosenberg, R. 2008. Spreading dead zones and consequences for marine ecosystems. *Science*, 321: 926–929. doi: 10.1126/science.1156401.
- Florin, A. B., and Höglund, J. 2008. Population structure of flounder (*Platichthys flesus*) in the Baltic Sea: differences among demersal and pelagic spawners. *Heredity*, 101: 27–38.
- Florin, A. B., Sundblad, G., and Bergström, U. 2009. Characterization of juvenile flatfish habitats in the Baltic Sea. *Estuarine, Coastal and Shelf Science*, 82: 294–300.
- Florin, A. B., and Lavados, G. 2010. Feeding habits of juvenile flatfish in relation to habitat characteristics in the Baltic Sea. *Estuarine, Coastal and Shelf Science*, 86: 607–612.
- Franck, H., Matthäus, E., and Sammler, R. 1987. Major Baltic Inflows During this Century, vol. 56, pp. 81–82. *Beitr. Meereskd*, Berlin.
- Grauman, G. B. 1981. Temporal distribution of flounder eggs and larvae in the Baltic Sea. *Fisheries research of the Baltic Sea basin*. Avots Riga, 16: 28–36 (in Russian).
- Hemmer-Hansen, J., Nielsen, E. E., Grønkjær, P., and Loeschcke, V. 2007. Evolutionary mechanisms shaping the genetic population structure of marine fishes; lessons from European flounder (*Platichthys flesus* L.). *Molecular Ecology*, 16: 3104–3118.
- Hinrichsen, H. -H., Böttcher, U., Köster, F. W., Lehmann, A., and St. John, M. A. 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., Böttcher, U., Oeberst, R., Voss, R., and Lehmann, A. 2001b. 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., Dickey-Collas, M., Huret, M., Peck, M. A., and Vikebo, F. B. 2011. Evaluating the suitability of coupled biophysical models for fishery management. *ICES Journal of Marine Science*, 68: 1478–1487.
- Hinrichsen, H. H., Hüsey, K., and Huwer, B. 2012. Spatio-temporal variability in western Baltic cod early life stage survival mediated by egg buoyancy, hydrography and hydrodynamics. *ICES Journal of Marine Science*, 69: 1744–1752.
- Hinrichsen, H. -H., Kraus, G., Böttcher, U., and Köster, 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.
- Hinrichsen, H. -H., Lehmann, A., Möllmann, C., and Schmidt, J. O. 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., Lehmann, A., Petereit, C., Nissling, A., Ustups, D., Bergström, U., and Hüsey, K. 2016. Spawning areas of eastern Baltic cod revisited: Using hydrodynamic modelling to reveal spawning habitat suitability, egg survival probability, and connectivity patterns. *Progress in Oceanography*, 143: 13–25.
- Hinrichsen, H. H., Lehmann, A., St. John, M. S., and Brügge, B. 1997. Modeling the cod larvae drift in the Bornholm Basin in summer 1994. *Continental Shelf Research*, 17: 1765–1784.
- Hinrichsen, H. -H., Möllmann, C., Köster, F. W., and Kornilovs, G. 2002a. Biophysical modelling 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., Aro, E., Grønkjær, P., and Voss, R. 2001a. 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., St John, M., Lehmann, A., MacKenzie, B. R., and Köster, F. W. 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.
- Hüsey, K., Hinrichsen, H. H., and Huwer, B. 2012. Hydrographic influence on the spawning habitat suitability of western Baltic cod (*Gadus morhua*). *ICES Journal of Marine Science*, 69: 1736–1743.
- ICES. 2014. Report of the Benchmark Workshop on Baltic Flatfish Stocks (WKBALFLAT), 27–31 January 2014, Copenhagen, Denmark. *ICES CM 2014/ACOM:39*. 320 pp.
- ICES. 2015. ICES Advice on fishing opportunities, catch and effort. Baltic Sea ecoregion. *ICES Advice Book 8*. Ch. 8.3.1–8.3.8. Flounder.
- Killworth, P. D., Stainforth, D., Webb, D. J., and Paterson, S. M. 1991. The development of a free-surface Bryan-Cox-Semtner ocean model. *Journal of Physical Oceanography*, 21: 1333–1348.
- Köster, F. W., Möllmann, C., Hinrichsen, H.-H., Wieland, K., Tomkiewicz, J., Kraus, G., Voss, R., et al. 2005. Baltic cod recruitment the impact of climate variability on key processes. *ICES Journal of Marine Science*, 62: 1408–1425.
- Kronsell, J., and Andersson, P. 2012. Total regional runoff to the Baltic Sea. *HELCOM Indicator Fact Sheets 2011*. Online. (<http://www.helcom.fi/environment2/ifs>).
- Lehmann, A., Hinrichsen, H. H., Getzlaff, K., and Myrberg, K. 2014. Quantifying the heterogeneity of hypoxic and anoxic areas in the Baltic Sea by a simplified coupled hydrodynamic-oxygen consumption model approach. *Journal of Marine Systems*, 134: 20–28.
- Lehmann, A., and Hinrichsen, H. H. 2000. On the thermohaline variability of the Baltic Sea. *Journal of Marine Systems*, 25: 333–357.
- Lehmann, A., Krauß, W., and Hinrichsen, H. H. 2002. Effects of remote and local atmospheric forcing on circulation and upwelling in the Baltic Sea. *Tellus*, 54A: 299–316.
- MacKenzie, B. R., Hinrichsen, H. -H., Plikshs, M., Wieland, K., and Zezera, A. S. 2000. Quantifying environmental heterogeneity: estimating the size of habitat for successful cod egg development in the Baltic Sea. *Marine Ecology Progress Series*, 193: 143–156.
- MacKenzie, B. R., Gislason, H., Möllmann, C., and Köster, F. 2007. Impact of 21st century climate change on the Baltic Sea fish community and fisheries. *Global Change Biology*, 13: 1348–1367.
- Martinsson, J. 2011. Ecology of juvenile turbot and flounder in the Central Baltic Sea. PhD Thesis, Department of Systems Ecology, Stockholm University. ISBN 978-91-7447-402-2.
- Martinsson, J., and Nissling, A. 2011. Nursery area utilization by turbot (*Psetta maxima*) and flounder (*Platichthys flesus*) at Gotland, central Baltic Sea. *Boreal Environmental Research*, 16: 60–70.
- Matthäus, W., and Lass, H. U. 1995. The recent salt inflow into the Baltic Sea. *Journal of Physical Oceanography*, 25: 280–286.
- Meier, H. E. M., Andersson, H. C., Arheimer, B., Blenckner, T., Chubarenko, B., Donnelly, C., Eilola, K., et al. 2014. Ensemble modeling of the Baltic Sea ecosystem to provide scenarios for management. *AMBIO*, 43: 37–48.
- Neumann, V., Köter, F. W., Schaber, M., and Eero, M. 2014. Recovery in eastern Baltic cod: is increased recruitment caused by

- decreased predation on early life stages? ICES Journal of Marine Science, 71: 1382–1392.
- Nissling, A., Johansson, U., and Jacobsson, M. 2006. Effects of salinity and temperature conditions on the reproductive success of turbot (*Scophthalmus maximus*) in the Baltic Sea. Fisheries Research, 80: 230–238.
- Nissling, A., Kryvi, H., and Vallin, L. 1994. Variation in egg buoyancy of Baltic cod (*Gadus morhua*) and its implications for egg survival in prevailing conditions in the Baltic Sea. Marine Ecology Progress Series, 110: 67–74.
- Nissling, A., Thorsen, A., and da Silva, F. F. G. 2014. Fecundity regulation in relation to habitat utilization of two sympatric flounder (*Platichthys flesus*) populations in the brackish water Baltic Sea. Journal of Sea Research, 95: 188–195.
- Nissling, A., Westin, L., and Hjerne, O. 2002. Spawning success in relation to salinity of three flatfish species, Dab (*Pleuronectes limanda*), Plaice (*Pleuronectes platessa*) and Flounder (*Pleuronectes flesus*), in the brackish water Baltic Sea. ICES Journal of Marine Science, 59: 93–108.
- Novotny, K., Liebsch, G., Lehmann, A., and Dietrich, R. 2006. Variability of sea surface heights in the Baltic Sea: an intercomparison of observations and model simulations. Marine Geodesy, 29: 113–134.
- Pacariz, S., Björk, G., Jonsson, P., Börjesson, P., and Svedäng, H. 2013. A model study of the large scale transportation of fish eggs in the Kattegat in relation to egg density. ICES Journal of Marine Science, 71: 345–355.
- Petereit, C., Hinrichsen, H. H., Franke, A., and Köster, F. W. 2014. Floating along buoyancy levels: Dispersal and survival of western Baltic fish eggs. Progress in Oceanography, 122: 131–152.
- Riley, J. D., Symonds, D. J., and Woolner, L. 1981. On the factors influencing the distribution of 0-group demersal fish in coastal waters. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 178: 223–228.
- Rudolph, C., and Lehmann, A. 2006. A model-measurements comparison of atmospheric forcing and surface fluxes of the Baltic Sea. Oceanologia, 48: 333–380.
- Schinke, H., and Matthäus, W. 1998. On the causes of major Baltic inflows - an analysis of long time series. Continental Shelf Research, 18: 67–97.
- Semtner, A. J., 1974. A general circulation model for the World Ocean. UCLA Department of Meteorology Technical Report, No. 8, 99 pp.
- Svedäng, H., Righton, D., and Jonsson, P. 2007. Migratory behavior of Atlantic cod *Gadus morhua*: natal homing is the prime stock-separating mechanism. Marine Ecology. Progress Series, 345: 1–12.
- Thompson, B. M., and 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.
- Ustups, D., Uzars, D., and Müller-Karulis, B. 2007. Size structure and feeding ecology of fish communities in the surf zone of the Eastern Baltic. Proceedings of Latvian Academy of Science. Section B, 61: 20–30.
- Ustups, D., Müller-Karulis, B., Bergstrom, U., Makarchouk, A., and Sics, I. 2013. The influence of environmental conditions on early life stages of flounder (*Platichthys flesus*) in the central Baltic Sea. Journal of Sea Research, 75: 77–84.
- Vallin, L., and Nissling, A. 2000. Maternal effects on egg size and egg buoyancy of Baltic cod, *Gadus morhua* – implications for stock structure effects on recruitment. Fisheries Research, 49: 21–37.
- Van der Veer, H. W., Berghahn, R., Miller, J. M., and Rijnsdorp, A. D. 2000. Recruitment in flatfish, with special emphasis on North Atlantic species: Progress made by the Flatfish Symposia. ICES Journal of Marine Science, 57: 202–215.
- Vitinsh, M. 1980. Ecological description of Eastern-Gotland population of flounder (*Platichthys flesus* L.). In Ecosystems of Baltic Sea, Vol. 1, pp. 213–236. Ed by G. Okolotovics. Sea Fishery Institute. Gdynia.
- Voipio, A. 1981. The Baltic Sea. Elsevier Oceanographic Series no. 30. Spreading Dead Zones and Consequences for Marine Ecosystems. Science, Vol. 321, pp. 926–929 Elsevier Scientific Company, Amsterdam.
- Voss, R., Hinrichsen, H.-H., Stepputtis, D., Bernreuther, M., Huwer, B., Neumann, V., and Schmidt, J. O. 2011. Egg mortality: predation and hydrography in the central Baltic. ICES Journal of Marine Science, 68: 1379–1390.

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Spatio-temporal trends in stock mixing of eastern and western Baltic cod in the Arkona Basin and the implications for recruitment

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In the Baltic Sea, two genetically distinct cod populations occur, the eastern and the western Baltic cod. Since 2006, cod abundance has increased substantially in the Arkona Basin (SD 24), the potential mixing area between the two stocks management areas, presumably due to spill-over from the eastern stock. In this study, the spatio-temporal dynamics of stock mixing were analysed using shape analysis of archived otoliths. Further, the impact of eastern cod immigration on recruitment in the western Baltic Sea was investigated using hydrographic drift modelling. The percentage of eastern Baltic cod in the Arkona Basin increased from ca. 30% before 2005 to >80% in recent years. Geographic patterns in stock mixing with a pronounced east–west trend suggest that immigration occurs north of Bornholm, but propagates throughout the Arkona Basin. The immigration cannot be attributed to spawning migration, as no seasonal trend in stock mixing was observed. Based on environmental threshold levels for egg survival and time-series of hydrography data, the habitat suitable for successful spawning of eastern cod was estimated to range between 20 and 50% of the maximum possible habitat size, limited by primarily low salinity. Best conditions occurred irregularly in May–end June, interspersed with years where successful spawning was virtually impossible. Using a coupled hydrodynamic modelling and particle-tracking approach, the drift and survival of drifters representing eastern cod eggs was estimated. On average, 19% of the drifters in the Arkona Basin survive to the end of the yolk-sac stage, with mortality primarily after bottom contact due to low salinity. The general drift direction of the surviving larvae was towards the east. Therefore, it is the immigration of eastern cod, rather than larval transport, that contributes to cod recruitment in the western Baltic Sea.

Keywords: Arkona Basin, Baltic cod, Baltic Sea, recruitment, stock mixing.

Introduction

Stock identification is a prerequisite for fisheries assessment and management. A stock is generally defined as a homogenous group of fish with respect to growth, maturity, and mortality patterns and with a self-sustaining recruitment of new generations (Cadrin *et al.*, 2013). Knowledge about stock structure and dynamics, the stocks' geographic boundaries, and migration patterns are among the basic input for a sustainable fisheries management (Secor, 2013). Cod in the Baltic Sea is managed as two separate stocks, i.e. eastern and western Baltic cod, located in ICES Subdivisions (SD) 25–32 and 22–24, respectively (Figure 1). There is ample evidence supporting the difference between the two populations, based on

tagging (Berner, 1967, 1974; Bagge, 1969; Berner and Borrmann, 1985; Otterlind, 1985), phenotypic differences (Birjukov, 1969; Berner and Vaske, 1985; Müller, 2002), and genetics (Nielsen *et al.*, 2003, 2005). However, the tagging programmes also provide documentation that eastern and western Baltic cod stocks co-occur in the Arkona Basin (SD 24; Aro, 1989; Nielsen *et al.*, 2013). In the late 2000s, the abundance of adult cod in the Arkona Basin rapidly increased, while the abundance remained stable and at a considerably lower level in the westernmost part of the Baltic Sea (SD 22; Eero *et al.*, 2014). This was hypothesized to be the result of an increasing proportion of cod of eastern origin in the Arkona Basin (Eero *et al.*, 2014), likely due to spill-over of cod from the currently

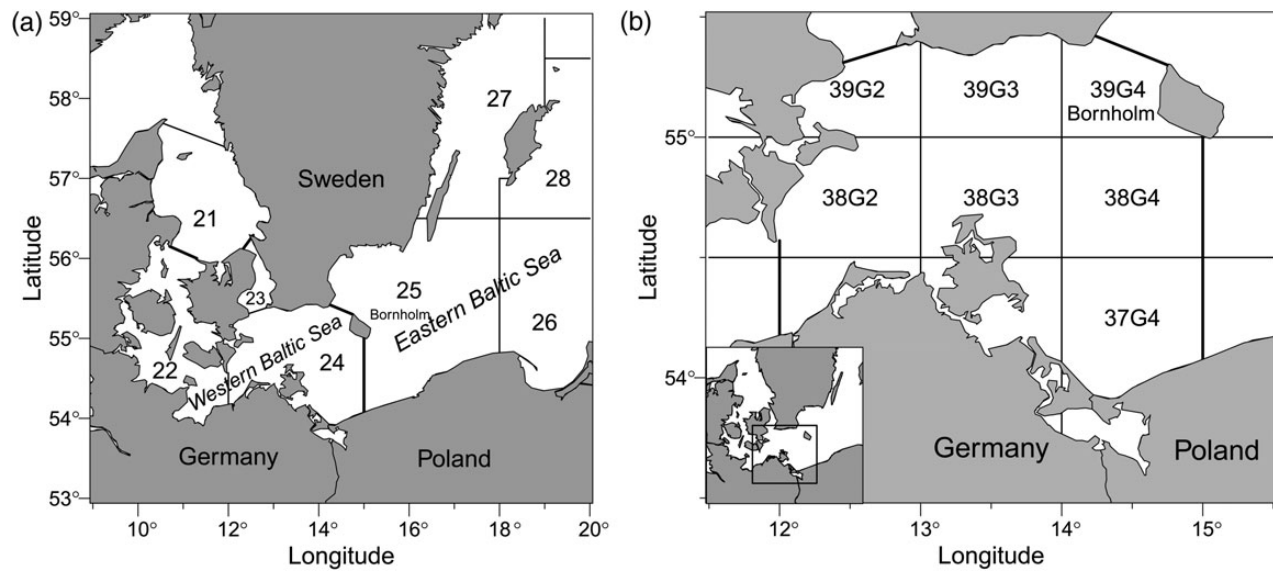


Figure 1. (a) Map of the Baltic Sea. Numbers indicate ICES SD, thin lines indicate SD boundaries, and solid lines the boundaries between the Kattegat, western and eastern Baltic Sea management areas. (b) Map of the Arkona Basin (SD24) in the western Baltic Sea. Lines indicate the statistical rectangles with rectangle names; bold lines mark the boundaries of SD 24. The inset shows the location of SD 24 in the Baltic Sea.

densely populated main distribution area of the eastern Baltic cod (SD 25; [Eero et al., 2012](#)). This presumed immigration of cod from the east has resulted in large spatial differences in abundance and biological parameters of cod in the western Baltic management area ([Eero et al., 2014](#)), which poses a number of challenges for fisheries management, including potential depletion of the true western Baltic cod population ([Eero et al., 2014](#)).

Although there is increasing focus on the potential importance of stock structure for sustainable fisheries management (e.g. [Ulrich et al., 2013](#); [Holmes et al., 2014](#)), stock assessment and fisheries management often do not take spatial heterogeneity or subpopulation structure in a given management unit into account (e.g. [Cadrin et al., 2013](#); [Kritzer and Liu, 2013](#)). Among the reasons for this are logistical constraints such as limitations in data availability and knowledge about exchange rates between areas, as well as limited familiarity of stock assessors with available methods ([Hammer and Zimmermann, 2005](#); [Kritzer and Liu, 2013](#); and references therein). However, there are a number of examples demonstrating that ignoring population structure can lead to unsustainable management and the failure of overfished stocks to recover ([Murawski, 2010](#); [Petitgas et al., 2010](#)) or depletion of local subpopulations (e.g. [Kell et al., 2009](#)). The eastern Baltic stock is approximately five times larger than the Western stock ([Eero et al., 2014](#)). Consequently, the Western stock is at risk for local depletion in a situation with increased immigration of cod from the neighbouring eastern stock.

To develop appropriate solutions to fisheries management in an area where stock mixing takes place, knowledge on temporal and spatial variation in mixing proportions is required ([Cadrin et al., 2013](#)). Further, tools are needed to allow for possible quantitative separation of the populations in the mixing area in routine stock assessments. In recent years, otolith shape analysis has developed into a useful tool for stock identification purposes ([Campana and Casselman, 1993](#); [Bolles and Begg, 2000](#); [Cardinale et al., 2004](#); [Mérigot et al., 2007](#)). Stock-specific otolith shape functions based on elliptic Fourier analysis provide means for classifying individuals

caught in a mixed-stock area to their respective natal stocks. In Baltic cod, this approach has recently been documented as a highly efficient tool to separate individuals belonging to the eastern and Western stock ([Hüsey et al., 2016](#)). Applied to archived otoliths, this technique thus provides an opportunity to estimate spatio-temporal trends in stock mixing within the Arkona Basin (SD 24).

Another central issue for managing mixed stocks is knowledge on their potential contribution to recruitment. This has impacts on defining appropriate biological reference points for sustainable exploitation status for a given geographical area or a population and for measuring the status of the stocks in relation to the defined targets. For Baltic cod, it is not known whether the eastern Baltic cod immigrating into the Arkona Basin are able to produce viable offspring in that Basin, and whether the offspring is retained within the management boundaries of the western Baltic Sea—or is advected into neighbouring management units. The Baltic Sea is a large estuary with shallow connections to the ocean and is governed by inflows of high saline Atlantic water and outflows of brackish surface water from the Baltic ([Lehmann et al., 2002](#)). The shallow sills cause a strong thermohaline stratification of the deep water areas, including the Arkona Basin, resulting in frequent hypoxia in the near bottom layers. Consequently, the hydrodynamic conditions within the Baltic Sea are extremely variable ([Matthäus and Franck, 1992](#); [Schinke and Matthäus, 1998](#)). The prevailing hydrographic conditions may have considerable impact on cod's spawning habitat suitability by affecting spermatozoa activity and the viability of the fertilized eggs ([Hüsey et al., 2012](#)). Particularly, low temperatures as well as sedimentation may also limit the survival of the egg- and larval stages during their transport from spawning to nursery area ([Hinrichsen et al., 2012](#)). Patterns of connectivity (as influenced by variable hydrographic and atmospheric forcing conditions) are known to affect recruitment success of fish stocks via changes in retention or dispersion of larvae from spawning grounds to areas suitable (or unsuitable) for subsequent survival (e.g. [Werner et al., 1996](#); [Heath and Gallego, 1997](#); [Hinrichsen et al., 2002a](#); [Bolle et al., 2009](#)).

The objectives of this paper are to provide new knowledge on the two issues described above. First, we estimate spatio-temporal trends in stock mixing within the Arkona Basin in relation to season, year, fish length, and spatial gradient, using otolith shape analyses. Second, to evaluate whether the eastern Baltic cod immigrating into the Arkona Basin contribute to recruitment in the western Baltic Sea, we use drift modelling to test the hypotheses that the environmental conditions in the Arkona Basin are (i) suitable for eastern Baltic cod spawning, (ii) suitable for early life stages (i.e. egg and larvae) survival, and (iii) retaining eastern Baltic cod recruits in the area of the Arkona Basin (or the western Baltic Sea in general).

Material and methods

Otolith samples

From the otolith archives of DTU Aqua, historical samples from the mixing area in the Arkona Basin (SD 24) were retrieved. Samples originated primarily from Danish harbour collections and discard samples. The majority of the samples were from landings in the Danish harbours of Klintholm, Neksø, Rødvig, Rønne, and Tejn. To capture the mixing dynamics within the last decades, where the stock size of the eastern Baltic cod has increased, we selected the years 1996, 1998, 2000, 2005, 2008, 2010, 2011, 2013, and 2014. The samples were selected carefully to ensure adequate sample numbers within each quarter of the years and size range (Q1: 1/1–31/3, Q2: 1/4–30/6, Q3: 1/7–30/9, Q4: 1/10–31/12). As the stock classification routine does not include juvenile cod, only individuals larger than 20 cm were used, resulting in a total of 6527 otoliths (Table 1). Biological data consisting of length, sex, and maturity stage associated with each fish/otolith were obtained from DTU Aqua's database BIA. These data are accompanied by information on catch location (ICES SD and statistical rectangle, longitude, latitude), catch date, trip type, station, and landing harbour.

Otoliths were viewed under a microscope (Leica MZ12) equipped with a circular reflected light source and a standard magnification ($15\ \mu\text{m pixel}^{-1}$). Images of otoliths were digitized with a Leica DFC290 camera and a standard setup (8 bit channel⁻¹, 2048×1536 pixel frame, 35 ms exposure). The otoliths were placed in a standardized orientation with the sulcus facing up to facilitate contour capture. Images were stored as JPG files. The contour of each otolith pair was captured using the “snake” routine of MatLAB developed for otolith images. Elliptic Fourier descriptors (EFD) were fit to the contours of each individual otolith and standardized following routine protocols (Kuhl and Giardina, 1982).

Otolith shape analysis

The classification of historical otolith samples to stock is essentially a two-step approach consisting of the development of stock-specific discrimination functions based on reference baseline samples if otolith shapes followed by the application of these functions to the historical mixed stock samples in the Arkona Basin. In the following, the approach is outlined, details of the analyses and baseline data used are described in Hüssy *et al.* (2016).

Development of stock-specific shape functions

To establish comprehensive baseline samples including the entire size range and all areas, spawning individuals from the eastern (SD 25) and western (SD 22) stock caught during the spawning season (410 and 1265 individuals, respectively) and 746 spawning and non-spawning individuals from the Arkona Basin (SD 24) were selected. Individuals from the Arkona Basin were assigned to biological population (east or west) based on a panel of 39 single-nucleotide polymorphism (SNP) markers identified to be particularly powerful for separating the two Baltic Sea populations (see Nielsen *et al.*, 2012 for concept) and using a Bayesian approach (Rannala and Mountain, 1997) implemented in the program GeneClass (Piry *et al.*, 2004).

Elliptic Fourier coefficients were fitted to the otolith silhouette contour and together with otolith area standardized to cod length to be used as descriptors for classification. Balanced subsets were selected by stratified random sampling from the total baseline to select the most robust descriptors for classification. The subsets were stratified into four length groups with group length intervals set to ensure at least 10 individuals within each size group of the baseline sample. The resulting four size groups were <32 , $32-39$, $40-47$, and ≥ 47 cm. This length stratification ensured a selection of random baseline subsets as calibration samples with all length classes present in constant proportions for further linear discriminant analyses. The descriptors with the highest discrimination power between stocks were identified by running a forward–backwards stepwise linear discriminant analysis (SAS PROC STEPWISE) 100 times on random subsets of the baseline samples. The 21 overall most frequent descriptors were selected as a robust variable list for all further analyses.

To estimate each individual's probability of belonging to either of the two stocks, a series of 100 linear discriminant analyses with randomized baseline subsets were subsequently carried out on both baseline and test samples (SAS PROC DISCRIM). For the baseline, this provided a matrix of correct and incorrect assigned individuals from each run, the so-called confusion matrix. The most likely

Table 1. Overview over samples by quarter and years.

Year	Quarter				Total
	1 (1 January – 31 March)	2 (1 April – 30 June)	3 (1 July – 30 September)	4 (1 October – 31 December)	
1996	199	279	110	54	642
1998	160	233	65	59	517
2000	254	175	270	256	955
2005	629	352	450	391	1822
2008	304	243	189	302	1038
2010	251	238	236	291	1016
2011	479	1264	118	207	2068
2013	477	144	123	205	949
2014	496	200	149	147	992
Total	3249	3128	1710	1912	9999

confusion matrix from all runs was then used for bias correction in the baseline as well as in the test samples.

Application to mixed stock samples

The bias-corrected proportional contribution of eastern and western otolith types were calculated for each year, quarter, size class, and statistical rectangle. Owing to the extensive problems with age reading of eastern Baltic cod (Hüsey, 2010), the stock mixing analyses were in the present study conducted for separate size groups (<32, 32–39, 40–47, and ≥ 47 cm) rather than age classes. Given a correct confusion matrix, the Monte Carlo approach provides information on the variability of the bias-corrected test samples caused by the baseline uncertainty and a way to calculate confidence limits. The baseline-introduced uncertainty was expressed as the 5 and 95% percentiles of the estimated proportions per size group in the time-series of mixed stock samples from the Arkona Basin.

Drift modelling

Hydrographic data

Temperature, salinity, and oxygen distributions are provided as prognostic variables by the hydrodynamic Kiel Baltic Sea Ice-Ocean Model (BSIOM, Lehmann and Hinrichsen, 2000; Lehmann et al., 2002). The horizontal resolution of the coupled sea ice-ocean model is at present 2.5 km. The horizontal model grid size is fine enough to capture the appropriate horizontal mixing processes (e.g. smaller than the internal Rossby radius; Hinrichsen et al., 2002b), which can influence the predicted fish egg and larval trajectories. Sixty vertical levels are specified, which enables the upper 100 m to be resolved into levels of 3 m thickness. The model domain comprises the Baltic Sea, including the Kattegat and the Skagerrak. The oxygen conditions in the entire Baltic Sea are described by an oxygen consumption submodel coupled to BSIOM (Lehmann et al., 2014). Details about the model configuration, boundary conditions, and atmospheric forcing can be found in Lehmann et al. (2014). The numerical model BSIOM has been run for the period 1970–2010. From the available time-series, data covering the years 1990–2010 were selected for the subsequent analysis of habitat suitability and early life stage survival in the Arkona Basin, covering the spawning period of eastern Baltic cod from May to August (Wieland et al., 2000; Bleil et al., 2009).

Spawning time

As the focus of this study is on the reproduction potential of eastern Baltic cod, the analyses were limited to the main spawning season of the eastern Baltic cod stock. This stock is known to spawn from March to October, with the main spawning season in May–August with considerable interannual variability in peak spawning (Wieland et al., 2000; Bleil et al., 2009).

Spawning area

The location of the spawning ground in the Arkona Basin was selected based on the review of all existing information on spawning activities of western Baltic cod's (Hüsey, 2011). The sampling locations for the estimation of spawning habitat suitability were based on environmental egg survival threshold levels for the Eastern Baltic cod stock as described below. Consequently, drifters representing newly spawned cod eggs were only released at those spawning ground locations for which environment-related egg survival was possible.

Environmental threshold levels

Environmental threshold levels for egg and larval survival were selected from published values on minimum values for salinity, temperature, and oxygen. The critical threshold levels used in this study were 11 psu for salinity, 1.5°C for temperature, and 2 ml O₂ l⁻¹ for oxygen, where survival was only possible at values above these levels. At salinity levels exceeding those at the bottom, eggs are buoyant and float in the water column while lower salinities presumably cause eggs to die due to sedimentation (Nissling et al., 1994). A salinity of >11 psu is also necessary for spermatozoa activation and egg fertilization (Nissling and Westin, 1997). Egg development time is strongly temperature-dependent, with development times decreasing exponentially from 18 to 7 d within the temperature range prevailing in the study area (Bleil, 1995; Peteret et al., 2014). Both high and low temperatures become increasingly detrimental to egg development. In the Arkona Basin, temperatures never rise to lethal levels; therefore, only the lower limit of 1.5°C was relevant to this study. At oxygen levels <2 ml O₂ l⁻¹, development fails and the eggs die (Wieland et al., 1994; Rohlf, 1999).

Spawning habitat suitability

To resolve the temporal variability of the spawning habitat in relation to ambient hydrography, time-series of hydrography data covering the years 1990–2010 were used in a similar way as described by Hüsey et al. (2012). Within the spawning area in the Arkona Basin (Figure 1b), positions on the regularly spaced 2.5 × 2.5 km hydrodynamic model grid were selected where the bottom depth was larger than 25 m. At these grid points, the model provided hydrographic data profiles at a vertical resolution of 3 m intervals. Covering the spawning season from 1 May to 31 August, spawning dates were defined at 10 d intervals. These data formed the basis for the calculation of the maximal possible habitat size suitable for spawning (HS_{\max}):

$$HS_{\max} = n_{ht} \times n_{vt},$$

where n_{ht} is the total number of horizontal locations within the spawning ground, and n_{vt} the total number of vertical egg release grid points at 3 m steps below 25 m water depth at these horizontal locations.

For each 10-d intervals within the spawning seasons from 1990 to 2010, the number of locations (in the horizontal and vertical dimension) which allowed egg survival was determined. The corresponding spawning habitat suitability (HS) in relation to the maximal possible spawning habitat size (HS_{\max}) was calculated for each individual date as:

$$HS = n_h \times n_v \times HS_{\max}^{-1},$$

where n_h is the number of horizontal locations at which n_v = number of surviving eggs at release (3 m intervals) were available. This value thus indicates the probability of successful egg release.

Estimation of survival and mortality

Simulated three-dimensional velocity fields were extracted (at 3 h intervals) from the hydrodynamic model to develop a database for particle tracking. This dataset offers the possibility to derive Lagrangian drift routes by calculating the advection of “marked” water particles. Simulated drift routes were obtained from Eulerian flowfields by utilization of a Lagrangian particle-tracking technique. The three-dimensional trajectories of the simulated drifters were

computed using a fourth-order Runge–Kutta scheme (Hinrichsen *et al.*, 1997). Particles representing cod eggs at developmental egg stage Ia were released into the simulated flowfields and tracked through the egg and yolk-sac stages, keeping the buoyancy constant over the entire drift duration. During their drift, eggs and yolk-sac larvae floated at the initially assigned density levels, but died due to bottom contact if their initially assigned density levels were found to be higher than those available at the bottom along the positions of the drift route, or due to lethal temperature ($<1.5^{\circ}\text{C}$) or oxygen ($<2\text{ ml l}^{-1}$) conditions. For individuals that died during the simulations, the positions where the death occurred were recorded, while for the surviving individuals, the final positions reached at the end of the yolk-sac stage were recorded.

The duration of the egg and yolk-sac larval drift depended on temperatures provided by the hydrodynamic model. For each of the 3 hourly time-steps of the drift model, these temperatures were used to calculate the corresponding temperature-dependent development times from stage Ia eggs to first-feeding larvae (Thompson and Riley, 1981) along the drift paths of each individual egg/larva. The simulations were stopped when yolk-sac larvae started to become first-feeding larvae characterized by beginning of the mouth opening at age 4 d (Thompson and Riley, 1981).

Results

Stock mixing trends

Season

To evaluate whether the mixing was subject to seasonal migration patterns, stock compositions was examined in relation to quarter for all years except 2005 and 2011, where not enough samples were available. Although stock mixing proportions varied over the season for all years (Pearson's χ^2 test, d.f. = 11, all $p < 0.05$), no consistent seasonal pattern was evident. This suggests that there is no apparent seasonal migration in and out of the Arkona Basin. Consequently, samples from all quarters were pooled in the subsequent analyses.

Year and size

The general trends in stock mixing within the Arkona Basin were examined based on the pooled data. The stock mixing proportions in the Arkona Basin have changed considerably since 1995 (Figure 2a). In the 1990s, the percentage of mature eastern Baltic cod in the Arkona Basin was estimated relative constant below 40%. Between 2005 and 2008, this percentage increased to $\sim 75\%$. Since then the percentage of eastern Baltic cod in the Arkona Basin has been increasing for each year to $>85\%$ in 2011 with a subsequent decrease to just over 65% in the last 2 years to a significantly higher level than before 2008 (Pearson's χ^2 test, d.f. = 8, $p < 0.05$). The majority of this immigration consisted up to 2011 primarily of fish $>32\text{ cm}$ (Figure 2b). In the smallest size group ($<32\text{ cm}$), eastern cod were present in the 1990s but not during the immigration period (2005–2011). Since 2011, all size groups have been present at statistically equal proportions (Pearson's χ^2 test, d.f. = 6, $p = 0.58$).

Spatial aspects of stock mixing

The analysis of the spatio-temporal stock mixing in the Arkona Basin reflects the general increase in the proportion of Eastern Baltic cod since 2005, but also reveals a clear geographic pattern. Stock proportions were estimated by ICES rectangle (Figure 3), arranged to match their relative positions within the Arkona

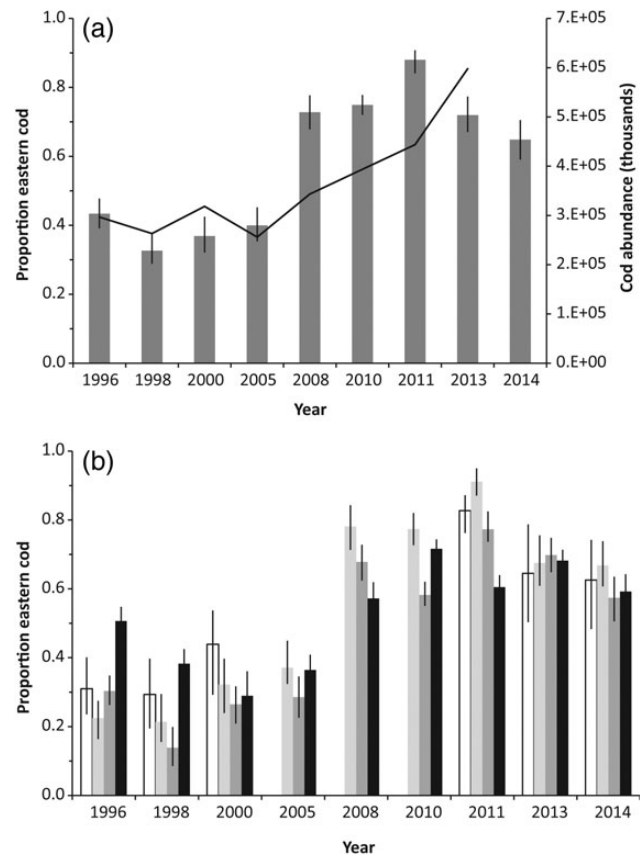


Figure 2. (a) Trends in proportion of eastern Baltic cod in the Arkona Basin (SD 24) over the years 1996–2014 (bars) with stock abundance of eastern Baltic cod during the same years (line; data from ICES, 2013), and (b) Proportion of eastern Baltic cod for each size group separately, where white $\leq 32\text{ cm}$, light grey = $32–39\text{ cm}$, dark grey = $40–47\text{ cm}$, black $\geq 47\text{ cm}$. Error bars in both histograms are baseline-introduced uncertainty expressed as the 5 and 95% percentiles of the estimated proportions per year and size group.

Basin. The highest percentage of Eastern Baltic cod occurred in the easternmost rectangles (39G4 and 38G4), the lowest in the westernmost rectangles 39G2 and 38G2). In the two rectangles in-between, the sample size was relatively limited but nevertheless suggested a gradual decrease in eastern Baltic cod from east to west. But despite the lower contribution of eastern Baltic cod to the westernmost rectangles within the Arkona Basin, the immigration from the east has nevertheless propagated throughout the entire Arkona Basin.

Early life stage survival

Spawning habitat suitability in the Arkona Basin was characterized by high variability both within and between years (Figure 4). Overall, habitat suitability ranged between 20 and 50%. Peaks in habitat suitability ($>70\%$) occurred primarily from mid-May to end June (Julian days 140–180), at irregular intervals interspersed by years with extremely low ($<30\%$) habitat suitability during the entire spawning season, averaging 37% over the entire spawning season. On average, half of these successfully spawned eggs survive to the end of the yolk-sac stage, while the rest die (Table 2). The majority of the mortality was attributable to bottom contact due to low salinity levels in the Arkona Basin. The remaining mortality was

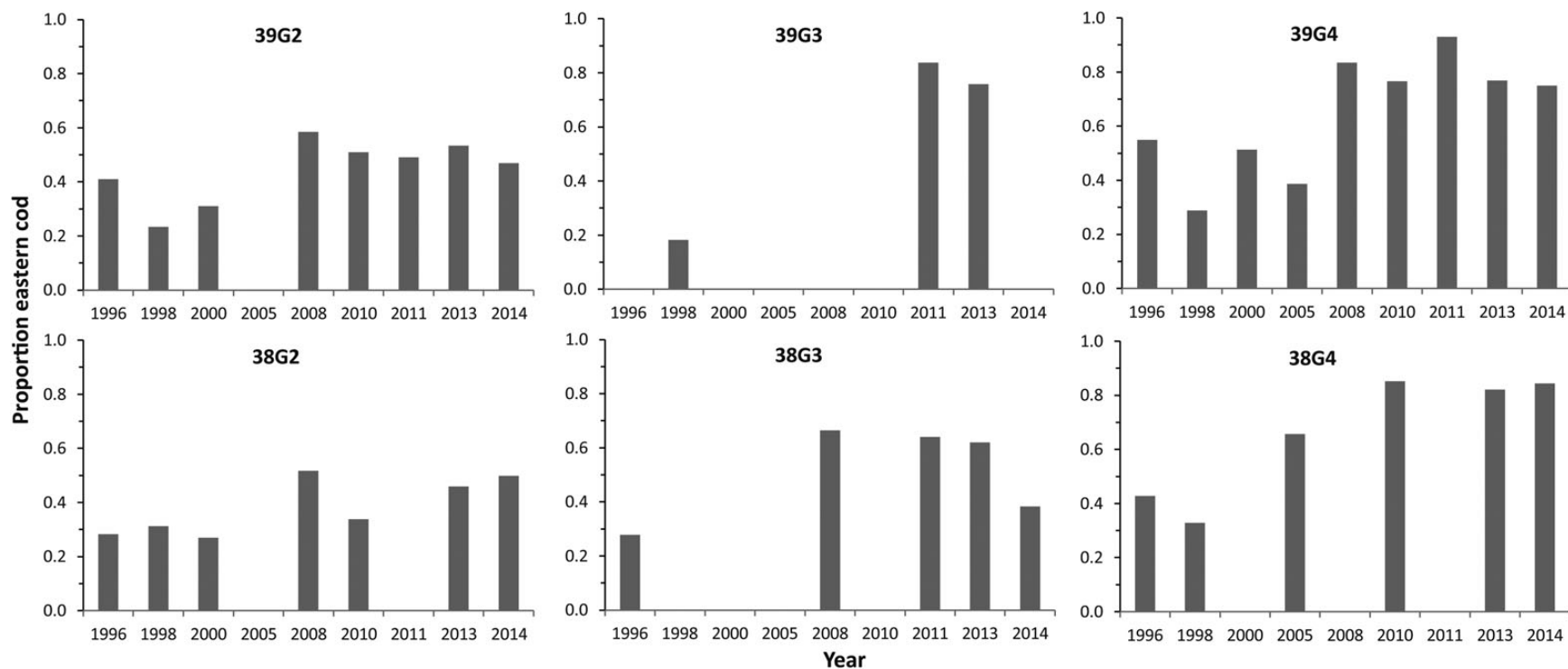


Figure 3. Proportion of eastern Baltic cod (> 20 cm) per year in the six ICES rectangles within the Arkona Basin (SD 24) for the years 1996–2014. Only years with > 10 fish per rectangle and year were used. Years without bars indicate lack of data. Rectangles are arranged to match their relative positions within the Arkona Basin from west to east.

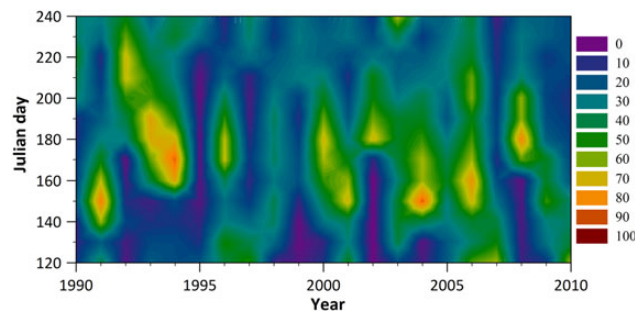


Figure 4. Habitat suitability in the Arkona Basin (SD 24) in relation to Julian day and year. Only data from eastern Baltic cod's main spawning time May–August (Julian days 120–240) are shown. Values represent per cent of maximum possible habitat size.

Table 2. Relative probabilities (mean \pm s.d.) of (1) successful egg release, (2–3) mortality of eggs and larvae due to bottom contact and temperature, and (4) survival to the yolk-sac larval stage of eastern Baltic cod spawned in the Arkona Basin.

	All	Retained	Drifted out
(1) Released eggs	0.373 \pm 0.216		
(2) Dead (bottom)	0.180 \pm 0.105	0.114 \pm 0.056	0.066 \pm 0.061
(3) Dead (temperature)	0.002 \pm 0.008	0.001 \pm 0.007	0.001 \pm 0.004
(4) Yolk-sac survivors	0.191 \pm 0.151	0.165 \pm 0.141	0.026 \pm 0.033

Values show the relative probabilities of all larvae together as well as those retained in and drifted out of SD 24.

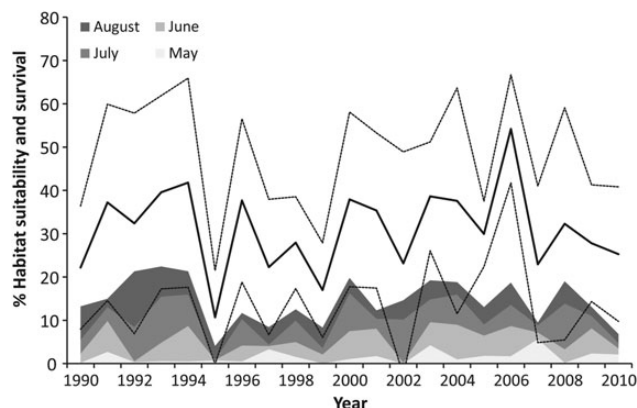


Figure 5. Average habitat suitability in May–August (average = solid black line, \pm s.d. = broken lines) and relative larval survival probability (shaded area) in the Arkona Basin (SD 24) in relation to years and spawning month, where May: white, June: light grey, July: grey, and August: dark grey.

relatively low ($<1\%$), caused by low temperatures, particularly early in the spawning season (May). Oxygen was unimportant as a mortality agent. The percentage of early life stages surviving to the end of the yolk-sack stage was relatively constant over the years (Figure 5).

To examine temporal trends in egg and larval drift/retention, the percentage of larvae ending outside of the Arkona Basin was analysed as the number of surviving drifters outside the Arkona Basin divided by total number of survivors. All transport from the Arkona Basin was towards the east (SD 25). This analysis showed considerable interannual variation, where the percentage of larvae

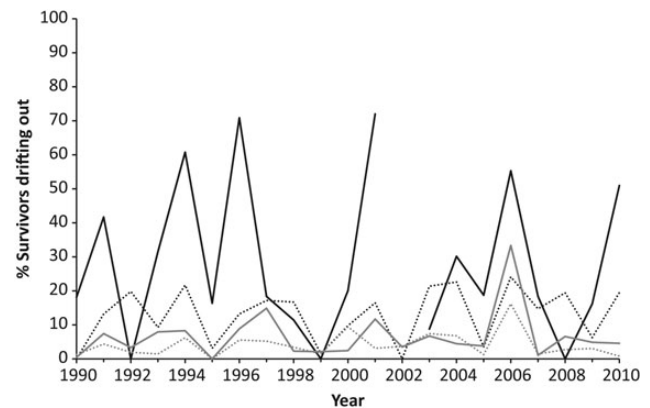


Figure 6. Percentage of surviving larvae drifting out of the Arkona Basin (SD 24) in relation to year for different months of hatch: May = solid black, June = dotted black, July = solid grey, and August = dotted grey. Missing values are the result of zero surviving larvae.

drifting out of the Arkona Basin ranged from 0 to 70% (Figure 6). Whether the surviving larvae are retained in the Arkona Basin depends on when they are spawned. Larvae spawned in May drifted to a large extent out of the area, whereas an increasing percentage of the larvae spawned later in the season were retained within the Arkona Basin. On average, the percentage of the surviving larvae that drift out of the Arkona Basin amounted to: May = $28 \pm 23\%$ (mean \pm s.d.), June = $13 \pm 8\%$, July = $7 \pm 7\%$, and August = $4 \pm 3\%$. For the surviving eggs in the Arkona Basin, a general tendency of drift from the central basin (north of the island of Rügen) towards more eastern areas of the basin was observed.

Discussion

Stock mixing dynamics

The results of the otolith shape-based stock discrimination analysis presented here confirmed that eastern Baltic cod have to some degree been present in the Arkona Basin since 1996. No consistent seasonal effects were observed, suggesting that the observed immigration patterns are not linked to spawning migrations as suggested by Müller (2002). The spatially resolved stock mixing pattern showed a consistent east–west gradient, with larger proportions of eastern cod towards the east. The topography within the Arkona Basin thus seems to promote immigration of eastern cod into the Arkona Basin, but may to some degree limit the expansion of their distribution range farther to the west. Also the historical tagging studies in this area have shown frequent migrations between the areas east and west of Bornholm, particularly through the deeper areas north of the island (Berner, 1981).

Earlier attempts at resolving stock discrimination in the Arkona Basin were based on length frequency analysis (Oeberst, 2001) and the number of dorsal fin rays (Berner and Müller, 1989; Müller, 2002). Proportions of eastern Baltic cod in the Arkona Basin were estimated at 72% (Berner and Müller, 1989) and 28–68% (Müller, 2002) with high variability between years and age classes and without consistent patterns except for a weak trend for larger proportions in older age classes (Müller, 2002). However, due to considerable classification error and strong environmental impact, these estimates probably do not reflect true mixing proportions.

Contrary to these earlier approaches estimating stock mixing, our stock separation based on otolith shape analysis found only

limited interannual variation. The most conspicuous result was the temporal trend in proportion of eastern Baltic cod with an increase from ca. 30% before 2005 to >80% in 2011. This is consistent with recent trends in stock size and biological parameters of cod for these size-groups (mean body weight, nutritional conditions) in SDs 22, 24, and 25 (Eero *et al.*, 2014). Genetic identification of individual cod from the Arkona Basin has recently confirmed that most fish in this area currently consists of eastern Baltic cod (Hüsey *et al.*, 2016). While the immigration of eastern cod consisted of all size classes >32 cm, the present study is not able to document whether the small cod (<32 cm) occurring from 2011 onward have moved into the Arkona Basin from the east as juveniles or offspring from the immigrants already residing in the Arkona Basin.

This study thus provides evidence for the hypothesis of Eero *et al.*'s (2014) hypothesis of an apparent increased spill-over of eastern Baltic cod into the Arkona Basin associated with an increase in abundance of the eastern Baltic cod. The otolith shape-based stock identification approach has proven useful for separating adult individuals of eastern and western origin for stock assessment and fisheries management purposes. However, the appropriate management solutions also depend on whether or not the eastern immigrants found in western Baltic are contributing viable offspring in their new resident area.

Contribution of eastern cod to recruitment in the western Baltic Sea

The spawning areas of cod in the Baltic are found in deep, saline waters below 20–40 m (Hüsey, 2011). The peak spawning season is area-specific with progressively later spawning towards the east, from January/February in Kattegat (SD 21) to March/April in Kiel and Mecklenburg Bays (SD 22) and June/July in the Bornholm Basin (SD 25; Tomkiewicz and Köster, 1999; Wieland *et al.*, 2000; Vitale *et al.*, 2005; Bleil *et al.*, 2009). Also the Arkona Basin has since the early 1990s been a known spawning area for cod (Bleil and Oeberst, 2002) with peak spawning in June/July, which suggests these cod to belong to the eastern stock (Bleil *et al.*, 2009). Contrary to this, spawning seems to have been restricted to early spring in the 1980s (Berner, 1985; Bagge *et al.*, 1994). These studies suggest considerable temporal variability in the degree to which eastern Baltic cod use the Arkona Basin as spawning area. In the light of the increased immigration of eastern cod, it is relevant to evaluate whether these immigrants produce viable offspring, and which stock the recruits contribute to. To that end, we tested the hypotheses that the Arkona Basin provides environmental conditions suitable for eastern Baltic cod spawning and early life stage survival (eggs and larvae), and that the offspring of the eastern cod are retained within the western Baltic management area.

The first step in this evaluation was to test whether the environmental conditions within the Arkona Basin are suitable for successful reproduction. With an average spawning habitat suitability of ca. 30%, the Arkona Basin is considerably below those of other known spawning areas such as the Kattegat (90%), Great Belt (80%), Sound (45%), Kiel Bay, and Mecklenburg Bay (50%; Hüsey *et al.*, 2012). Common for all areas is that habitat suitability is restricted primarily due to low salinity and only on few occasions by low temperatures. Peaks in habitat suitable for reproduction seldom seem to last for more than 1 month and primarily occurred during mid-May–end of June. In some years (1995, 1999, 2002, 2007, 2010), habitat suitability was observed to be low throughout the entire season. These results clearly demonstrate that reproductive success of eastern Baltic cod in the Arkona Basin may be restricted to narrow temporal

windows of opportunity, with overlap between peak spawning and maximum habitat suitability in some years only.

The next hypothesis tested addressed whether suitable environmental conditions existed in the Arkona Basin for early life stage survival (i.e. eggs and larvae) of eastern Baltic cod. Mortality of these life stages was relatively high, in that ~50% of the successively released eggs died. Mortality was almost exclusively attributable to death due to bottom contact caused by low environmental salinity and the increasing density of the eggs during development (Petereit *et al.*, 2014). For eastern Baltic cod, no information on changes in buoyancy during egg development was available. As observed for western Baltic cod eggs (Petereit *et al.*, 2014), it could be expected that an egg buoyancy decrease during the last quarter of egg development would result in reduced egg survival probability, mainly caused by an increase in sedimentation or further exposure of eggs to detrimental oxygen concentrations. Previous observations on larval survival of western Baltic cod showed that survival of early life stages is also low in the Kiel and Mecklenburg Bays, which are found next to the Arkona Basin, and also limited by low environmental salinity (Hinrichsen *et al.*, 2012).

The final hypothesis addressed the suitability of the environmental conditions in the Arkona Basin for retaining eastern Baltic cod recruits in the western Baltic Sea management unit. In this study, early life stage survival was lowest in May and highest in July. Concurrently, retention within the Arkona Basin was lowest in May and highest in July/August, with eggs primarily drifting eastward. Windspeed and direction are the key drivers of these drift/retention patterns (Hinrichsen *et al.*, 2001). The peak spawning time of eastern Baltic cod in June/July (Tomkiewicz and Köster, 1999; Wieland *et al.*, 2000; Bleil *et al.*, 2009) thus coincides with the temporal window ensuring highest survival and retention with the Arkona Basin. Nevertheless, one should bear in mind that the probability of successful egg release is low and mortality of early life stages is substantial. Ichthyoplankton surveys support these observations, in that only few cod larvae were observed in the Arkona area throughout the 1990s and 2000s (Klenz, 1999, 2006).

This study has shown that eastern Baltic cod immigrating into the Arkona Basin may contribute to recruitment in the western Baltic management area, but that the survival potential of eggs and larvae is limited. Only in years characterized by specific conditions can they contribute to recruitment: after inflow of saline water and with the major spawning taking place in July/August. This supports the observations that recruitment of cod in the entire western Baltic Sea (ICES, 2013) has been low in recent years, despite the high stock size in the Arkona Basin.

Implications for stock assessment and management

Catch quota setting based on estimates of fishing mortality is a common management tool in commercial fisheries. In fisheries targeting several stocks of the same species, subquotas can be set based on spatially structured assessment models or through spatially resolved harvest control rules (Kritzer and Liu, 2013). Spatially structured assessment models integrate stock composition information from multiple interconnected areas, though the stock status as well as reference points are determined for the combined stock (Kritzer and Liu, 2013 and references therein). However, applications of such frameworks remain rare (Cadrian and Secor, 2009). If spatially resolved assessment models are not feasible and single stock assessment models have to be used despite the presence of distinct stock components (Hammer and Zimmermann, 2005),

management strategies with spatial allocation of catch quotas are an option for sustainable fisheries management.

The two Baltic cod stocks differ from these scenarios, in that they are now assessed and managed as separate stocks, despite their overlapping distribution area. Until 2015, the stock assessment of the western Baltic cod represented a specific geographical area (SDs 22–24), regardless of the origin of cod residing in this area. The quantitative analyses of stock mixing presented in this paper were an important contribution to facilitate the transition from area-based to stock-based assessments of cod in the Baltic Sea in 2015 (ICES, 2015). Information on the annual proportions of eastern and western cod found in the western Baltic management area allowed allocating fisheries catch to the populations of origin, and performing stock assessments for the two biological populations separately. This change provides a more realistic picture of the dynamics of western Baltic cod population that were masked in the earlier area-based assessments by increasing proportions of the eastern Baltic cod in the area. Continued monitoring of the proportions of eastern and western cod populations within the western Baltic Sea is needed for long-term sustainable management of the two stocks.

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References

- 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.
- Bagge, O. 1969. Preliminary results of the cod tagging experiments in the western Baltic. ICES Document CM 1969/F: 29.
- Bagge, O., Thurow, F., Steffensen, E., and Bay, J. 1994. The Baltic cod. *Dana*, 10: 1–28.
- Berner, M. 1967. Results of cod taggings in the western and central Baltic in the period 1962–1965. ICES Document CM 1967/F: 05.
- Berner, M. 1974. Some results of cod tagging experiments of the GDR in the Baltic 1968–1971. ICES Document CM 1974/F: 32.
- Berner, M. 1981. Dislocation parameters of tagging experiments on cod in the Baltic (Sub-divisions 22–25) from 1959–1975. ICES Document CM 1981/J: 15.
- Berner, M. 1985. Die periodische Veränderung der Gonadenmasse und der Laichzyklus des “Ostsee-” und “Beltseedorsches” (*G. morhua callarias*? *G. morhua morhua*) in verschiedenen Regionen der Ostsee. *Fischerei-Forschung*, 23: 49–57.
- Berner, M., and Borrmann, U. 1985. Zum saisonalen Längenwachstum des Dorsches der Mecklenburger Bucht nach Wiederfangdaten von Markierungsexperimenten und Bestandsvergleichen. *Fischerei-Forschung*, 23: 63–69.
- Berner, M., and Müller, H. 1989. Discrimination between “Baltic cod” (*Gadus morhua callarias* L.) and “Belt Sea cod” (*Gadus morhua morhua*) by means of morphometric and meristic characters. ICES Document CM 1989/J: 13.
- Berner, M., and Vaske, B. 1985. Morphometric and meristic characters of cod stocks in the Baltic Sea. ICES Document CM 1985/J: 11.
- Birjukov, N. P. 1969. Spawning communities of Baltic cod and the extent of their mixing. ICES Document CM 1969/F: 7.
- Bleil, M. 1995. Untersuchungen zur Aufzucht von Dorsch (*Gadus morhua*) der Westlichen Ostsee. 3. Aufbau und Hälterung eines Laichfischbestandes sowie Erbrütung der gewonnenen Eier. *Informationen aus der Fischwirtschaft und Fischereiforschung*, 42: 133–146.
- Bleil, M., and 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., and Urrutia, P. 2009. Seasonal maturity development of Baltic cod in different spawning areas: importance of the Arkona Sea for the summer spawning stock. *Journal of Applied Ichthyology*, 25: 10–17.
- Bolle, L. J., Dickey-Collas, M., van Beek, J. K. L., Erftemeijer, P. L. A., Witte, J. I. J., van der Veer, H. W., and Rijnsdorp, A. D. 2009. Variability in transport of fish eggs and larvae. III. Effects of hydrodynamics and larval behaviour on recruitment in place. *Marine Ecology Progress Series*, 390: 195–211.
- Bolles, K. L., and Begg, G. A. 2000. Distinctions between silver hake (*Merluccius bilinearis*) stocks in U.S. waters of the northwest Atlantic based on whole otolith morphometric. *Fishery Bulletin*, 98: 451–462.
- Cadrin, S. X., Kerr, L. A., and Mariani, S. 2013. Stock identification methods: an overview. In *Stock Identification Methods: Applications in Fishery Science*, 2nd edn, pp. 1–5. Ed. by S. X. Cadrin, L. A. Kerr, and S. Mariani. Elsevier Academic Press, Burlington, USA. 588 pp.
- Cadrin, S. X., and Secor, D. H. 2009. Accounting for spatial population structure in stock assessment: past, present, and future. In *The Future of Fisheries Science in North America*, pp. 405–426. Ed. by R. J. Beamish, and B. J. Rothschild. Springer, The Netherlands. 736 pp.
- Campana, S. E., and Casselman, J. M. 1993. Stock discrimination using otolith shape analysis. *Canadian Journal of Fisheries and Aquatic Sciences*, 50: 1062–1083.
- Cardinale, M., Doering-Arjes, P., Kastowsky, M., and Mosegaard, H. 2004. Effects of sex, stock, and environment on the shape of known-age Atlantic cod (*Gadus morhua*) otoliths. *Canadian Journal of Fisheries and Aquatic Sciences*, 61: 158–167.
- Eero, M., Hemmer-Hansen, J., and Hüsey, K. 2014. Implications of stock recovery for a neighbouring management unit: experience from the Baltic cod. *ICES Journal of Marine Science*, 71: 1458–1466.
- Eero, M., Köster, F. W., and Vinther, M. 2012. Why is the eastern Baltic cod recovering? *Marine Policy*, 36: 235–240.
- Hammer, C., and Zimmermann, C. 2005. The role of stock identification in formulating fishery management advice. In *Stock Identification Methods: Applications in Fishery Science*, 1st edn, pp. 631–658. Ed. by S. X. Cadrin, K. D. Friedland, and J. R. Waldman. Elsevier Academic Press, Burlington, USA. 681 pp.
- Heath, M., and Gallego, A. 1997. The effect of growth-dependent mortality, external environment and internal dynamics on larval fish otolith growth: an individual-based modelling approach. *Journal of Fish Biology*, 51: 121–134.
- Hinrichsen, H. H., Hüsey, K., and Huwer, B. 2012. Spatio-temporal variability in western Baltic cod early life stage survival mediated by egg buoyancy, hydrography and hydrodynamics. *ICES Journal of Marine Science*, 69: 1744–1752.
- Hinrichsen, H. H., Lehmann, A., St John, M. A., and Brügge, B. 1997. Modelling the cod larvae drift in the Bornholm Basin in summer 1994. *Continental Shelf Research*, 17: 1765–1784.
- Hinrichsen, H-H., Möllmann, C., Köster, F. W., and Kornilovs, G. 2002b. Biophysical modelling 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., Aro, E., Grønkjær, P., and Voss, R. 2001. Testing the larval drift hypothesis in the Baltic Sea: retention versus dispersion caused by wind-driven circulation. *ICES Journal of Marine Science*, 58: 973–984.
- Hinrichsen, H.-H., St John, M., Lehmann, A., MacKenzie, B. R., and Köster, F. W. 2002a. Resolving the impact of short-term variations in physical processes impacting on the spawning environment of eastern Baltic cod: application of a 3-D hydrodynamic model. *Journal of Marine Systems*, 32: 281–294.
- Holmes, S. J., Millar, C. P., Fryer, R. J., and Wright, P. J. 2014. Gadoid dynamics: differing perceptions when contrasting stock vs. population trends and its implications to management. *ICES Journal of Marine Science*, 71: 1433–1442.
- Hüsey, K. 2010. Why is age determination in Baltic cod (*Gadus morhua* L.) so difficult? *ICES Journal of Marine Science*, 67: 1198–1205.
- Hüsey, K. 2011. Review of western Baltic cod (*Gadus morhua*) recruitment dynamics. *ICES Journal of Marine Science*, 68: 1459–1471.
- Hüsey, K., Hinrichsen, H. H., and Huwer, B. 2012. Hydrographic influence on the spawning habitat suitability of western Baltic cod (*Gadus morhua*). *ICES Journal of Marine Science*, 69: 1736–1743.
- Hüsey, K., Mosegaard, H., Albertsen, C. M., Nielsen, E. E., Hemmer-Hansen, J., and Eero, M. 2016. Evaluation of otolith shape as a tool for stock discrimination in marine fishes using Baltic Sea cod as a case study. *Fisheries Research*, 174: 210–218.
- ICES. 2013. Report of the Baltic Fisheries Assessment Working Group (WGBFAS), 10–17 April 2013, ICES Headquarters, Copenhagen, Denmark. ICES CM 2013/ACOM: 10. 747 pp.
- ICES. 2015. Report of the Benchmark Workshop on Baltic Cod Stocks (WKBALTCOD), 2–6 March 2015, Rostock, Germany. ICES CM 2015/ACOM: 35. 172 pp.
- Kell, L. T., Dickey-Collas, M., Hintzen, N. T., Nash, R. D. M., Pilling, G. M., and Roel, B. A. 2009. Lumpers or splitters? Evaluating recovery and management plans for metapopulations of herring. *ICES Journal of Marine Science*, 66: 1776–1783.
- Klenz, B. 1999. Ichthyoplanktonaufnahmen als Beitrag zu Biodiversitätsuntersuchungen in der westlichen Ostsee. *Informationen aus der Fischwirtschaft und Fischereiforschung*, 46: 27–31.
- Klenz, B. 2006. Fish larvae in the western Baltic Sea—biodiversity studies from 2000 to 2005. *Informationen aus der Fischereiforschung*, 53: 35–39.
- Kritzer, J. P., and Liu, W. R. 2013. Fishery management strategies for addressing complex spatial structure in marine fish stocks. *In* Stock Identification Methods: Applications in Fishery Science, 2nd edn, pp. 29–57. Ed. by S. X. Cadrin, L. A. Kerr, and S. Mariani. Elsevier Academic Press, Burlington, USA. 588 pp.
- Kuhl, F. P., and Giardina, C. R. 1982. Elliptic features of a closed contour. *Comparative Graphics and Image Processing*, 18: 237–258.
- Lehmann, A., and Hinrichsen, H.-H. 2000. On the thermohaline variability of the Baltic Sea. *Journal of Marine Systems*, 25: 333–357.
- Lehmann, A., Hinrichsen, H.-H., Getzlaff, K., and Myrberg, K. 2014. Quantifying the heterogeneity of hypoxic and anoxic areas in the Baltic Sea by a simplified coupled hydrodynamic-oxygen consumption model approach. *Journal of Marine Systems*, 134: 20–28.
- Lehmann, A., Krauss, W., and Hinrichsen, H.-H. 2002. Effects of remote and local atmospheric forcing on circulation and upwelling in the Baltic Sea. *Tellus*, 54A: 299–316.
- Matthäus, W., and Franck, H. 1992. Characteristics of major Baltic inflows—a statistical analysis. *Continental Shelf Research*, 12: 1375–1400.
- Mérogot, B., Letourneur, Y., and Lecomte-Finiger, R. 2007. Characterization of local populations of the common sole *Solea solea* (Pisces, Soleidae) in the NW Mediterranean. *Marine Biology*, 151: 997–1008.
- Müller, H. 2002. The distribution of “Belt Sea cod” and “Baltic cod” in the Baltic Sea from 1995 to 2001 estimated by discriminant analysis of the number of dorsal fin rays. *ICES Document CM 2002/L: 16*.
- Murawski, S. A. 2010. Rebuilding depleted fish stocks: the good, the bad, and, mostly, the ugly. *ICES Journal of Marine Science*, 67: 1830–1840.
- Nielsen, B., Hüsey, K., Neuenfeldt, S., Tomkiewicz, J., Behrens, J. W., and Andersen, K. H. 2013. Individual behaviour of Baltic cod *Gadus morhua* in relation to sex and reproductive state. *Aquatic Biology*, 18: 197–207.
- Nielsen, E. E., Cariani, A., Mac Aoidh, E., Mae, G. E., Milano, I., Ogden, R., Taylor, M., et al. 2012. Gene-associated markers provide tools for tackling illegal fishing and false eco-certification. *Nature Communications*, 3: 851.
- Nielsen, E. E., Grønkjær, P., Meldrup, D., and Paulsen, H. 2005. Retention of juveniles within a hybrid zone between North Sea and Baltic Sea Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences*, 62: 2219–2225.
- Nielsen, E. E., Hansen, M. M., Ruzzante, D. E., Meldrup, D., and Grønkjær, P. 2003. Evidence of a hybrid-zone in Atlantic cod (*Gadus morhua*) in the Baltic and the Danish Belt Sea revealed by individual admixture analysis. *Molecular Ecology*, 12: 1497–1508.
- Nissling, A., Kryvi, H., and Vallin, L. 1994. Variation in egg buoyancy of Baltic cod *Gadus morhua* and its implications for egg survival in prevailing conditions in the Baltic Sea. *Marine Ecology Progress Series*, 110: 67–74.
- Nissling, A., and Westin, L. 1997. Salinity requirements for successful spawning of Baltic and Belt Sea cod and the potential for cod stock interactions in the Baltic Sea. *Marine Ecology Progress Series*, 152: 261–271.
- Oeberst, R. 2001. The importance of the Belt Sea cod for the eastern Baltic cod stock. *Archive of Fishery and Marine Research*, 49: 83–102.
- Otterlind, G. 1985. Cod migration and transplantation experiments in the Baltic. *Zeitschrift für angewandte Ichthyologie*, 1: 3–16.
- Petereit, C., Hinrichsen, H.-H., Franke, A., and Köster, F. W. 2014. Floating along buoyancy levels: dispersal and survival of western Baltic fish eggs. *Progress in Oceanography*, 122: 131–152.
- Petitgas, P., Secor, D. H., McQuinn, I., Huse, G., and Lo, N. 2010. Stock collapses and their recovery: mechanisms that establish and maintain life-cycle closure in space and time. *ICES Journal of Marine Science*, 67: 1841–1848.
- Piry, S., Alapetite, A., Cornuet, J.-M., Paetkau, D., Baudouin, L., and Estoup, A. 2004. GeneClass2: a software for genetic assignment and first-generation migrant detection. *Journal of Heredity*, 95: 536–539.
- Rannala, B., and Mountain, J. L. 1997. Detecting immigration by using multilocus genotypes. *Proceedings of the National Academy of Sciences of the United States of America*, 94: 9197–9201.
- Rohlf, N. 1999. Verhaltensänderungen der Larven des Ostseesardines (*Gadus morhua callarias*) während der Dottersackphase. *Berichte aus dem Institut für Meereskunde*, 50 pp.
- Schinke, H., and Matthäus, W. 1998. On the causes of major Baltic inflows—an analysis of long time series. *Continental Shelf Research*, 18: 67–97.
- Secor, D. H. 2013. The unit stock concept: bounded fish and fisheries. *In* Stock Identification Methods: Applications in Fishery Science, 2nd edn, pp. 7–28. Ed. by S. X. Cadrin, L. A. Kerr, and S. Mariani. Elsevier Academic Press, Burlington, USA. 588 pp.
- Thompson, B. M., and 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.
- Tomkiewicz, J., and Köster, F. W. 1999. Maturation process and spawning time of cod in the Bornholm Basin of the Baltic Sea: preliminary results. *ICES Document CM 1999/Y: 25*.

- Ulrich, C., Boje, J., Cardinale, M., Gatti, P., LeBras, Q., Andersen, M., Hemmer-Hansen, J., *et al.* 2013. Variability and connectivity of plaice populations from the Eastern North Sea to the Western Baltic Sea, and implications for assessment and management. *Journal of Sea Research*, 84: 40–48.
- Vitale, F., Cardinale, M., and Svedäng, H. 2005. Evaluation of the temporal development of the ovaries in *Gadus morhua* from the Sound and Kattegat, North Sea. *Journal of Fish Biology*, 67: 669–683.
- Werner, F. E., Perry, R. I., Lough, R. G., and Naimie, C. E. 1996. Trophodynamic and advective influence on Georges Bank larval cod and haddock. *Deep Sea Research II*, 43: 1793–1822.
- Wieland, K., Jarre-Teichmann, A., and Horbowa, K. 2000. Changes in the timing of spawning of Baltic cod: possible causes and implications for recruitment. *ICES Journal of Marine Science*, 57: 452–464.
- Wieland, K., Waller, U., and Schnack, D. 1994. Development of Baltic cod eggs at different levels of temperature and oxygen content. *Dana*, 10: 163–177.

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Connectivity of larval cod in the transition area between North Sea and Baltic Sea and potential implications for fisheries management

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Connectivity of pelagic, early life stages via transport by ocean currents may affect survival chances of offspring, recruitment success, and mixing of stocks across management units. Based on drift model studies, transport patterns of particles representing exogenously feeding cod larvae in the transition area between North Sea and Baltic were investigated to (i) determine long-term trends and variability in advective transport of larvae from spawning grounds to juvenile nursery areas, (ii) estimate the degree of exchange between different management areas, and (iii) compare the results with spatial distributions of juvenile cod. The transport of particles showed considerable intra- and interannual variability, but also some general patterns of retention within and dispersion to different management areas. Good spatial overlap of particle end positions, representing potential juvenile settlement areas, with observed distributions of juveniles in bottom trawl surveys suggests that the drift simulations provide reasonable estimates of early life stage connectivity between cod populations in the investigated areas. High exchange rates of particles between management areas of up to ca. 70% suggest that cod populations in the investigated areas are demographically correlated. Results are discussed in relation to their relevance for stock structure, fish stock assessment, and management.

Keywords: connectivity, early life stages, fisheries management, juvenile nursery areas, spatial management, stock structure.

Introduction

The exchange of individuals among populations and habitats is an important process from an ecological perspective, affecting, e.g. species distribution ranges, the demographic and genetic structure of populations, population dynamics, density-dependent processes and species interactions (Roughgarden *et al.*, 1988; Gaines and Lafferty, 1995; Gaylord and Gaines, 2000; Grosberg and Cunningham, 2001; Hixon *et al.*, 2002). In the marine world, connectivity of pelagic early life stages via ocean currents is of particular interest (e.g. Cowen and Sponaugle, 2009), as retention in or transport to favourable or unfavourable habitats may lead to variability in survival chances and eventually in recruitment success (Sinclair, 1988; Baumann *et al.*, 2006; Huwer *et al.*, 2014). In commercially important marine fish stocks which are annually assessed to estimate stock size and status and to inform about resulting fishing opportunities, the exchange of individuals between different management units is particularly important (Selkoe *et al.*, 2008; Reiss *et al.*, 2009; Eero *et al.*, 2014).

According to Gulland (1983) a 'stock' is assumed to be a discrete group of fish which show little mixing with adjacent groups and which have the same growth and mortality parameters across a particular geographical area. If large numbers of individuals are moving across boundaries of management units, either by active migration or by passive transport, this may lead to erroneous assumptions about stock–recruitment relationships, growth and mortality parameters needed in stock assessment and, due to variable fishing effort between management units, to overexploitation of certain stocks or stock units (Heath *et al.*, 2013; Eero *et al.*, 2014). Thus, management strategies will benefit from increased understanding of movement patterns in space and time and linkages among populations by exchange of eggs, larvae, juveniles, or adults, i.e. population connectivity (Palumbi, 2004).

Many marine fish stocks are managed in large areas, which often have limited connection to management areas of neighbouring stocks, e.g. the Arcto-Norwegian cod north of Norway and the

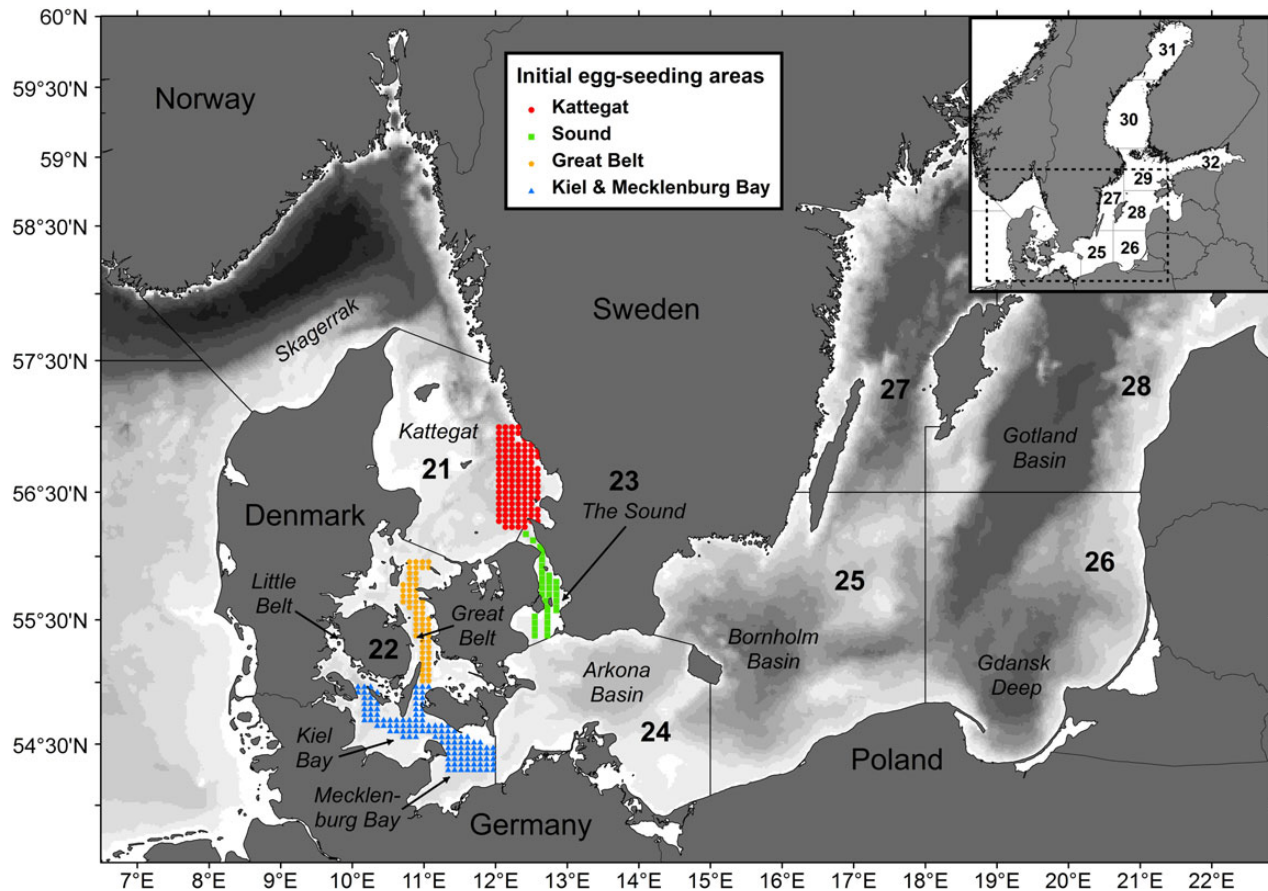


Figure 1. Overview of the study area. Symbols represent areas of historical spawning activity and grid of cod egg particle release positions in the Kattegat, the Sound, the Great Belt, and the Kiel & Mecklenburg Bay. Numbers indicate ICES Subdivisions. For a colour representation of the figure, it is referred to the online version. This figure is available in black and white in print and in colour at *ICES Journal of Marine Science* online.

northern cod in the Southern Labrador and eastern Newfoundland area (ICES, 2005), or Baltic sprat which is managed as a single unit in ICES Subdivisions 22–32 (ICES, 2015a) with only a very small border to one adjacent management unit in the area of the Belt Sea (see Figure 1).

In contrast, in the transition area between North Sea and Baltic Sea, there are four cod stocks which are managed in separate, relatively small management units, which are in close vicinity to each other (Figure 1): (i) Skagerrak (together with North Sea), (ii) Kattegat in ICES SD 21, (iii) western Baltic cod in SDs 22–24, and (iv) eastern Baltic cod in SDs 25–32 (see Figure 1; ICES, 2015a,b).

The spawning grounds of cod in these areas are generally well described and their spatial distribution seems to be rather stable over the years (see Hüsey, 2011; Hüsey et al., 2012 and references therein). Although a number of relevant processes for recruitment success of cod in the western Baltic and the Kattegat have been identified, recruitment dynamics and potential exchange of recruits between the different spawning and management areas are poorly known (Hüsey, 2011) and it is generally recognized that the cod stock structure and the borders of distribution areas of populations inhabiting the transition area from the North Sea to the Baltic are unclear (Nielsen et al., 2005; Svedäng and Svenson, 2006). Cod populations in this region apparently consist of a mixture of resident and migratory stocks (Svedäng and Svenson, 2006; Svedäng et al., 2007, 2010a; Hüsey, 2011). Consequently, considerable mixing of

stocks in this region may be anticipated as a result of both migrations of adult fish as well as drift of early life stages (Hüsey, 2011).

Despite this evidence of connectivity between areas, the standard stock assessments for cod in the Baltic and North Sea region have only recently begun to consider mixing between management areas, e.g. for eastern and western Baltic cod stocks mixing in SD 24 (Hüsey et al., 2015; ICES, 2015a,c). Stock mixing in the areas from Skagerrak and Kattegat over the Belt Sea to the Arkona basin (ICES SD's 20–24, see Figure 1) is not taken into account. From a management perspective, it must be emphasized to gain a better understanding of connectivity in this region at different life history stages to elucidate the resulting recruitment and stock dynamics as well as the recovery potential and appropriate management measures for the cod stocks.

In previous studies, we have assessed the importance of variability in environmental conditions for egg survival within different spawning grounds of cod stocks in the North Sea-Baltic Sea transition area (Hüsey et al., 2012) as well as the advective transport and the variability in environmentally mediated survival of eggs and yolk-sac larvae along drift routes in relation to both spatial and temporal dynamics (Hinrichsen et al., 2012). The aim of the present study was to go a step further in the life cycle by exploring the fate of offspring during the exogenously feeding larval stage. We utilized a hydrodynamic model to simulate the drift of exogenously feeding cod larvae which were originally released on different spawning

Table 1. Sizes of spawning grounds, larval hatching grounds and spatial overlap of hatching grounds with spawning grounds for early, middle, and late western Baltic cod spawners (all values are in km²).

Area	Spawning ground size	Hatching ground size			Spatial overlap between hatching grounds and spawning grounds											
		Early	Mid	Late	Kattegat			Øresund			Great Belt			Western Baltic		
					Early	Mid	Late	Early	Mid	Late	Early	Mid	Late	Early	Mid	Late
Kattegat	2825	6675	6675	5700	450	100	900	1125	300	1500	0	0	0	0	0	0
Øresund	850	6475	6825	3775	0	0	0	25	0	75	0	0	0	0	0	0
Great Belt	1440	8225	9225	5125	0	0	0	0	0	0	900	885	900	300	830	325
Western Baltic	3085	6325	7750	5425	0	0	0	0	0	0	80	0	55	1125	1290	950

grounds in the western Baltic and the Kattegat. The objectives of the study were to (i) determine long-term trends and variability in advective transport of larvae from spawning grounds to juvenile nursery areas; (ii) estimate the degree of exchange between the management areas of eastern and western Baltic, Kattegat, and North Sea; and (iii) compare the results with spatial distributions of juvenile cod. The results are discussed in the light of their potential influence on genetic diversity as well as their relevance for stock assessment and management in the transition area between the North Sea and the Baltic.

Material and methods

Identification of larval release areas

In previous studies, major spawning grounds of cod in the transition area between North Sea and Baltic (Figure 1) were identified to be located in the Kattegat, the Sound, the Little and Great Belt, Kiel Bay, the Fehmarn Belt, and to a limited degree in Mecklenburg Bay (Hüssy, 2011; Hüssy *et al.*, 2012 and references therein). Based on spatio-temporal distributions of drifting particles representing yolk-sac larvae of western Baltic cod at the end of the endogenous feeding period obtained from a previous modelling study (Hinrichsen *et al.*, 2012), spatial distributions of seeding areas for particles representing feeding larvae were identified. This was done by calculation of dispersal kernels (Edwards *et al.*, 2007) from principal component analysis (Hinrichsen *et al.*, 2012) for particles which were initially released as spawned eggs at each of the specific spawning grounds (Figure 1). Based on the duration of the spawning season from December to May, particles were seeded at the centre of the grid cells every 10 days from December 11 to June 10, resulting in 19 different release dates throughout the spawning season. To account for seasonal variations, we chose different release areas of feeding larvae for the early (December–January), mid (February–March), and late (April–June) spawning season. As a second step, we used results from hydrodynamic model runs, combined with a drift model approach considering feeding larval cod as drifting particles, to hindcast long-term spatio-temporal distributions of these late larval stages.

Hydrodynamic model

The hydrodynamic model 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 made, necessary to adapt the model to the Baltic Sea can be found in Lehmann (1995) and Lehmann and Hinrichsen (2000). The model domain comprises the entire Baltic Sea. The horizontal resolution is 5 km, with 60 vertical levels specified. The Baltic Sea model is driven by atmospheric data provided by the Swedish

Meteorological and Hydrological Institute (Norrköping, Sweden) and river run-off taken from a monthly mean run-off database (Bergström and Carlsson, 1994). 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 *et al.*, 1997; Lehmann and Hinrichsen, 2000).

Drift model

The drift model tracks individual feeding larvae through space and time. To consider the seasonal variability of the environmental conditions in relation to its spatial and temporal variability, locations were extracted at the hydrodynamic model 5 × 5 km grid within the estimated hatching areas. In the vertical domain, particles were released between 1.5 and 28.5 m depths at a 3 m depth interval (Hinrichsen *et al.*, 2001). This range was chosen based on the only study of larval cod vertical distribution in the western Baltic Sea, where larvae were found in the depth range 0–30 m, with spatio-temporal differences in depths of highest densities (Westerberg, 1994). To estimate potential effects of vertical migration behaviour, a sensitivity analysis was performed by analysing the drift of particles for three different depth layers (0–10, 10–20, and 20–30 m) separately. The spatio-temporal variability of habitat size of larval release areas is given in Table 1. A total of 494 (26 years × 19 release dates) drift model runs were performed. The larval particles were tracked for a duration of 90 days. The seeding positions were located in the four subregions representing the above defined larval release areas. Finally, to obtain some simple indications for the connectivity of the early life stages of the western Baltic cod stock, we calculated the spatial overlap between their spawning and hatching grounds in terms of sizes for commonly utilized areas.

Model run

Simulated three-dimensional velocity fields were extracted (at 1 h intervals) from the hydrodynamic model to develop a database for particle tracking. This dataset offers the possibility to derive Lagrangian drift routes by calculating the advection of “marked” water particles. Simulated drift routes were obtained from Eulerian flowfields using a Lagrangian particle-tracking technique. The three-dimensional trajectories of the simulated particles were computed using a fourth-order Runge–Kutta scheme (Hinrichsen *et al.*, 1997). The distribution of particles at the end of the 90 days drift duration, representing relative abundances of late larval/early juvenile stages, was recorded. The model runs addressed the question how many particles originating in the different release areas were retained and how many were transported into adjacent areas. To quantify retention within and dispersal to adjacent areas, we produced time series of average proportions of particle end positions for the four spawning

areas for the entire season as well as seasonally resolved for early, mid, and late season for each year from 1979 to 2004. Area-specific averages and standard deviations of proportions of final drift destinations for all years from 1979 to 2004 were determined for the four release areas in early, mid, late, and total spawning season.

Comparison of particle end positions with spatial distribution of juvenile cod

To test the results from the drift modelling, we compared maps of average particle end positions per ICES quarter square, representing potential juvenile settlement areas, with the observed spatial distribution of juvenile cod. To that end, catch per unit effort (cpue) data of 0-group cod from regularly conducted standard bottom trawl surveys in the area were downloaded from the ICES trawl database (ICES Database of Trawl Surveys, 2015, International Bottom Trawl Survey (IBTS) and Baltic International Trawl Survey, ICES, Copenhagen). For more details, see Supplementary Material.

Results

In the following sections, results concerning the extent of larval release areas and particle end positions are mainly described for the entire spawning season, while their seasonal variations are presented in detail in Supplementary Material.

Release areas of feeding larvae

Seeding areas for particles representing feeding larvae of western Baltic cod (Figure 2; Supplementary Figure S1) were generally only partly located within their original spawning grounds but showed a high degree of spatial overlap between areas of origin (Table 1, Figure 2). For the Kattegat spawners, larval release areas were generally also located in the south-central Kattegat, as well as north of the initial spawning area along the Swedish west coast (Figure 2). Offspring originating in the Sound were generally not found in the Sound at the end of the yolk-sac stage, but in the southern and central Kattegat, resulting in a high degree of overlap with the Kattegat release area (Figure 2). A large part of offspring originating in the Great Belt was also found to be located in the original spawning ground at the end of the endogenously feeding period, but there was also a relatively high degree of spatial overlap with the larval release areas of offspring of Kattegat and Sound origin in the south-central Kattegat (Figure 2). Compared with the three other spawning areas, offspring originally spawned in the Kiel Bight and Mecklenburg Bay were found to be closer connected to their initial spawning area, covering the eastern part of Kiel Bay and parts of the Mecklenburg Bay, however, there was also a certain degree of spatial overlap with the larval release area of Great Belt offspring (Figure 2).

Particle end positions

The model runs conducted in the present study addressed the question how many particles, representing different larval cohorts originating in the different western Baltic cod spawning grounds (Figure 1) ended up within the different ICES Subdivisions of the western and the central Baltic Sea. A sensitivity analysis of particle depth on drift patterns showed that depth of occurrence has an impact on drift direction and distance. The deeper the particles, the further were they transported towards the east (Supplementary Figure S2). At present, no information exists on the vertical migration patterns of larvae in the Kattegat/western Baltic Sea, and drift patterns of larvae are therefore integrated over the entire depth range where they have been observed in the field (Westerberg, 1994). Time series of yearly averages of retention within release areas and dispersal

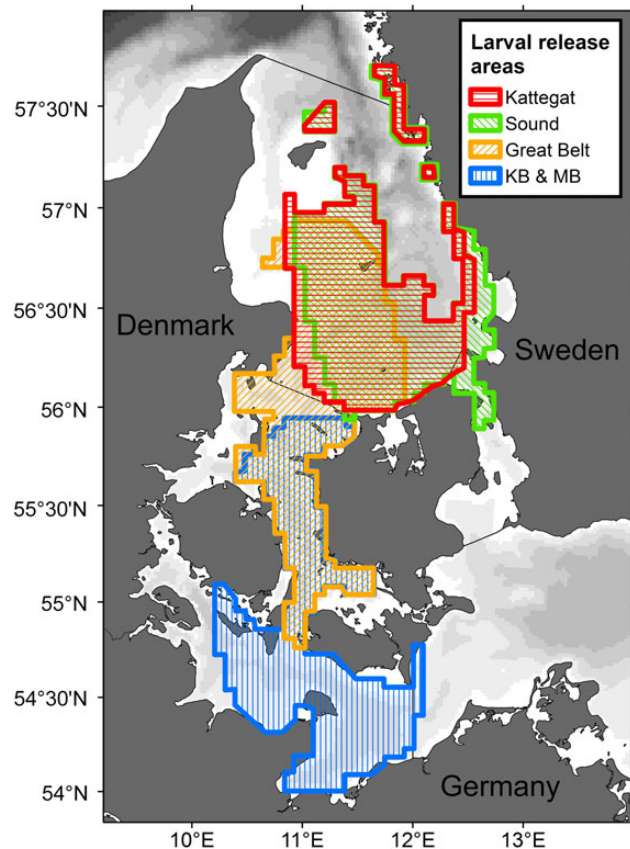


Figure 2. Extent and overlap of release areas of larvae originating in the four spawning grounds in Kattegat, Sound, Great Belt, and Kiel & Mecklenburg Bay. For a colour representation of the figure, it is referred to the online version. This figure is available in black and white in print and in colour at ICES Journal of Marine Science online.

to adjacent areas for the entire spawning season (Figure 3a–d) and seasonally resolved for the early, mid, and late spawning season (Supplementary Figures S3–S6) are presented, as well as averages and standard deviations of proportions of final drift destinations in the different areas for all years from 1979 to 2004 in early, mid, late, and total spawning season (Table 2).

Particles initially released in the Kattegat did mainly end up in the Kattegat and Skagerrak, with high interannual variability (Figure 3a, Table 2). In the 1980s, a particularly strong northward drift occurred, with a very large share of particles transported into Skagerrak, reaching values between 50 and 60%, while fewer particles stayed in Kattegat. Since the 1990s, relatively stable shares of 40–50 and 10–15% were transported to Skagerrak and Kattegat and south into SD22, respectively, whereas only very few particles were transported to the more eastern subdivisions 24–28. On average, 46% of particles were transported to Skagerrak, 12% to SD 22, 2% to SD 24, 1% to SD 25 and <1% to SDs 23, 26 and 28, while 38% stayed in Kattegat (Table 2).

The particles released in the Sound show a very similar pattern as the particles released in Kattegat (Figure 3b), with almost identical average shares of particles ending in the different areas (Table 2). This means that there was basically no retention of particles in the Sound ($0.6 \pm 0.2\%$). Instead, all offspring originating in this area were transported into adjacent areas, with on average >80% in northern direction (45% to SD20 and 38% to SD 21), a smaller share of 12% towards south in SD 22 and very few further east. Another

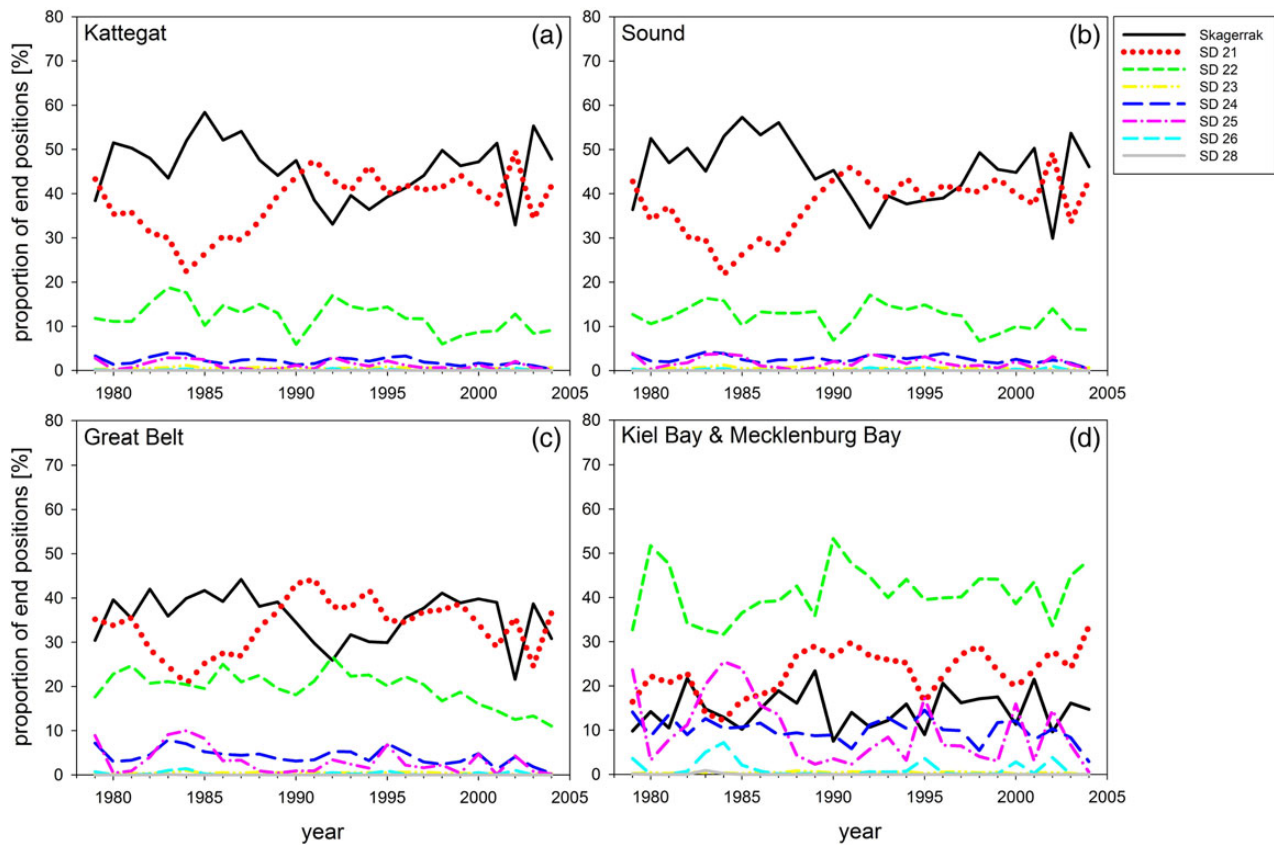


Figure 3. Time series of proportions of particles ending in Skagerrak and ICES SD's 21–28 for particles originating in (a) Kattegat, (b) Sound, (c) Great Belt, and (d) Kiel & Mecklenburg Bay. For a colour representation of the figure, it is referred to the online version. This figure is available in black and white in print and in colour at *ICES Journal of Marine Science* online.

Table 2. Averages and standard deviations (1979–2004) of proportions [%] of particle end positions by initial spawning areas and destination areas for early (December–January), mid (February–March), late (April–June), and total (December–June) spawning season.

Release area	Release period	Destination area							
		Skagerrak	SD21	SD22	SD23	SD24	SD25	SD26	SD28
Kattegat (SD 21)	Early	45.6 ± 12.0	35.2 ± 9.2	13.4 ± 4.8	0.8 ± 0.3	2.9 ± 1.9	2.0 ± 2.1	0.2 ± 0.5	0.0 ± 0.0
	Middle	51.5 ± 10.8	37.4 ± 10.0	8.2 ± 3.6	0.4 ± 0.4	1.4 ± 1.3	1.1 ± 1.4	0.1 ± 0.1	0.0 ± 0.0
	Late	39.2 ± 9.2	42.3 ± 7.3	15.3 ± 6.1	0.6 ± 0.4	2.2 ± 1.3	0.6 ± 1.0	0.0 ± 0.0	0.0 ± 0.0
	Total	45.8 ± 6.8	38.1 ± 6.8	12.1 ± 3.4	0.6 ± 0.2	2.2 ± 0.9	1.2 ± 1.0	0.1 ± 0.2	0.0 ± 0.0
Sound (SD 23)	Early	45.1 ± 12.2	34.7 ± 9.0	13.5 ± 4.6	0.6 ± 0.3	3.3 ± 2.0	2.6 ± 2.6	0.3 ± 0.7	0.0 ± 0.0
	Middle	50.0 ± 10.6	37.5 ± 9.6	9.0 ± 3.5	0.4 ± 0.4	1.7 ± 1.3	1.4 ± 2.6	0.2 ± 0.3	0.0 ± 0.0
	Late	37.0 ± 8.9	42.0 ± 7.1	15.7 ± 4.9	0.9 ± 0.6	3.2 ± 1.4	1.4 ± 1.8	0.0 ± 0.0	0.0 ± 0.0
	Total	45.3 ± 7.2	37.5 ± 6.8	12.1 ± 2.8	0.6 ± 0.2	2.6 ± 0.9	1.8 ± 1.2	0.2 ± 0.3	0.0 ± 0.0
Great Belt (SD 22 N)	Early	31.5 ± 10.2	31.6 ± 8.1	27.4 ± 6.6	0.6 ± 0.4	4.8 ± 2.9	3.7 ± 4.4	0.4 ± 0.8	0.0 ± 0.0
	Middle	42.6 ± 10.6	36.3 ± 8.5	14.3 ± 4.3	0.3 ± 0.3	3.4 ± 2.1	3.0 ± 3.7	0.2 ± 0.4	0.0 ± 0.0
	Late	33.4 ± 11.0	36.9 ± 6.8	21.6 ± 6.9	0.4 ± 0.3	5.2 ± 2.8	2.7 ± 3.6	0.0 ± 0.1	0.0 ± 0.0
	Total	35.8 ± 5.5	33.7 ± 6.1	19.7 ± 3.9	0.4 ± 0.2	4.2 ± 1.8	3.1 ± 3.1	0.3 ± 0.4	0.0 ± 0.0
KB & MB (SD 22 S)	Early	8.2 ± 4.2	16.4 ± 6.1	50.4 ± 11.8	0.6 ± 0.5	11.4 ± 5.3	11.3 ± 10.7	1.9 ± 3.9	0.0 ± 0.1
	Middle	19.2 ± 9.4	26.3 ± 7.9	35.9 ± 6.9	0.2 ± 0.1	8.2 ± 3.9	9.0 ± 8.8	1.3 ± 2.3	0.1 ± 0.4
	Late	15.0 ± 7.0	25.7 ± 4.5	38.7 ± 7.5	0.4 ± 0.4	11.1 ± 4.0	9.0 ± 6.9	0.3 ± 0.5	0.0 ± 0.0
	Total	14.7 ± 4.3	23.1 ± 5.3	41.2 ± 5.9	0.4 ± 0.2	10.0 ± 2.7	9.7 ± 7.6	1.2 ± 1.9	0.0 ± 0.2

interesting fact about the Sound is that this area did basically not receive any particles from adjacent areas either, with total average values of particles ending in SD 23 ranging between 0.4 and 0.6%.

Particles released in the Great Belt in the northern part of SD 22 also showed similar general drift patterns as Kattegat and Sound, with high interannual variability and a generally high transport

towards north (Table 2, Figure 3c). Also for this release area, northward drift was particularly pronounced during the 1980s when a higher fraction was transported to Skagerrak than to Kattegat, while during the early 1990s more particles ended in Kattegat than in Skagerrak. Since the mid-1990s more or less equal shares ended in Skagerrak and Kattegat. However, the overall share of particles

transported to Skagerrak and Kattegat was $\sim 35\%$ and thus smaller than for particles released in Kattegat and the Sound, while there was a higher share of retention within SD 22 (on average ca. 20%). Also, a higher average share of 4 and 3% were drifted eastward to SD 24 and SD 25, respectively, with some years (e.g. 1979, 1983–1985, 1995) ranging between 5 and 10%.

Particles released in Kiel Bay and Mecklenburg Bay in the southern part of SD 22 showed the highest retention (41%) of all four investigated release areas (Table 2, Figure 3d). However, also from this area considerable shares of on average 15 and 20% were transported to Skagerrak and Kattegat. Furthermore, this area also showed a high variability with respect to drift into other areas, with some years characterized by high shares of northward drift and others by high shares of eastward drift. This variability becomes particularly evident when comparing the time series for SD 21 and SD25, which were showing alternating patterns, with low transport to SD 25 and high transport to SD 21 in 1980–1982, 1988–1994, and 1996–1999 and an opposite pattern in 1979, 1983–1985, 1995, and 2000. In these latter years up to 26% were transport to SD 25 and up to 7% reached as far east as SD 26. The high interannual variability of transport to SD 25 is also witnessed by the high standard deviation of 7.6 at an average of 9.7% (Table 2). In contrast to the alternating pattern between SD 21 and SD 25, northward transport to Skagerrak and eastward transport to SD 24 were rather stable at values of ca. 10–20 and 10–15%, respectively. It should also be noted that SD 24 belongs to the same management unit as SD 22, which means if particles ending in SD 22 and SD 24 are combined, more than half of the particles released in Kiel and Mecklenburg Bay were retained within that management unit.

To further illustrate the potential for variability in transport between areas, we have mapped two extreme examples of eastward and northward transport for particles released in the Kiel and Mecklenburg Bay area (see Supplementary Figure S7a and b).

Comparison of particle end positions with spatial distribution of juvenile cod

For particles initially released in the Kattegat, there is a good match between large numbers of particle end positions (Figure 4a) and abundance of juvenile cod (Figure 4d) at the border between Kattegat and Skagerrak, as well as in the eastern Skagerrak along the coast of Sweden. A large number of particles ended also in the central Skagerrak, but for this area no trawl data were available for comparison with juvenile occurrence.

Within the Kattegat, there is a good spatial match, with high abundance of particle end positions and juveniles in the southeastern Kattegat, while lower values of particles in the western part of the Kattegat correspond to low or zero catches of juveniles. However, when considering the overall picture of all particles and juvenile abundance in the entire investigation area, the proportions do not match well, as there is a low juvenile abundance in the southeastern Kattegat compared with the large numbers of particles in this area.

Particles initially released in the Sound show an almost identical pattern as particles released in the Kattegat, and therefore no separate map is shown for this release area.

Particles initially released in the Great Belt also show a similar pattern as particles released in the Kattegat and the Sound (Figure 4b), with centres of aggregations along the Swedish Skagerrak coast, at the border between Skagerrak and Kattegat and in the southeastern Kattegat. However, there are also areas of increased accumulations of particles in the southwestern Kiel Bay as well as in

the central Mecklenburg Bay, which matches high juvenile abundances in these areas.

Finally, for the release area Kiel Bay and Mecklenburg Bay, there is a good match between particle end positions and juvenile cpues in the southern part of the study area, with high accumulations in the western and southern Kiel Bay as well as in central parts of Mecklenburg Bay (Figure 4c and d).

Discussion

Larval drift, hydrography, juvenile nursery areas, and connectivity

Connectivity, or the exchange of individuals among populations, is an important process from an ecological perspective, but also for conservation and management of harvested species (e.g. Selkoe *et al.*, 2008; Cowen and Sponaugle, 2009; Reiss *et al.*, 2009). The connectivity of Atlantic cod (*Gadus morhua*) populations in the transition area between the North Sea and the Baltic has been the topic of a number of studies (Pihl and Ulmestrand, 1993; Nielsen *et al.*, 2003, 2005; Svedäng and Svenson, 2006; Svedäng *et al.*, 2007, 2010a, b). However, these investigations were focused on migrations and genetic structure of adults and larger juveniles, while transport of early life stages has not been considered, although pelagic eggs and larvae can be transported over large distances via ocean currents. In previous studies, Hüsey *et al.* (2012), Hinrichsen *et al.* (2012), and Pacariz *et al.* (2014a, b) have analysed the fate of cod eggs and yolk-sac larvae in this transition area. These studies showed that environmentally mediated mortality and survival success were predominantly affected by egg buoyancy, ambient temperatures, and transport into suitable or unsuitable habitats, and that transport patterns are highly variable within and between years, with average transport directions towards the north.

As for the egg stage, the transport patterns during the exogenous-ly feeding larval stage investigated in the present study were generally also very dynamic and showed high intra- and interannual variability of particle end positions. However, recurring patterns of larval transport were found, e.g. the general drift in northward direction for the three northern spawning areas and the high retention for the spawning area in Kiel Bay and Mecklenburg Bay. Furthermore, a striking feature of our modelling study was the high overlap of larval release areas in the middle (February–March) and partly also the early (December–January) spawning season, while late in the spawning period (April–June) the larval release areas were more distinct with only little overlap. This can be related to lower ambient temperatures in mid and partly also early season and the correspondingly longer temperature-dependent egg and yolk-sac larval developmental times associated with longer drift durations resulting in larger drift distances. In contrast, higher ambient temperatures associated with shorter development times and shorter drift durations at the end of the spawning season (Hinrichsen *et al.*, 2012) resulted in smaller release areas for feeding larvae, which were more concentrated near the initial spawning areas. Another interesting result was that the Sound showed basically no retention but transport of $>80\%$ of particles towards the north, and generally an identical drift pattern as the Kattegat. This is caused by the fact that eggs spawned in the Sound are more or less immediately flushed northward into the Kattegat (Hinrichsen *et al.*, 2012) and the release area of larvae initially originating in the Sound is therefore very similar to the release area of larvae from the Kattegat spawning ground.

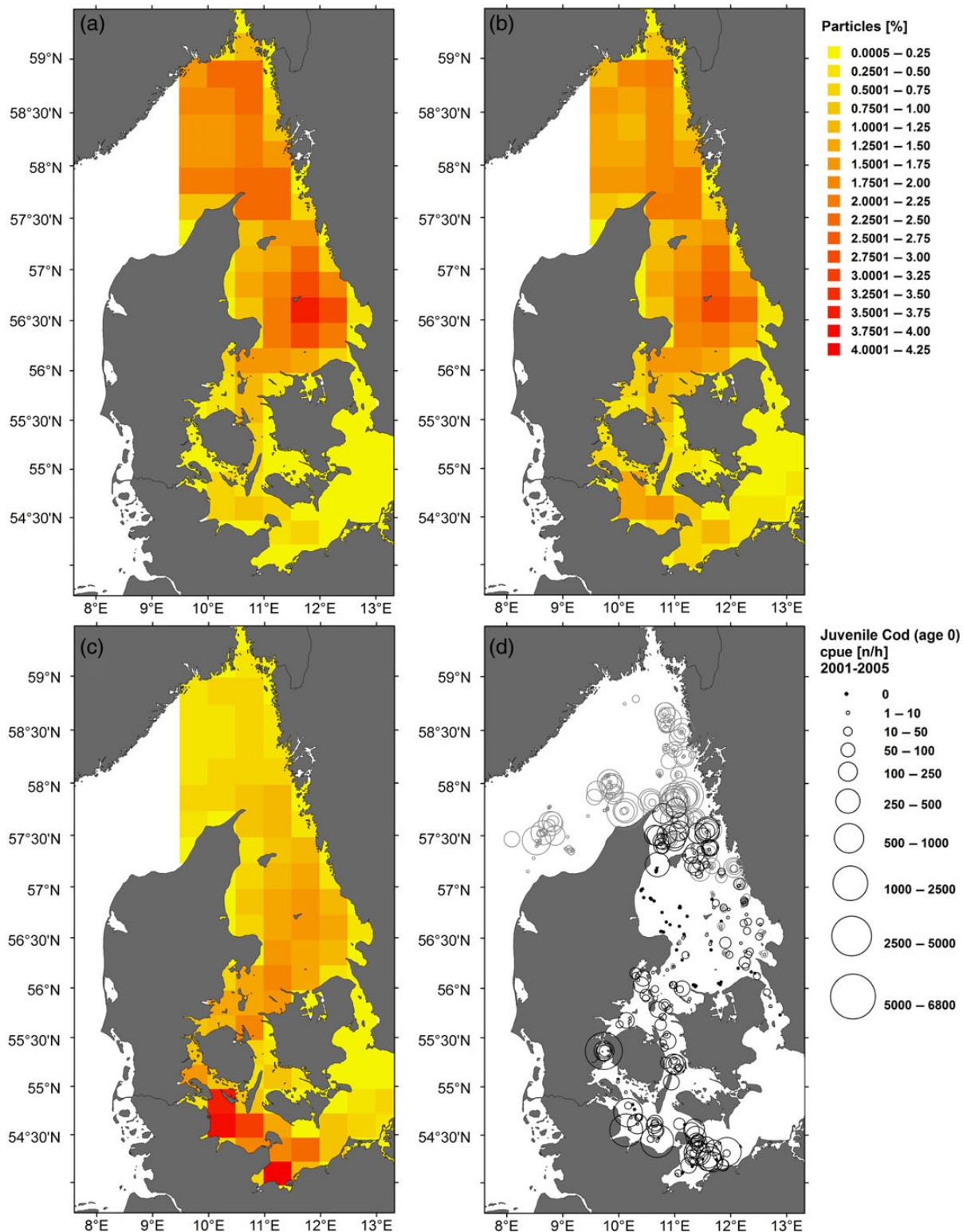


Figure 4. Comparison of average (1979–2004) particle end positions (%) for particles released in (a) Kattegat, (b) Great Belt, and (c) Kiel & Mecklenburg Bay with (d) catch per unit effort (cpue, n/hour) of juvenile cod from bottom trawl surveys (grey circles: IBTS – International Bottom Trawl Survey, black circles: BITS – Baltic International Trawl Survey) in the period 2001–2005. For a colour representation of the figure, it is referred to the online version. This figure is available in black and white in print and in colour at *ICES Journal of Marine Science* online.

The comparison of particle end positions with catches of juvenile cod from bottom trawl surveys showed a high degree of concurrence, with centres of nursery areas around Skagen at the northern

tip of Denmark and along the Swedish coast, as well as in Kiel and Mecklenburg Bay. However, there were also some discrepancies with large numbers of particles but no concurrent juvenile

occurrence in the central Skagerrak, which can be explained by the local topography. Although not sampled in the IBTS, juvenile cod are likely not able to find a suitable settling habitat in this area due to the large depths in the eastern part of the Norwegian Trench. Considering Kattegat alone, there is actually a good spatial match, with a juvenile nursery area in the southeast and no juvenile occurrence in the western part. However, the proportions of particles and juvenile catches did not agree well, with relatively low juvenile catches compared with the large number of particles ending in this area. This may be related to the fact that the exchange rates between areas and the associated particle end positions represent relative, general patterns rather than actual abundances, as no information on spawning intensity and estimates of actual numbers of eggs and larvae released in the different spawning areas were available. Furthermore, there is an important difference between “total connectivity”, i.e. the number of transported particles and “realized connectivity”, i.e. the number of transported particles which actually survive and contribute to successful recruitment and eventually reproduction (Selkoe *et al.*, 2008). This issue has at least partly been considered in our previous studies on cod eggs, which estimated egg mortality due to unfavourable environmental conditions in the spawning areas and along the drift routes (Hinrichsen *et al.*, 2012; Hüsey *et al.*, 2012). However, analyses of realized connectivity during the larval stage would require estimates of larval mortality by linking the drift model with a bioenergetics growth model and realistic prey fields as well as absolute measures of initially released eggs and their attributes (i.e. size, buoyancy) based on spawning stock size, stock composition and fecundity. As these necessary data and tools for estimation of absolute numbers are not available, drift patterns can at present only be captured as probability distributions. Nevertheless, the overall good agreement between spatial patterns of particle end positions and juvenile catches suggests that our modelling study provides reasonable estimates of larval drift and juvenile settling areas, and thus of general patterns of early life stage connectivity between cod populations in the investigated areas, while the actually realized connectivity between areas awaits further quantification.

The strong differences of retention and dispersal patterns of larval cod in space and time are a consequence of the specific, spatially, and temporally highly variable physical environmental conditions in our study area, which in turn lead to a highly dynamic ocean circulation (for details, see e.g. Stigebrandt, 1983; Schinke and Matthäus, 1998; Lehmann *et al.*, 2002). The combination of these highly variable environmental conditions with the small size and close vicinity of the cod management units in the transition area between North Sea and Baltic lead to a high potential for exchange of individuals between management units via advective transport during the pelagic stages of the life cycle.

Evidence of stock structure in the transition area between North Sea and Baltic

In the transition area between the North Sea and the Baltic Sea there is ample evidence of complex stock structuring from area-specific stock indices (Svedäng and Svenson, 2006; Svedäng *et al.*, 2010a), tagging experiments (Pihl and Ulmestrand, 1993; Svedäng *et al.*, 2007), chemical signatures in otoliths (Svedäng *et al.*, 2010b), and genetics (Nielsen *et al.*, 2003). Cod in the Kattegat (SD 21) consist of a mixture of resident and migratory stocks undertaking migrations as far as the North Sea (Svedäng *et al.*, 2007). Throughout the area from the Belt Sea (SD 22) to the Arkona Basin (SD 24) spawning migrations occur towards the southern Kattegat and Great Belt, respectively, with return migrations to their respective

feeding grounds (Hüsey, 2011 and references therein). In the Sound however, cod seem to be exclusively resident (Svedäng *et al.*, 2007).

Despite this apparent stock structuring driven by individual fish's behaviour, there seems to be limited genetic differentiation. While North Sea, Kattegat, Sound, and Belt Sea cod are genetically similar (Nielsen *et al.*, 2003; Svedäng *et al.*, 2010b), they differ significantly from cod in the Baltic Sea east of Bornholm (Nielsen *et al.*, 2003). To explore the connectivity between stocks from different areas, Nielsen *et al.* (2005) examined the genetic linkage between adults and juveniles within each area. Juvenile cod in the North Sea, Kattegat/Skagerrak, Belt Sea, and Eastern Baltic are genetically related to adults in the same areas indicative of limited exchange with other areas. Juveniles from the Western Baltic Sea on the other hand were closer related to adults from the Belt Sea (Nielsen *et al.*, 2005). This suggests early life stage dispersal from the Belt Sea towards the east. Additionally, a number of genetically distinct local populations occur along the Skagerrak coast, with no apparent trend of isolation by distance. This suggests that the primary driver for genetic stock structuring is not migration of adults but drift of early life stages without subsequent return migration as juveniles or adults (Knutsen *et al.*, 2003).

Extensive and temporally variable drift of North Sea cod larvae into coastal waters in the Skagerrak are known to occur, and between 1 and 10% of juveniles in the Skagerrak were estimated to be of North Sea origin (Knutsen *et al.*, 2004; Stenseth *et al.*, 2006). In combination with results from the present study, this suggests that the Skagerrak/Kattegat may be an area where cod originating in the North Sea, the Skagerrak, the Kattegat, and the western Baltic are mixing via larval drift, while the eastern Baltic is isolated through limited exchange of both early life stages and adults.

Although there is evidence of a certain degree of natal homing in cod in the area of investigation, the lack of genetic differentiation documents that extensive gene flow occurs between stocks in the transition area between the North Sea and the western Baltic. The high dispersal rates between areas observed in the present study suggest that dispersal of early life stages may be the driving force for this lack in genetic differentiation.

Implications for fisheries management

Hinrichsen *et al.* (2011) documented the usefulness of hydrodynamic and coupled biophysical models for fisheries management, owing to their ability to estimate the transport and survival chances of early life stages, the settlement probability of juvenile fish and the spatio-temporal scales of connectivity between stocks.

Stock identity and geographical boundaries used to define fish stocks are of particular concern for fisheries management as a failure to recognize biological populations could result in non-optimal or unsustainable management of the resources (Heath *et al.*, 2013; Eero *et al.*, 2014). Development of various stock separation techniques can potentially allow accounting for mixing of biological populations in stock assessment, as demonstrated by a recent example for Eastern and Western Baltic cod (Hüsey *et al.*, 2015; ICES 2015a, c). Our analyses in the present paper demonstrate that the stock structure in the transition area between North Sea and Baltic may be even more complex when considering early life stages and involve four different cod management units: Skagerrak/North Sea, Kattegat, Western Baltic, and Eastern Baltic.

Evaluations of fishing opportunities based on stock assessments are mostly focused on the adult components of the stocks. The exchange of offspring between different stock assessment or

management units may not be an issue for assessing the adult biomass levels or fishing pressure, given that homing takes place (Robichaud and Rose, 2001; Svedäng *et al.*, 2007). However, the relationship between parent stock biomass and resulting recruitment is an important basis for defining biological reference points used for fisheries management. Stock–recruitment relationships may be blurred extensively if large parts of the eggs and larvae spawned in a given management unit do not remain as recruits in the same area, but instead contribute as recruits to adjacent stock units. Exchange of recruits needs to be considered for small adjacent assessment units with extensive water movement as demonstrated in this study for the transition area from the North Sea to the Baltic. Drift of early life stages can thus be one of the reasons for the lack of well-defined relationships between recruitment and the size of parent stock within the assessment units, in addition to drivers affecting recruitment survival.

The “realized connectivity” (Selkoe *et al.*, 2008), i.e. the numbers of transported particles which actually survive and contribute to recruitment in the investigated cod stock areas, is currently not quantified. Therefore, it is difficult to evaluate the magnitude of the potential problem that the apparently substantial drift of early life stages causes for stock assessment and management. However, given the high probability of substantial exchange of recruits between the defined assessment units, stock–recruitment relationships within a given unit should be treated with caution. Quantitative analyses of the origin of recruitment in different areas are recommended as a next step, for example, using otolith chemistry (Svedäng *et al.*, 2010b). Furthermore, studies on larval vertical migration behaviour and regular ichthyoplankton surveys are advocated to improve the input for drift modelling and to further quantify connectivity between areas.

From a management point of view, one could consider combining the smaller units into one single assessment covering a larger geographical area to avoid violating the closed population assumption that is the basis for stock assessment. However, a shortcoming of this approach is that weaker subpopulations may not get sufficiently protected as the most abundant substock will mask the developments in smaller populations (e.g. Eero *et al.*, 2014). In fact, a number of recent studies have argued for a finer spatial resolution in fisheries management to account for subpopulations structure, e.g. for cod in the North Sea (Heath *et al.*, 2013). Ideally, spatial processes should be modelled as part of stock assessment, which however increases the complexity of stock assessments and data demands (Goethel *et al.*, 2011). Thus, there is a need for both better understanding of connectivity to quantify the exchange of recruits between areas as well as further development of stock assessment modelling tools to identify most appropriate solutions for stock assessment and fisheries management purposes taking into account spatial processes.

Hydrodynamic and coupled biophysical models such as the one used in this study are considered valuable tools to estimate spatio-temporal scales of connectivity within and between stocks, to identify potential issues with stock area definitions and thereby to contribute to conservation, management, and recovery of fish stocks.

Supplementary material

Supplementary material is available at the ICESJMS online version of the paper.

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References

- Baumann, H., Hinrichsen, H.-H., Möllmann, C., Köster, F. W., Malzahn, A. M., and Temming, A. 2006. Recruitment variability in Baltic sprat (*Sprattus sprattus*) is tightly coupled to temperature and transport patterns affecting the larval and early juvenile stages. *Canadian Journal of Fisheries and Aquatic Sciences*, 63: 2191–2201.
- Bergström, S., and Carlsson, B. 1994. River runoff to the Baltic Sea: 1950–1990. *Ambio*, 23: 280–287.
- Bryan, K. 1969. A numerical method for the study of the circulation of the world ocean. *Journal of Physical Oceanography*, 15: 1312–1324.
- Cowen, R. K., and Sponaugle, S. 2009. Larval dispersal and marine population connectivity. *Annual Review of Marine Science*, 1: 443–466.
- Cox, M. D. 1984. A primitive equation 3-dimensional model of the ocean. GFDL Ocean Group Technical Report No. 1, Geophysical Fluid Dynamics Laboratory, Princeton, NJ, 75 pp.
- Edwards, K. P., Werner, F. E., Seim, H., and Hare, J. A. 2007. Using 2-dimensional dispersal kernels to identify the dominant influences on larval dispersal on continental shelves. *Marine Ecology Progress Series*, 352: 77–87.
- Eero, M., Hemmer-Hansen, J., and Hüsey, K. 2014. Implications of stock recovery for a neighbouring management unit: experience from the Baltic cod. *ICES Journal of Marine Science*, 71: 1458–1466.
- Gaines, S. D., and Lafferty, K. D. 1995. Modeling the dynamics of marine species: the importance of incorporating larval dispersal. In *Ecology of Marine Invertebrate Larvae*, pp. 389–412. Ed. by L. R. McEdward. CRC Press, Boca Raton, FL, USA.
- Gaylord, B., and Gaines, S. D. 2000. Temperature or transport? Range limits in marine species mediated solely by flow. *American Naturalist*, 155: 769–789.
- Goethel, D. R., II, Quinn, T., and Cadrin, S. X. 2011. Incorporating spatial structure in stock assessment: Movement modeling in marine fish population dynamics. *Reviews in Fisheries Science*, 19: 119–136.
- Grosberg, R. K., and Cunningham, C. W. 2001. Genetic structure in the sea: from populations to communities. In *Marine Community Ecology*, pp. 61–84. Ed. by M. D. Bertness, M. E. Hay, and S. D. Gaines. Sinauer, Sunderland, MA, USA.
- Gulland, J. A. 1983. Fish stock assessment: a manual of basic methods. FAO Wiley Series on food and agriculture. Vol. 1. Wiley Interscience, Chichester, UK. 223 pp.
- Heath, M. R., Culling, M. A., Crozier, W. W., Fox, C. J., Gurney, W. S. C., Hutchinson, W. F., Nielsen, E. E., *et al.* 2013. Combination of genetics and spatial modelling highlights the sensitivity of cod (*Gadus morhua*) population diversity in the North Sea to distributions of fishing. *ICES Journal of Marine Science*, 71: 794–807.
- Hinrichsen, H.-H., Boettcher, U., Oeberst, R., Voss, R., and Lehmann, A. 2001. 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., Dickey-Collas, M., Huret, M., Peck, M. A., and Vikebø, F. B. 2011. Evaluating the suitability of coupled biophysical models for fishery management. *ICES Journal of Marine Science*, 68: 1478–1487.
- Hinrichsen, H.-H., Hüsey, K., and Huwer, B. 2012. Spatio-temporal variability in western Baltic cod early life stage survival mediated by egg buoyancy, hydrography and hydrodynamics. *ICES Journal of Marine Science*, 69: 1744–1752.

- Hinrichsen, H.-H., Lehmann, A., St. John, M. S., and Brüggel, B. 1997. Modeling the cod larvae drift in the Bornholm Basin in summer 1994. *Continental Shelf Research*, 17: 1765–1784.
- Hixon, M. A., Pacala, S. W., and Sandin, S. A. 2002. Population regulation: historical context and contemporary challenges of open vs closed systems. *Ecology*, 83: 1490–1508.
- Hüssy, K. 2011. Review of western Baltic cod (*Gadus morhua*) recruitment dynamics. *ICES Journal of Marine Science*, 68: 1459–1471.
- Hüssy, K., Hinrichsen, H.-H., Eero, M., Mosegaard, H., Hemmer-Hansen, J., Lehmann, A., and Lundgaard, L. S. 2015. Spatio-temporal trends in stock mixing of eastern and western Baltic cod in the Arkona Basin and the implications for recruitment (under revision). doi: 10.1093/icesjms/fsv227.
- Hüssy, K., Hinrichsen, H.-H., and Huwer, B. 2012. Hydrographic influence on the spawning habitat suitability of western Baltic cod (*Gadus morhua*). *ICES Journal of Marine Science*, 69: 1736–1743.
- Huwer, B., Hinrichsen, H.-H., Böttcher, U., Voss, R., and Köster, F. W. 2014. Characteristics of juvenile survivors reveal spatio-temporal differences in early life stage survival of Baltic cod. *Marine Ecology Progress Series*, 511: 165–180.
- ICES. 2005. Spawning and life history information for North Atlantic cod stocks. ICES Cooperative Research Report No. 274. 152 pp.
- ICES. 2015a. Report of the Baltic Fisheries Assessment Working Group (WGBFAS), 14–21 April 2015, ICES Headquarters, Copenhagen, Denmark. ICES CM 2015/ACOM:10.
- ICES. 2015b. Report of the International Bottom Trawl Survey Working Group (IBTSWG), 23–27 March 2015, Bergen, Norway. ICES CM 2015/SSGIEOM:24. 278 pp.
- ICES. 2015c. Report of the Benchmark Workshop on Baltic Cod Stocks (WKBALTCOD). ICES CM 2015/ACOM:35.
- Killworth, P. D., Stainforth, D., Webb, D. J., and Paterson, S. M. 1991. The development of a free-surface Bryan-Cox-Semtner ocean model. *Journal of Physical Oceanography*, 21: 1333–1348.
- Knutsen, H., André, C., Jorde, P. E., Skogen, M. D., Thuróczy, E., and Stenseth, N. C. 2004. Transport of North Sea cod larvae into the Skagerrak coastal populations. *Proceedings of the Royal Society B-Biological Sciences*, 271: 1337–1344.
- Knutsen, H., Jorde, P. E., André, C., and Stenseth, N. C. 2003. Fine-scaled geographical population structure in a highly mobile marine species: the Atlantic cod. *Molecular Ecology*, 12: 385–394.
- Lehmann, A. 1995. A three-dimensional baroclinic eddy-resolving model of the Baltic Sea. *Tellus*, 47A: 1013–1031.
- Lehmann, A., and Hinrichsen, H.-H. 2000. On the thermohaline variability of the Baltic Sea. *Journal of Marine Systems*, 25: 333–357.
- Lehmann, A., Krauß, W., and Hinrichsen, H.-H. 2002. Effects of remote and local atmospheric forcing on circulation and upwelling in the Baltic Sea. *Tellus*, 54: 299–316.
- Nielsen, E. E., Grønkjær, P., Meldrup, D., and Paulsen, H. 2005. Retention of juveniles within a hybrid zone between North Sea and Baltic Sea Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences*, 62: 2219–2225.
- Nielsen, E. E., Hansen, M. M., Ruzzante, D. E., Meldrup, D., and Grønkjær, P. 2003. Evidence of a hybrid-zone in Atlantic cod (*Gadus morhua*) in the Baltic and the Danish Belt Sea revealed by individual admixture analysis. *Molecular Ecology*, 12: 1497–1508.
- Pacariz, S., Björk, G., Jonsson, P., Börjesson, P., and Svedäng, H. 2014a. A model study of the large-scale transport of fish eggs in the Kattegat in relation to egg density. *ICES Journal of Marine Science*, 71: 345–355.
- Pacariz, S., Björk, G., and Svedäng, H. 2014b. Interannual variability in the transport of fish eggs in the Kattegat and Öresund. *ICES Journal of Marine Science*, 71: 1706–1716.
- Palumbi, S. R. 2004. Marine reserves and ocean neighborhoods: the spatial scale of marine populations and their management. *Annual Review of Environment and Resources*, 29: 31–68.
- Pihl, L., and Ulmestrand, M. 1993. Migration pattern of juvenile cod (*Gadus morhua*) on the Swedish west coast. *ICES Journal of Marine Science*, 50: 63–70.
- Reiss, H., Hoarau, G., Dickey-Collas, M., and Wolff, W. J. 2009. Genetic population structure of marine fish: mismatch between biological and fisheries management units. *Fish and Fisheries*, 10: 361–395.
- Robichaud, D., and Rose, G. A. 2001. Multiyear homing of Atlantic cod to a spawning ground. *Canadian Journal of Fisheries and Aquatic Sciences*, 58: 2325–2329.
- Roughgarden, J., Gaines, S., and Possingham, H. 1988. Recruitment dynamics in complex life cycles. *Science*, 241: 1460–1466.
- Schinke, H., and Matthäus, W. 1998. On the causes of major Baltic inflows – an analysis of long time series. *Continental Shelf Research*, 18: 67–97.
- Selkoe, K. A., Henzler, C. M., and Gaines, S. D. 2008. Seascape genetics and the spatial ecology of marine populations. *Fish and Fisheries*, 9: 363–377.
- Semtner, A. J. 1974. A general circulation model for the World Ocean. UCLA Department of Meteorology Technical Report, No. 8, 99 pp.
- Sinclair, M. 1988. Marine populations: an essay on population regulation and speciation. University of Washington Press, Seattle.
- Stenseth, N. C., Jorde, P. E., Chan, K. S., Hansen, E., Knutsen, H., André, C., Skogen, M. D., et al. 2006. Ecological and genetic impact of Atlantic cod larval drift in the Skagerrak. *Proceedings of the Royal Society Series B – Biological Sciences*, 273: 1085–1092.
- Stigebrandt, A. 1983. A model for the exchange of water and salt between Baltic and the Skagerrak. *Journal of Physical Oceanography*, 13: 411–427.
- Svedäng, H., André, C., Jonsson, P., Elfman, M., and Limburg, K. E. 2010a. Migratory behaviour and otolith chemistry suggest fine-scale sub-population structure within a genetically homogenous Atlantic Cod population. *Environmental Biology of Fish*, 89: 383–397.
- Svedäng, H., Righton, D., and Jonsson, P. 2007. Migratory behaviour of Atlantic cod *Gadus morhua*: natal homing is the prime stock-separating mechanism. *Marine Ecology Progress Series*, 345: 1–12.
- Svedäng, H., Stål, J., Sterner, T., and Cardinale, M. 2010b. Consequences of subpopulation structure on fisheries management: Cod (*Gadus morhua*) in the Kattegat and Öresund (North Sea). *Reviews in Fisheries Science*, 18: 139–150.
- Svedäng, H., and Svenson, A. 2006. Cod *Gadus morhua* L. populations as behavioural units: inference from time series on juvenile abundance in the eastern Skagerrak. *Journal of Fish Biology*, 69 (Suppl. C): 151–164.
- Westerberg, H. 1994. The transport of cod eggs and larvae through Öresund. ICES Document CM 1994/Q:4.

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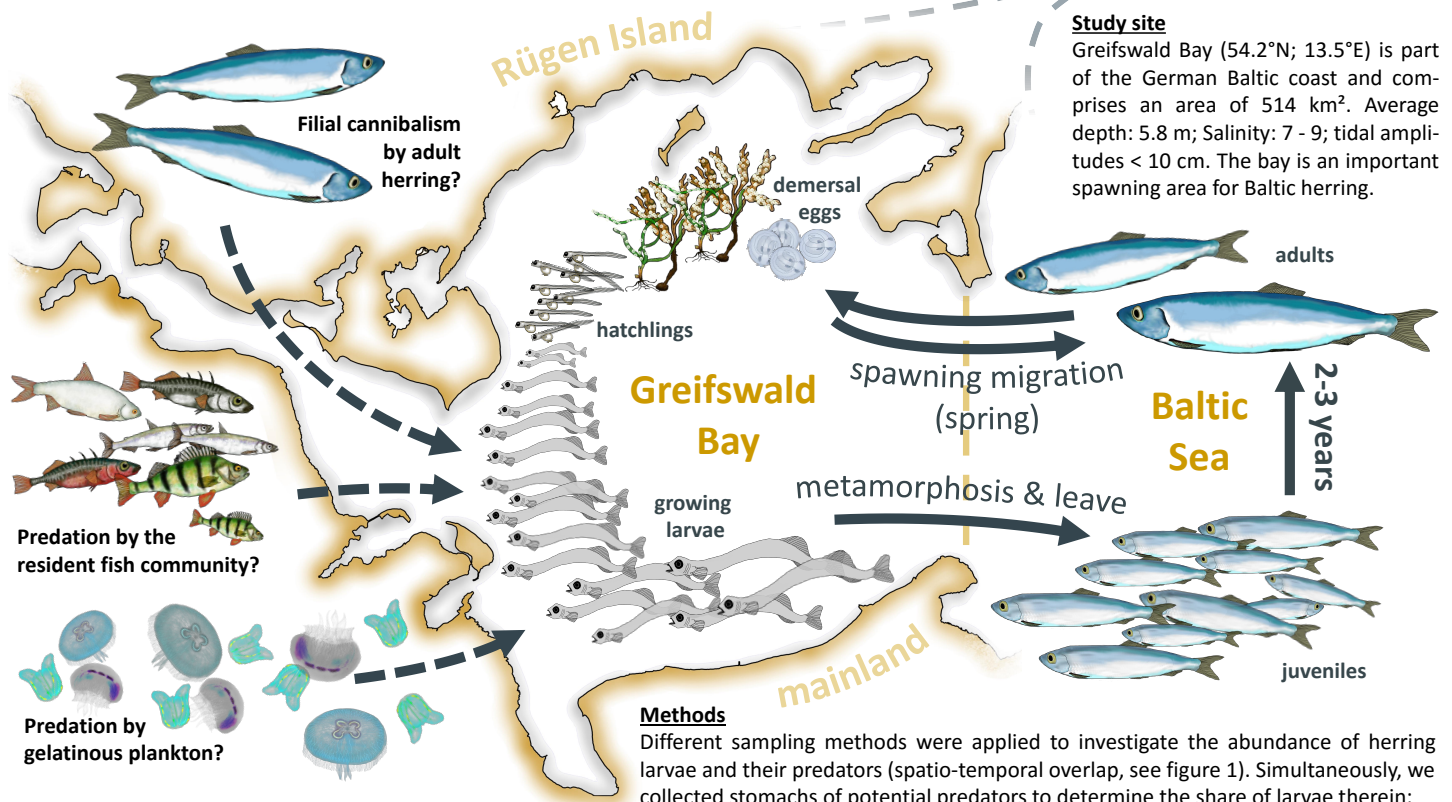
Predator impacts on inshore Baltic herring (*Clupea harengus*) larvae: Lions, tigers and bears – but where?

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Background

Predation on marine fish larvae is considered to be a major cause of their mortality. For example, in offshore retention areas of Pacific and Atlantic herring (*Clupea* spp.) larvae, a broad variety of different predators such as pelagic fish species and gelatinous plankton (Scyphozoa and Ctenophora) is assumed to significantly affect the survival of herring larvae. Furthermore, herring itself has been documented to conduct filial cannibalism. Alike other herring subpopulations, Baltic herring usually spawns in transitional waters and lagoons that are characterized by a different set of environmental factors and potential larvae predators. Are top-down mechanisms observed in offshore areas then transferable to inshore systems at all?



Herring larvae: Oblique Bongo net hauls at 36 distinct stations (25 years data series) & trawls with a modified epibenthic sledge in the littoral zone (2011). **Potential predators:** Bongo net bycatches; frame trawl catches in the bay (2011); beach seine hauls in the littoral (2011-2015). Adult herring were sampled with a gill net (2010-2015). Stomach samples were immediately fixated onboard (frozen on dry ice or with 4% formalin) & later analyzed in the laboratory.

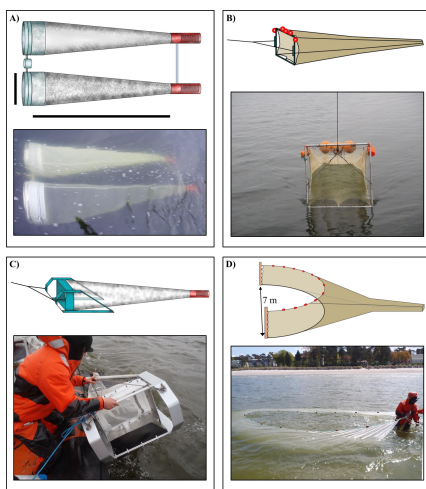


Figure 1. Sampling techniques. A) Bongo-net (oblique haul plankton net with meshes of 335 & 780 µm) B) Frame trawl with 2.1 m opening and 5 mm meshes. C) Modified epibenthic sledge, equipped with a plankton net (500 µm) D) Beach seine with 7 m opening and 5 mm meshes.

Results

predator group:	adult herring	fish community	gelatin. plankton
spatio-temporal overlap?	strong overlap	strong overlap (see figure 2)	temporal mismatch
larvae predation?	nearly no larvae in the stomachs	nearly no larvae in the stomachs	no predation

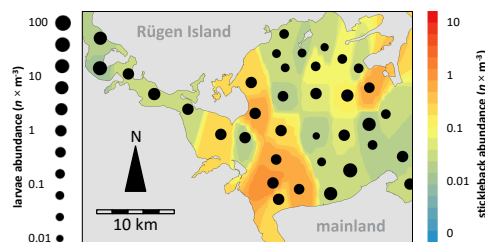


Figure 2. Spatial overlap of herring larvae and threespine stickleback (*Gasterosteus aculeatus*) in May 2011 (calendar week 19) based on the Bongo-net sampling at 36 stations within Greifswald Bay. Larvae abundances are given as black circles (area = proportional to abundance) while the stickleback abundance (color scale) was interpolated using a spatial kriging approach.

Conclusions

Unexpectedly, we found no significant predation on herring larvae within Greifswald Bay. We conclude that in these types of nursery grounds, larval mortality due to predation is negligible and that observations from offshore areas should not be transferred. Moreover, low predation rates might act synergistically with favorable temperatures and nutritional conditions for larval growth - making transitional waters even more valuable as spawning & nursery grounds for marine fishes.

We gratefully thank all colleagues at the Thünen-Institute and the crew of the research vessel "Clupea". This work resulted from the BONUS BIO-C3 and INSPIRE projects and was supported by BONUS (Art 185), funded jointly by the EU and the Federal Ministry of Education and Research of Germany (BMBF).

Migration of spring spawning herring in the Western Baltic Sea

Thuenen Institute of Baltic Sea fisheries; Daniel Oesterwind, Paul Kotterba

Throughout the last years, P11 conducted a variety of different field studies to examine the connectivity of coastal inshore lagoons with the offshore areas of the Baltic Sea. We used Atlantic herring (*Clupea harengus*) as an example to analyze interactions between these systems since the species undergoes intensive annual migrations for reproduction between offshore and inshore waters. Field studies included acoustic surveys in offshore areas close to Rügen Island to gain insights into the herring migration from offshore to inshore and the number of individuals (and the corresponding biomass) that migrate to coastal waters. Other ecological studies were focused on the trophodynamic interactions of different life stages of herring within inshore waters (predation on herring larvae, feeding behavior of adult herring) and are discussed in detail in other parts of this report.

Investigating offshore-inshore migrations by the means of acoustic surveys

In 2014, 2015 and 2016 several acoustic research cruises were conducted to investigate the spring spawning migration and spawning aggregation of herring close to Rügen Island.

In general, all acoustic cruises were performed with the following standards: On each transect acoustic records were performed with a Simrad EK60 and fishing stations were conducted with a modified pelagic trawl called 'Krake'. The only exception was FRV Solea cruise number 715 because another echo sounder (Simrad EK80) was used. Fishing time was variable and depended on the NASC (Nautical Area Scattering Coefficient) values and catch signals from the gear sensor. At the beginning and at the end of each transect a CTD station with a Seabird CTD was performed. Additional CTD data were recorded at least in the middle / or deepest point of each transect and / or at every fishing station. The total catch was weighed, for each species an appropriate subsample was measured (individual total lengths) while for a subsample of herring, more detailed individual fish data (age, maturity, gonad weight etc.) were collected.

In 2014 three acoustic cruises with FRV Clupea (cruise number 279, 280, 286, see appendices 1 - 3) were performed to test different survey designs. A standardized survey design was optimized and then consistently applied during several cruises in 2015 (Fig. 2). However, the first acoustic cruise in 2015 started in February with FRV Solea (Cruise No. 699, see Appendix 4). Within eleven days acoustic signals were recorded in ICES SD 22 and 24 to get a broader insight into the clupeid distribution (Fig. 1).

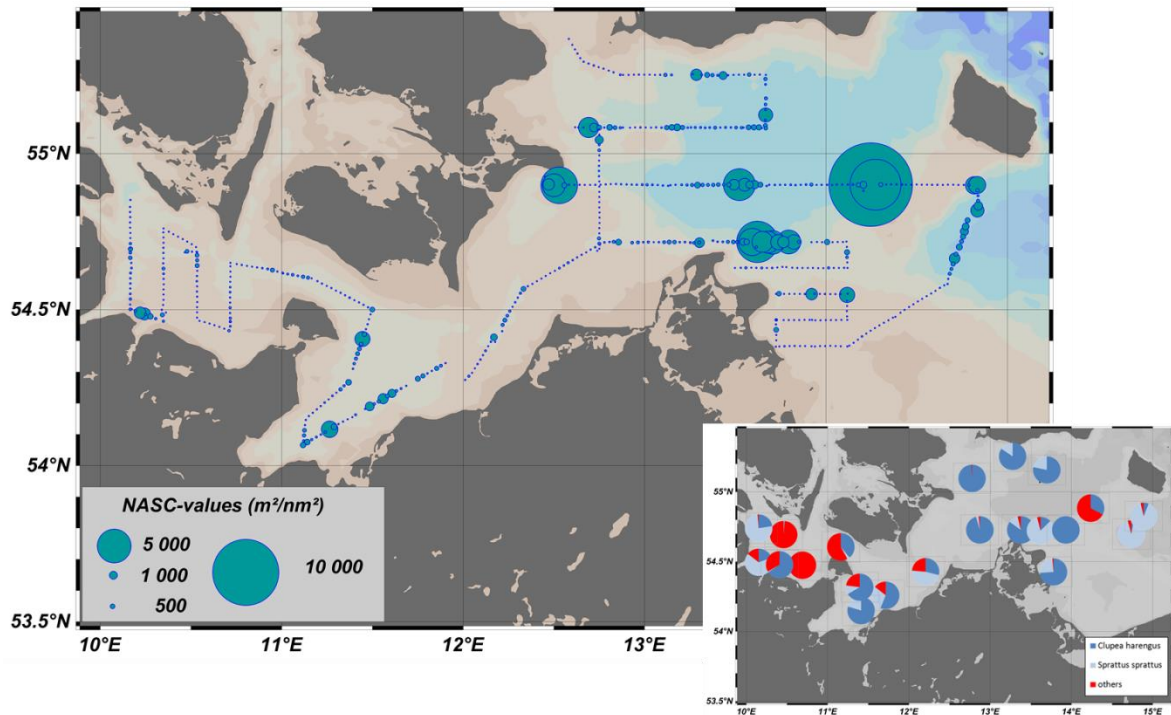


Figure 1. Cruise track and NASC values from FRV Solea cruise 699 (February 2015), right panel catch composition and haul position.

During the following weeks we focused on a smaller area to collect acoustic records in a higher spatio-temporal resolution. Therefore we performed an acoustic survey every second week from week 11 (March) to week 19 (May) with FRV Clupea (Cruise number 290, see appendix 5). To do so, we choose the area of Rügen Island where intensive spawning migration and aggregation can be observed. We established fixed hydro-acoustic transects (Fig. 2) covering the adjacent waters of Rügen Island. A total of 5 cruises with trip durations of 3 to 4 days each could be realized.

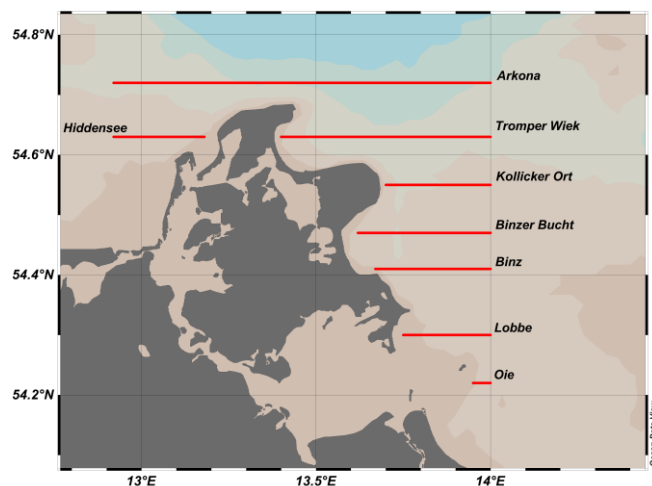


Figure 2. Fixed acoustic transects for FRV Clupea Cruise 290 and 297 in 2015.

The first cruise part started on the 10th of March and ended at the 13th of March (week 11). All eight transects were recorded and a total of six fishery hauls and 24 CTD stations were performed. The second cruise part was performed between the 26th of March and 28th of March (week 13). Again, all eight transects were sampled but due the low acoustic signals (NASC values) the cruise lasted only three days and a total of 6 fishery hauls were performed. In addition 22 CTD stations were

completed. The third cruise part took place between the 10th and 12th of April (week 15). During this cruise, the north western transect called 'Hiddensee' was excluded due to technical reasons. However, 7 fishery hauls were performed and 23 CTD station conducted. The fourth cruise part started at the end of April (24.04 – 26.04.; week 17). Again, transect 'Hiddensee' was not recorded but a total of seven hauls and 21 CTD stations were conducted at the other transects. The last cruise part was performed between the 7th and 10th of May (week 19). All transects were sampled and eight hauls and 25 CTD stations were completed (Fig 3).

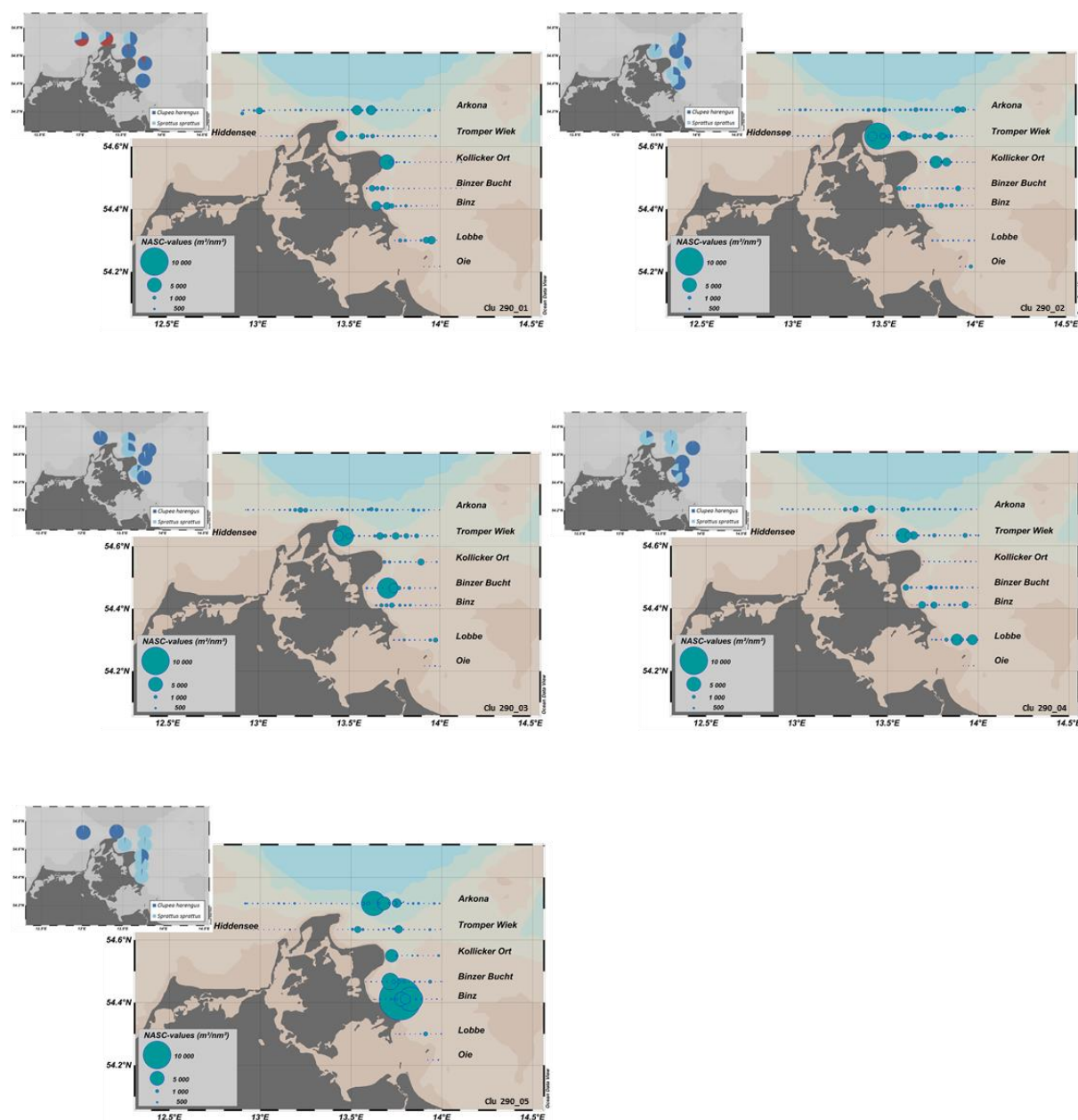


Figure 3. Recorded acoustic transects and estimated mean NASC values (1 nm intervals, dots) during the biweekly FRV Clupea Cruise 290 (10.03.2015 – 10.05.2015). First row, left: week 11; right: week 13; middle row, left: week 15; right: week 17; lower row: week 19. Upper left panel of each figure: Catch composition and haul position for each sub-cruises.

The third acoustic cruise with the focus on herring migration (Clu 297) in 2015 started in November. Due to very bad weather conditions (wind forces up to nine Beaufort) we only recorded acoustic signals on three transects ('Binz', 'Lobbe', 'Oie') and could not perform any fishing haul, but

conducted 7 CTD stations. Thus lacking the groundtruthing data of fishing hauls, the data of this cruise were not included in further analyses.

We completed the acoustic survey work within the task with FRV Solea Cruise No. 715 in February 2016 (see Appendix 6, Fig.4).

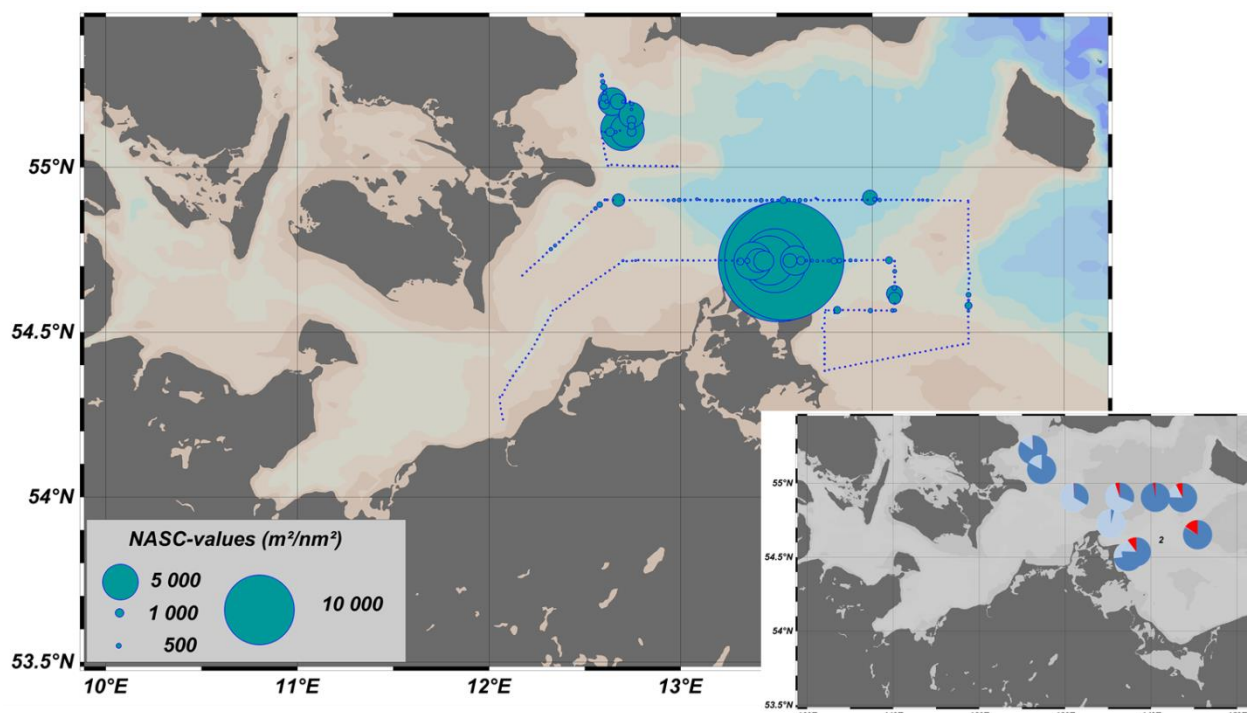


Figure 4. Cruise track and mean NASC values (1 nm intervals, dots) from FRV Solea cruise 715 (February 2016), right panel catch composition and haul position.

Results

NASC-values – catch composition

In February 2015 (SO 699; week 6), NASC values (indicating clupeid aggregations) were highest in the Arkona Sea (SD 24) with highest measurements north of Rügen Island as well as in the central Arkona Sea (Fig. 1). Notable NASC values were also measured in nearshore areas of the western Arkona Sea. In SD 22, NASC levels were highest in the Mecklenburg Bight and to a lesser degree in southeastern parts of Kiel Bight. Reference fishing hauls showed a dominant share of herring close to the Øresund and in the Northern part of the Arkona Sea, as well as close to Rügen Island and the Bay of Mecklenburg, while sprat dominated hauls were mainly recorded in the Arkona Sea and in the south west of the Bornholm Basin.

During the first cruise part in week 11 higher NASC values were recorded in the north-eastern and eastern waters of Rügen Island. The biomass of the corresponding easterly performed reference fishing hauls were dominated by herring, while the northern hauls were a mixture of herring, sprat and others (Fig. 3). During the following cruises it seems that sprat migrated into the study area and preferred the nearshore waters in the eastern bights ('Tromper Wiek' and 'Prorer Wiek') while it seems that herring preferred the eastern entrance of the Sassnitz Channel and the Sassnitz Channel itself. However, during the last cruise part the catch compositions were mainly dominated by sprat,

only the catch compositions of two hauls on the northern transect were dominated by herring indicating an emigration of herring out of the study site.

In the following February (2016; Fig. 4), high NASC values were recorded in the North of Rügen Island and relatively high NASC values were observed close to the Øresund. The reference fishing hauls showed a dominant herring share in the catches from the south eastern area of the study site between the eastern part of Rügen Island and in the south of the Adlergrund as well as close to the Øresund. The catch composition was mainly dominated by sprat in the Arkona Basin and westerly of the Darß-Zingst peninsula. The enormously high NASC values in the North of Rügen Island were caused by an unusual large sprat school.

Estimated biomass and numbers within the study area

Combining the NASC values and the information from the fishing hauls the total number and biomass of herring and sprat were estimated with small modifications, as described in the ICES WGBIFS BIAS Manual (ICES 2014). To do so, the investigated area was divided into three rectangles (Fig. 5). But in contrast to the ICES manual where only an area deeper than 10 meters were used for the estimations, we decided to use an area deeper than 5 meters, increasing the area included. The proportion (in numbers) of each fish species was calculated per rectangle (lumpsucker and all species with less than 1 percentage were excluded) and the mean length and weight per species and rectangles were determined. Afterwards the mean target strength (the measure of the reflection coefficient of a sonar target, which depends on the fish size) was estimated for each species and rectangle. The size of the rectangle, the mean NASC value of the rectangle, the mean target strength and the proportion of the species within the rectangles was used to estimate the total number of each species in every rectangle. This was then multiplied with the species' mean weight to calculate the total biomass of the species within the rectangle.



Figure 5. Rectangles to estimate the total number and biomass within the study area. Excluded were only areas with a water depth lower than 2 meters.

During week 6 in 2015 (FRV Solea Cruise number 699) an estimated total biomass of around 8 700 tons of herring and around 200 million individuals occur in the three selected rectangles (Fig 5). During the following weeks the total biomass and the total number of individuals increased. Between week 11 and week 19 the estimated total biomass of herring reached between 39 200 and 6 200 tons with the lowest biomass in week 19 (Fig. 6). Two peaks can be observed in week 11 and week 15 with

around 39 000 tons biomass of herring each. After week 15 the biomass decreases to a minimum of around 6 200 tons. The estimated total number of individuals was between 672 million and 122 million with the maximum peak in week 15. The results reveal an immigration and emigration of herring within the study area during our study period. As indicated above, the estimated total number and estimated total biomass of sprat increased in the investigated rectangles between week 11 and week 19 from 728 million to 3 239 million individuals and from 8 500 tons to 29 400 tons (Fig.6) revealing an immigration of sprat during our study period.

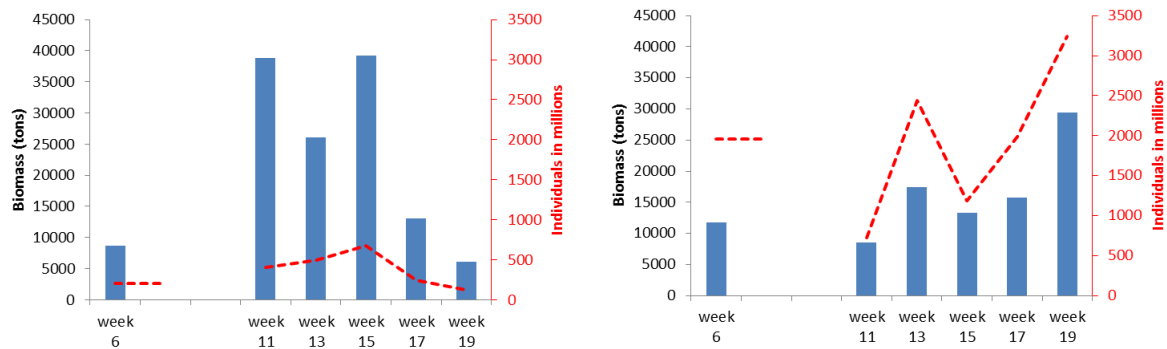


Figure 6. Estimated total biomass and total numbers over time within the three selected rectangles. Left panel: herring; right panel: sprat.

Temporal length analysis

A temporal length analysis show that in week six (2015), the mean length of herring occurring in the study area close to Rügen Island was 190 mm (\pm 62 mm) (Fig. 7). While at the beginning of the spawning season in week 11 the herring spawning aggregation close to Rügen Island is characterized by larger herring individuals and that length decreased during the following eight weeks. In week 11, the mean length of herring was 218 mm (\pm 60 mm) while in week 13 and 15 the length did not differ significantly and the mean length decreased to 204 mm (\pm 44 mm) and 201 mm (\pm 46 mm), respectively. The significant smallest mean length similar to week 6 was observed within the last two cruise parts in week 17 and 19 with 191 mm (\pm 41 mm) and 190 mm (\pm 38 mm).

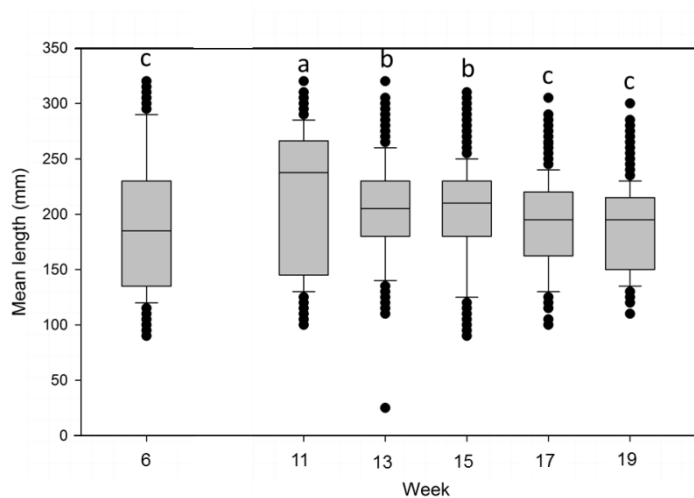


Figure 7. Box plot median, 10th, 25th, 75th and 90th percentile with outliers to visualize temporal length trend for herring in 2015. Letters indicate significant groups (Kruskal-Wallis One Way Analysis of Variance on Ranks, Dunn's Method).

Temporal condition analysis

The gonadosomatic-index (GSI) and the Fulton's condition-factor (k -factor) were estimated for herring in the area of Rügen Island (Fig.8). GSI was estimated through the formula $GSI = W_g / W_t * 100$; where W_g is the weight (in gram) of the gonads; and W_t is the total weight (in gram) of the individual. The k -factor was estimated through the formula $k = W_t / L_t^3 * 100$ where W_t is the total weight (in gram) and L_t the total length (in cm) of the individual.

In week 6 (2015) the mean GSI value was around $10.4 (\pm 7.01)$ for females and $12.1 (\pm 5.2)$ for males. In week 11 highest mean values were observed for both, females (15.7 ± 7) and males (12.5 ± 5.9). In the following weeks the mean GSI value decreased to $8.4 (\pm 5.8)$ for females and $6.5 (\pm 4.8)$ for males, respectively. The trend of the k -factor is quite similar. In week 6 the k -factor is significant lower for females (0.646 ± 0.1) and males (0.625 ± 0.09) compared to week 11 (females: 0.739 ± 0.1 and males: 0.696 ± 0.09) while in the following weeks the k -factor decreased significantly to $0.643 (\pm 0.06)$ for females and $0.635 (\pm 0.07)$ for males in week 19 with a second peak in week 17 (females: 0.662 ± 0.06 ; males: 0.644 ± 0.06).

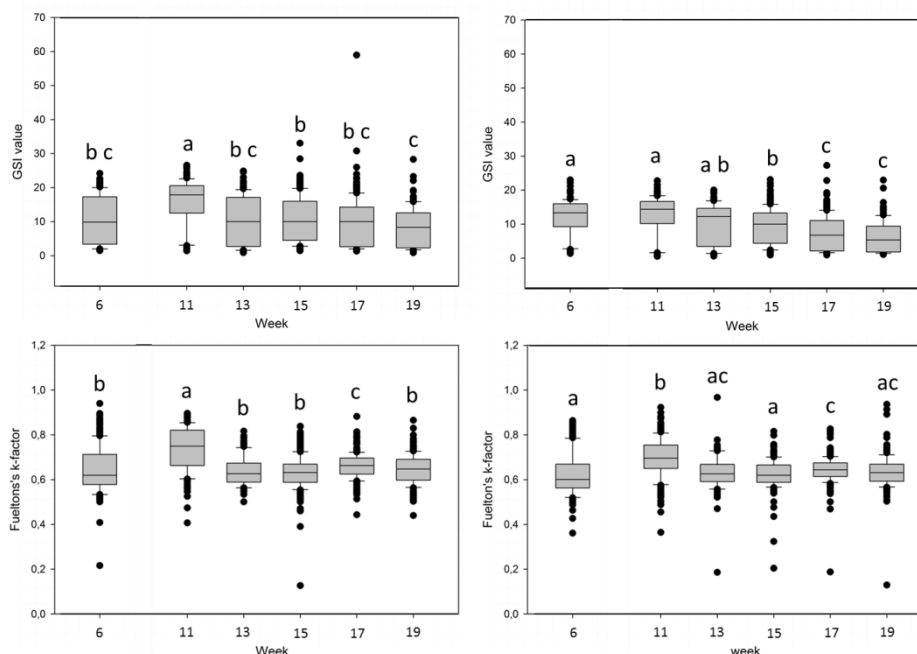


Figure 8. Box plot median, 10th, 25th, 75th and 90th percentile with outliers to show temporal trends for GSI and k -factor during 2015. Upper row, GSI values: left panel females, right panel males. Lower row k -factor: left panel females, right panel males. Letters indicate significant groups (Kruskal-Wallis One Way Analysis of Variance on Ranks, Dunn's Method).

Maturity

Maturity stages were determined in five classes (Fig. 9). At the beginning, in week 6 most of the individuals occurring close to Rügen Island were in the stage of maturation (52 %) only 1.68 % were running ripe. The maximum percentage of individuals which had already spent (14.19 %) and which were running ripe (42.09 %) were observed in the study site of Rügen Island in week 11. Between week 11 and week 15 the percentage of individuals which were running ripe decreased to 2.29 % and increased in week 17 and 19 up to 11.45 % and 17.90 %, respectively. In week 19 a higher number of individuals which already have spent occur in the study site. The results reveal at least two different spawning peaks. A summation of the maturation stage 'spent', 'spawning' and 'maturation' gives a number of 'active' spawners in the area. In week 6 the percentage of active spawners was around 54 %. Between week 11 and week 17 the percentage is around 80 and decreases in week 19 to 63 %.

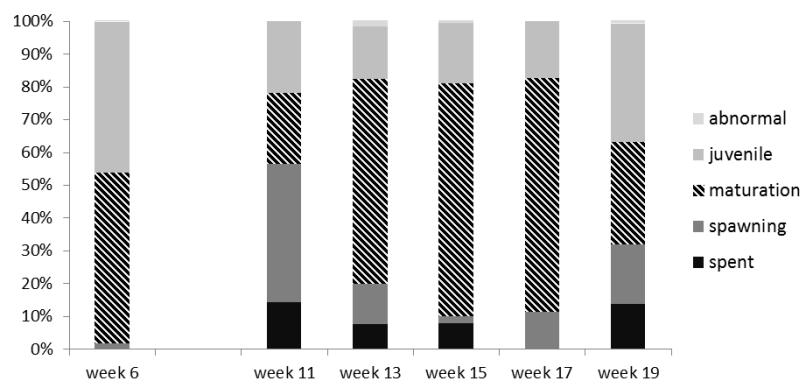


Figure 9. Percentage of different maturity stages within the study site close to Rügen Island over time.

In summary

The study was conducted to give an overall idea about the herring migration and the biomass of herring migrating to the coastal waters of Rügen Island which are considered to be of exceptional importance for the reproduction of herring in the Western Baltic Sea. Combined with the ICES coordinated acoustic survey in autumn, our survey gives new insights of the herring migration close to Rügen Island. Within the ICES survey numbers of herring were estimated for the whole Baltic on the basis of ICES rectangles. In the western Baltic (SD 21 – 24) a total of 3,707 million herring individuals were estimated (Gröhsler & Schaber 2016) in autumn 2015. Most of the herring occurred in the Øresund (approx. 1,200 million individuals). While highest fish densities in SD 24 were recorded north and east of Rügen Island and in the central parts of the Arkona Sea, resulting in about 140 million herring individuals in ICES rectangle '38G3' which is almost congruent to our study area. In contrast, our results show significant more herring individuals at the beginning of the year (week 6) and during the spawning season (week 11 – 17). However, in the last week (week 19) of our investigation numbers of herring decreased to a similar level as the autumn values. Even if the estimations and the size of the area differ slightly between both studies and the residence time of the individuals is unknown, our results reveal a clear important herring migration to the coastal waters of Rügen Island. Larger individuals arrive at first, which might be related to the speed of migration assuming larger individuals swim faster compared to their smaller conspecifics. Regarding the maturation of the migrating individuals, it was not always easy to distinguish between 'spent' individuals and 'maturation' individuals and no clear boarder between the five defined classes exists. However, with a proportion of 80 % of active spawners between week 11 and 17, the herring migration can be assumed to transfer a notable amount of energy and biomass from offshore feeding areas to the inshore spawning grounds.

References

ICES 2014. SISP Manual of international Baltic Acoustic surveys (IBAS). ICES Addendum 2: Series of ICES survey protocols, version 1.02. 24pp.

Gröhsler T & Schaber, M., 2016: Survey Report fort FRV "Solea" German Acoustic Autumn Survey (GERAS) 01 – 19 October 2015. ICES WGIPS Report 2016: 165 – 189.

Combining hydrodynamic modelling with genetics: Can passive larval drift shape the genetic structure of Baltic *Mytilus* populations?

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Running title: Drift model explores Baltic *Mytilus* hybridization

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1 **Abstract**

2 While secondary contact between *Mytilus edulis* and *M. trossulus* in North America
3 results in mosaic hybrid zone formation, both species form a hybrid swarm in the
4 Baltic. Exploring mechanisms underlying these contrasting patterns will allow an
5 understanding of processes such as speciation or adaptation to extreme
6 environments (e.g., low salinity). The previous discovery of discordant allele
7 frequency clines across the Baltic secondary contact zone suggested only weak
8 interspecific reproductive barriers resulting in a semi-permeable barrier to gene
9 flow. This investigation tests an alternative hypothesis and asks whether
10 discordant allele frequency clines result from founder events, i.e., long-distance
11 dispersal of passively drifting *Mytilus* larvae beyond a transition zone. Genetic
12 analyses of allele/haplotype frequency clines and Bayesian inference found
13 highest admixture proportions in southern Baltic populations west of Rügen Island.
14 Consequently, a virtual line between this area and the previously characterized
15 admixture zone in the Öresund describes the position of the Baltic *Mytilus*
16 transition zone. Hydrodynamic modelling and Lagrangian particle tracking showed
17 short distance dispersal routes (10 - 30 km) of Baltic *Mytilus* larvae that do not
18 reach far beyond this area. Consequently, one can reject the possibility that
19 founder events shape discordant allele frequency clines and cause pervasive
20 hybridization. The Baltic *Mytilus* transition zone is characterized by significant
21 environmental changes (e.g., West to East salinity gradient from approx. 15 to
22 below 10 PSU). Thus, we discuss whether introgressive hybridization of certain
23 alleles/allele combinations is adaptive and whether weak reproductive isolation in
24 combination with reduced post-zygotic incompatibility results in high admixture
25 proportions.

26

1 Introduction

2 Blue mussels of the *Mytilus edulis* species complex (*M. edulis*, *M. trossulus*, *M.*
 3 *galloprovincialis*) are keystone species in coastal ecosystems worldwide.
 4 Particularly their ability to hybridize in zones of secondary contact bears the
 5 potential to ask questions related to reproductive traits (e.g., Heß et al. 2012,
 6 Bartel et al. 2012) and hence to analyse speciation processes or to investigate the
 7 relationship between genotype, phenotype and adaptation to environmental
 8 conditions (e.g., Riginos and Cunningham 2005). Species of the *Mytilus edulis*
 9 species complex usually form mosaic hybrid zones, i.e., genetically pure parental
 10 species coexist with their interspecific hybrids and amalgamation of gene pools is
 11 prevented by existing but incomplete reproductive barriers or local adaptation. Well
 12 studied mosaic hybrid zones are between *M. trossulus* and *M. galloprovincialis*
 13 along the Pacific coast of northern America (e.g., Rawson and Hilbish 1996a),
 14 between *M. edulis* and *M. galloprovincialis* along the Atlantic coast of Europe (e.g.,
 15 Bierne et al. 2003a) or between *M. edulis* and *M. trossulus* along the Atlantic coast
 16 of northern America (e.g., Saavedra et al. 1996). In contrast, Baltic Sea *Mytilus*
 17 populations show no mosaic like structure but a pattern of massive interspecific
 18 gene flow. Although morphological and allozyme studies suggested a classification
 19 of populations in the western Baltic Sea (Kattegat/Skagerrak) as *M. edulis* and
 20 populations in the central Baltic Sea (Baltic Proper) as *M. trossulus* (Bulnheim and
 21 Gosling 1988; Koehn 1991), the application of DNA markers revealed a complex
 22 pattern of bidirectional but asymmetric gene flow. While introgression of *M.*
 23 *trossulus* specific alleles into the *M. edulis* populations of the Kattegat/Skagerrak
 24 region was observed at only few genetic loci, introgression of *M. edulis* alleles into
 25 the *M. trossulus* populations of the Baltic Proper is pervasive (e.g., Riginos et al.
 26 2002; Quesada et al. 2003; Kijewski et al. 2006; Stuckas et al. 2009). Given that

1 introgression is detectable at almost all tested genetic loci of the *M. trossulus*
2 populations in the Baltic Proper, Riginos and Cunningham (2005) classified these
3 populations as hybrid swarm. Irrespective of pervasive gene flow, populations in
4 the Kattegat/Skagerrak and the Baltic Proper maintain a distinct genetic,
5 morphological and physiological integrity. Mechanisms underlying and maintaining
6 this pattern are not yet understood. Riginos and Cunningham (2005) were the first
7 to state the hypothesis that reproductive barriers might have been eroded while
8 local adaptation to environmental conditions caused strong genetic differentiation.
9 In fact, the Baltic Sea is an extreme environment with a strong salinity gradient
10 from the Skagerrak (approx. 30 PSU) via the Belt Sea (approx. 15 PSU) into the
11 Baltic Proper (up to 5 PSU). Stuckas et al. (2009) found discordant allele
12 frequency clines when investigating different nuclear loci and mitochondrial DNA.
13 These authors observed a high level of asymmetric gene flow at neutral markers,
14 while sharp allele frequency clines were found at loci that are functionally related
15 to reproductive traits (M7 lysin) and cyto-nuclear incompatibility (paternally
16 transmitted mtDNA). These findings were interpreted as evidence for weak
17 reproductive barriers leading to a semi-permeable barrier to gene flow. In general,
18 discordances between allele frequency clines may result from neutral
19 introgression, genetic drift, hybrid zone movement, selection in favour or against
20 certain alleles and/or allele combinations, asymmetric introgression caused by
21 differences in pre- and postzygotic reproductive barriers, or chromosomal
22 rearrangements (Stuckas et al. 2009 and citations therein).

23 The study presented here aims at exploring founder events as one additional
24 mechanism causing discordances between allele frequency clines (Barton 1993).
25 Founder events can result from passive dispersal of larvae far beyond the limits of
26 the secondary contact zone. In fact, passive larval drift has been previously shown

1 to shape the structure of *Mytilus* secondary contact zones (*M. edulis* x *M.*
2 *galloprovincialis*, Gilg and Hilbish 2003; a, b) and hydrodynamic forces can act as
3 barriers to gene flow in Mediterranean *M. galloprovincialis* (Almera-Oran
4 oceanographic front, Quesada et al. 1995). We used hydrodynamic modelling and
5 Lagrangian particle tracking covering recent time scales (one decade from 1997 to
6 2008) to explore i) whether *Mytilus* larvae are passively dispersed over long or
7 short distances and/or ii) whether oceanographic barriers to dispersal exist. In
8 addition, we performed genetic analyses of *Mytilus* populations along the German
9 Baltic coastline for 25 populations using one mitochondrial and five nuclear
10 markers to exactly determine the position where genetic transition occurs. We
11 hypothesized that if passive larval dispersal was an important mechanism that
12 shapes hybrid swarm formation, one would expect larval drift routes to
13 substantially exceed the limits of the transition zone. Similarly, congruence
14 between larval drift routes and genetic structure would support the argument that
15 hydrodynamic conditions have a strong influence on genetic structure, e.g.,
16 complete or incomplete barriers to larval dispersal may causally maintain
17 phenotypic and genetic integrity of Baltic *Mytilus* species.

1 **Material and Methods**

2 **Hydrodynamic modelling and Lagrangian particle tracking**

3 Lagrangian particle tracking models simulate drift trajectories of virtually released
4 and passively moving particles (mussel larvae) and have been successfully used
5 to explore larval drift routes in the Baltic (e.g., Hinrichsen et al. 1997).
6 Temperature, salinity, and oxygen distributions as well as 3-D current velocity
7 fields are provided as prognostic variables by the hydrodynamic Kiel Baltic Sea
8 Ice-Ocean Model (BSIOM, Lehmann and Hinrichsen 2000; Lehmann et al. 2002).
9 The oxygen conditions in the entire Baltic Sea are described by an oxygen
10 consumption sub-model coupled to BSIOM (Lehmann et al. 2014). The horizontal
11 resolution of the coupled sea-ice ocean model is at present 2.5 km, while in the
12 vertical 60 levels are specified, which enables the upper 100 m to be resolved into
13 levels of 3 m thickness. The model domain comprises the Baltic Sea, including the
14 Kattegat and the Skagerrak. At the western boundary, a simplified North Sea is
15 connected to the Skagerrak to represent characteristic North Sea water masses.
16 The coupled sea ice-ocean model is forced by realistic atmospheric conditions
17 taken from the Swedish Meteorological and Hydrological Institute (SMHI
18 Norrköping, Sweden) meteorological database (Lars Mueller, pers. Comm.). This
19 database includes surface pressure, precipitation, cloudiness, air temperature,
20 water vapour mixing ratio and geostrophic wind. Additionally, river runoff was
21 prescribed from a monthly mean runoff data set (Kronsell and Andersson 2012).
22 The numerical model BSIOM was run for the period 1997–2008. From the
23 available time series, data were selected for the subsequent analysis of Baltic
24 *Mytilus* early life stage drift and survival patterns along the German coast line,
25 covering the reproduction period of *Mytilus* from April to July.

26

1 **Prediction of *Mytilus* larval drift routes in the Baltic**

2 Simulated three-dimensional velocity fields (Eulerian flow fields) were provided (at
 3 a 3 hours interval) by the BSIOM model in order to develop a database for a
 4 Lagrangian particle tracking exercise for Baltic *Mytilus* larvae. This data set offers
 5 the possibility to derive Lagrangian drift routes by calculating the advection of
 6 "marked" water particles. Vertical velocities were calculated from the divergence of
 7 the horizontal velocity fields. The positions of the drifters varied over time as a
 8 result of the three-dimensional velocities that they experienced. The three-
 9 dimensional trajectories of the simulated drifters were computed using a 4th order
 10 Runge-Kutta scheme (Hinrichsen et al. 1997).

11 Drift routes were predicted using a combination of the hydrodynamic modelling
 12 spanning a time period of 12 years from 1997 to 2008 and Lagrangian particle
 13 tracking as basically described above. Lagrangian particle tracking is a tool to
 14 describe the position of particles in terms of geographic coordinates and time.
 15 *Mytilus* larvae can be considered as particles given that they are passively drifted
 16 during their pelagic life cycle prior to permanent settlement at a larval size of
 17 <0.5mm. Particles were released along Baltic coasts on a regular spaced grid
 18 enclosed by the 40 m isobath representing the main occurrence area. Drifters
 19 were released every year (1997–2008) between April 21st and July 10th
 20 (encompassing the spawning period of Baltic *Mytilus* species), 19 releases at a 5
 21 days interval were performed every year, and ca. 200 000 particles were inserted
 22 into the model per release and allowed to drift for 450 degree days (temperature in
 23 °C * time in days), an interval that roughly corresponds to the larval phase of *M.*
 24 *trossulus* and *M. edulis* within their natural thermal window (Rayssac et al. 2010).
 25 Particle tracking was performed assuming a mortality depending on the number of
 26 degree days (calculated as percent mortality per degree day = 0.0011

1 (temperature in °C)² - 0.0329 (temperature in °C) + 0.3204) (average mortality for
 2 *M. edulis* and *M. trossulus* derived from Rayssac et al. 2010, Figure 1) but no
 3 further assumptions with respect to mortality were made (e.g., mortality depending
 4 on salinity or water depth at drift endpoints). Endpoints of particles were recorded
 5 to obtain their spatial distribution and corresponding transport patterns.
 6 Furthermore, the distribution of particles released at certain localities was
 7 quantitatively investigated. We first applied spatial overlap analysis according to
 8 Horn (1966) to investigate the relationship between *Mytilus* larvae initially released
 9 in different areas along the German coast during their spawning season. To
 10 determine how many larvae of different release locations were simultaneously
 11 present in the specified subarea of the investigated area, a coefficient of overlap
 12 (C) was calculated, which is 0 when there is no overlap of particles, and 1 when
 13 two distributions are identical. This was done using the following equation:

$$14 \quad C = 2 \sum_{i=1}^n (A_i \times B_i) / \left(\sum_{i=1}^n A_i^2 + \sum_{i=1}^n B_i^2 \right)$$

15 Variable “n” is the number of statistical rectangles. Spatial overlap analysis was
 16 applied to study the degree of mixing between Baltic *Mytilus* larvae initially
 17 released within different spawning areas represented by the final distributions A
 18 and B. This method was used as a descriptive tool to quantitatively assess the
 19 importance of overlap between different Baltic localities.

20 Quantitative analyses of drifter further included calculating densities of particle
 21 endpoints in space. Release point specific densities were plotted using the R
 22 package (R Development Core Team 2012).

23

24 **Sampling, tissue dissection, DNA extraction**

25 Mussels were sampled at 25 different localities between 2004 and 2013 (Figure 1;

1 Table S1). They were dissected and tissue samples were stored at -80°C. DNA
 2 was extracted from frozen tissue samples using the innuPrep DNA Mini Kit
 3 (Analytik Jena, Jena, Germany) following the manufacturer's instructions (protocol
 4 for DNA isolation from tissue samples or rodent tails) but extending tissue lysis
 5 overnight and including RNA digestion.

6

7 **Genotyping**

8 Genotyping was based on PCR amplification of DNA and a standard PCR reaction
 9 was performed in a total volume of 20µl using 20-40 ng DNA, 1 unit DFS-Taq
 10 polymerase (Bioron, Ludwigshafen, Germany) in the recommended buffer, 2.5 mM
 11 MgCl₂ (Bioron), 0.2 mM of each dNTP (Fermentas, St. Leon-Rot, Germany), and
 12 0.37 µM of each primer. Standard PCR cycling condition were as follows: 35 to 38
 13 cycles were used with denaturation at 94°C (20 - 30s but 3 - 5 minutes for the first
 14 cycle), annealing at a primer pair specific temperature (20 - 30s), and extension at
 15 72°C (45s - 1 minute but 10 minutes for the last cycle).

16 Given that *Mytilus* species show doubly uniparental inheritance (DUI, Zouros et al.
 17 1994; Skibinski et al. 1994), only maternally transmitted mitochondrial DNA
 18 (mtDNA) was investigated as this type occurs in both sexes (Zouros et al., 1994;
 19 Skibinski et al., 1994) and allows the use of unsexed samples. New PCR primers
 20 (VD1_Fb.for, RNAY.rev, Table S2) were developed to detect length variation of the
 21 mitochondrial control region taking into account that native *M. trossulus* mtDNA
 22 was replaced by *M. edulis* mtDNA in all Baltic *Mytilus* populations (Quesada et al.
 23 2003) and considering specific patterns of length variation in the control region of
 24 maternally transmitted mtDNA (Burzynski et al. 2006). These new PCR primers
 25 are expected to give amplicons of 694 bp length (representing *M. edulis* from
 26 Kattegat/Skagerrak) or larger (representing length variant as described for Baltic

1 *M. trossulus*). Mitochondrial DNA was amplified in a multiplex PCR reaction
 2 together with the nuclear marker Glu-5' (5' part of the giant exon encoding the
 3 polyphenolic adhesive foot protein; primers ME15/16; Inoue et al. 1995) and mac-
 4 1 (first intron of the actin gene; mac-1 primer according to Bierne et al. 2003b)
 5 (Table S2). Multiplex PCR followed standard conditions but employed 3.75 mM
 6 MgCl₂, 55°C annealing temperature, and adjusted amounts of PCR primers
 7 (VD1_Fb.for, RNAY.rev: 0.125 µM; ME15/16: 0.125 µM; mac-1: 0.37 µM). The use
 8 of fluorescently labelled forward primers allowed fragment length analyses of PCR
 9 products on an ABI capillary sequencer (ABI 3130xl or ABI 3730 Genetic Analyser;
 10 Applied Biosystems, Darmstadt, Germany) using the Gene Scan TM 1200 LIZ
 11 Standard and Hi-Di TM formamide (1µl DNA sample dilution, 8.6 µl formamide, 0.4
 12 µl size standard; denaturation at 95°C prior to analysis).
 13 Specimens with ambiguous Glu-5' alleles were PCR amplified with an alternative
 14 primer set (JH-5/JH-54; Rawson et al. 1996b) using standard PCR conditions with
 15 annealing at 56°C. PCR products were Sanger sequenced after enzymatic clean-
 16 up with ExoSAP-IT (USB Europe GmbH, Stauf, Germany), cycle sequencing
 17 using the PCR primers, the BigDye Terminator v3.1 Cycle Sequencing Kit (Applied
 18 Biosystems) and an ABI 3130xl Genetic Analyser (Applied Biosystems, Foster City,
 19 CA, USA). In addition, these specimens were also analysed using the Glu-3'
 20 marker (3' part of the giant exon encoding the polyphenolic adhesive foot protein
 21 and adjacent intron; primers PR-8/JH4; Rawson et al. 1996b). PCR was performed
 22 using standard PCR conditions and annealing at 52°C. The Glu-3' marker
 23 becomes species diagnostic upon restriction digest (DdeI; NEB, Frankfurt Main,
 24 Germany) of PCR products and is in combination with the Glu-5' marker indicative
 25 for interspecific recombinants in secondary contact zones (Rawson et al. 1996b).
 26 Genotyping of the nuclear locus EFbis (intron of the elongation factor 1 alpha) was

1 basically performed according to Kijewski et al. (2006) and Stuckas et al. (2009)
2 using standard PCR conditions and annealing at 54°C. PCR products were
3 digested with restriction enzymes HhaI and RsaI (NEB, Frankfurt Main, Germany).
4 Genotyping of the nuclear locus MAL-I (*Mytilus* anonymous locus 1) marker was
5 basically performed according to Rawson et al. (1996a) and standard PCR
6 conditions with annealing at 52°C. PCR products were subsequently digested
7 with the restriction enzyme SpeI (NEB, Frankfurt Main, Germany) to distinguish
8 between species specific alleles.

9 Finally, two PCR assays were designed in order to amplify species specific
10 fragments (*M. edulis*, *M. trossulus*) from exon 5 of the M7 lysin gene (acrosomal
11 protein M7 lysin, Riginos et al. 2006) using either fluorescently labelled or
12 unlabelled forward primers (Table S2). Standard PCR conditions were used with
13 annealing at 55°C (assay with unlabelled forward primer) or 65°C (assay with
14 labelled forward primer). Fragment length analyses of fluorescently labelled PCR
15 products were performed as described above.

16

1 **Bayesian Inference, admixture proportions and genetic divergence**

2 The software package STRUCTURE was used to analyse datasets based on 8
 3 different model assumptions for the prior distribution considering all combinations
 4 between different settings of i) ancestry model (admixture or no admixture), ii)
 5 allele frequency model (correlated or not correlated), and iii) allocation of
 6 specimens to sampling localities (with or without *loc prior*) (Pritchard et al. 2003;
 7 models STR1 to STR8 outlined in Table 1). Bayesian inference was performed
 8 under the hypothesis that strong population structure should be reflected
 9 independent from different model assumptions. Allele frequencies of 5 nuclear loci
 10 (numerically coded species specific alleles of loci Glu-5', MAL-1, M7 lysin, EFbis
 11 together with mac-1 allele fragment lengths) at all sampling localities were used.
 12 Each run was performed 20 times independently with a MCMC (Markov Chain
 13 Monte Carlo) chain length of 10^6 repetitions including a 25% burnin and K (putative
 14 genetic clusters) ranging from one to ten. We plotted the average posterior
 15 probabilities over K and applied the method by Evanno et al. (2005) to choose the
 16 most reasonable value for K. Algorithms implemented in STRUCTURE express
 17 admixture proportions as Q-values (ranging from 0-1) which can be interpreted as
 18 hybrid indices.

19 Admixture proportions were also calculated as rather descriptive hybrid indices for
 20 populations predefined by sampling site and their amount of *M. edulis* genotypes
 21 for four nuclear loci (EFbis, Glu-5', MAL-I, M7 lysin). These calculations resulted in
 22 hybrid indices ranging from zero (genetically pure *M. trossulus*) to 8 (genetically
 23 pure *M. edulis*), with indices between 2 to 7 indicating interspecific hybrids
 24 (considering diploidy of the organism). Divergence between *a priori* defined
 25 populations was expressed using an analysis of molecular variance (locus by
 26 locus AMOVA) and by calculating pairwise F_{ST} values. These calculations were

1 done using the software package ARLEQUIN (Excoffier et al. 2005) and based on
 2 a distance matrix derived from the number of different alleles. Significance of F_{ST}
 3 values was tested using a permutation test (10^4 permutations) and P values
 4 derived from pairwise F_{ST} value calculations were Bonferroni corrected for multiple
 5 comparisons (Rice 1989).

6

7 **Cline shape analyses**

8 Genetic changes along the coastline (Kattegat, Belt Sea, Baltic Proper) were
 9 analysed using i) average STRUCTURE Q-values at each sampling site and ii)
 10 single locus allele frequencies (EFbis, MAL-I, M7 lysin, Glu-5', D-Loop). Clines
 11 were explored as in Stuckas et al. (2009) but using the statistical software package
 12 HZAR (Derryberry et al. 2014). HZAR works with the Metropolis Hastings Markov
 13 Chain Monte Carlo algorithm and performs cline fitting in a maximum-likelihood
 14 framework. Several different models are implemented in this software that allow
 15 estimating parameters describing the curve. The two most important parameters to
 16 be estimated were the cline centre and the cline width. The cline centre (c)
 17 describes the position in space where the estimated marker frequency equals to
 18 0.5 and is given by the distance from the starting point of the transect in km
 19 (position of a locality along the transect is given in Table S1). The cline width (w) is
 20 defined as $1/\text{slope}$ at the cline centre. In addition, the frequencies at the outer
 21 ends of the transect were estimated. Distances (km) between localities were
 22 measured along the coastline with the “Ocean Basemap” for ArcGis software using
 23 GCS_MGI geographic coordinate system (Figure 1B, Table S1).

24 Calculations were performed with the HZAR package for R (Derryberry et al. 2014)
 25 using the example script “Data S2” with few modifications. All 15 models
 26 implemented were tested, our measuring inaccuracy was 4 km (for the

1 approximately 1168 km long transect), we used own randomized numbers for the
 2 initial value of each fit, and MCMC chains were run with 10^6 iterations. Within the
 3 *hzar.multiFitRequest* command, options were: *BaseSeed* option with ten random
 4 picked numbers between 100 and 9000, *RotateSeed* was set to “true”,
 5 *BaseChannel* and *adjChannel* were both set to 50, and *skip* was set to zero. The
 6 model performance was compared using both Akaike information criterion (AIC)
 7 and the AIC score corrected for small sample size (AICc) to check for differences
 8 in the resulting best fitting model. Since no differences in the fitting models were
 9 observed, no further modifications to the calculation approach by Derryberry et al.
 10 (2014; example script “Data S2”) were done. Parameters were estimated and
 11 confidence intervals of each parameter were expressed as 2 log likelihood
 12 intervals. This enables comparing parameters of different cline shape estimates
 13 and parameters were considered statistically significant to each other if the
 14 confidence intervals did not overlap (conservative estimate).

15

16 **Results**

17 **Hydrodynamic modelling and Lagrangian particle tracking**

18 An overall analysis of the advection distance of all drifters observed in this model
 19 indicates that the majority of drifters remained in relative proximity of the release
 20 point. In particular, more than 50% moved within a surrounding of 10 to 30 km and
 21 only a vast minority of drifters reached distances between 30 and 100 km (Figure
 22 2A).

23 In order to qualitatively explore drift patterns in more detail, the transport of
 24 particles released at 70 selected localities scattered all over the coastlines along
 25 the Skagerrak, Kattegat, Belt Sea and Baltic Proper were qualitatively analysed
 26 (Table S3). This was done by depicting endpoints of released particles at each

1 locality resulting in pictograms best described as drifter endpoint distributions
 2 (example shown in Figure 2B). These pictograms illustrate that travel distances
 3 are short and follow a stepping stone like manner along coastlines. In addition,
 4 overlap between drifter endpoint distributions of all 70 selected localities were
 5 quantified according to Horn (1966). Overlap coefficients between directly adjacent
 6 localities (69 comparisons) can reach values between 0.10 and 0.96 (26 cases)
 7 but were mostly low between 0 and 0.10 (9 cases) or even 0 (34 cases). The high
 8 number of low overlap coefficients reflects short distance dispersal instead of
 9 providing evidence for absolute drift barriers caused by hydrodynamic forces.
 10 Drifters did not reach offshore areas in the Skagerrak, Kattegat and the Baltic
 11 Proper.

12 However, as drifter endpoint distributions of localities in the Belt Sea area
 13 (mainland and Belt Sea Islands) were overlapping, the Belt Sea islands probably
 14 facilitate step-wise distribution of *Mytilus* species between the opposing coastlines.
 15 Model data from selected localities at the southern Baltic coast, the Belt Sea area,
 16 and the Öresund region were additionally analysed using an alternative
 17 quantitative approach. This quantitative analysis divided the total area of the drifter
 18 endpoint cloud into areas where densities per unit ($1^\circ \times 1^\circ$) were i) at least 1000
 19 drifters, ii) at least 500 drifters, or iii) at least 10 drifters. This allowed analysing to
 20 what extent particles released from two adjacent localities can admix and gave an
 21 impression whether larval admixture between two localities is quantitatively high or
 22 low.

23 When analysing the southern Baltic coastline, localities showed different
 24 quantitative levels of overlap (Figure 3). For instance, drifter endpoint clouds of
 25 localities Warnemünde, Ahrenshoop, and Barhöft overlapped in areas where
 26 densities were generally high (at least 500 drifter endpoints per unit; Figure 3B, C,

1 D). This is also reflected by overlap coefficients ranging between 0.24 and 0.66
 2 (Table 2). In contrast, while drifter endpoint clouds of localities Barhöft and Rügen
 3 Island were still overlapping in areas with low densities (at least 10 drifters per
 4 unit), no overlap was observed in the model at higher densities (500 or 1000
 5 drifters per unit) (Figure 3D, E). This observation is supported by a low overlap
 6 coefficient between Barhöft and Rügen (0.09; Table 2). Quantification of drifter
 7 endpoint clouds at selected localities in the Belt Sea area suggested that
 8 distribution of *Mytilus* larvae via Belt Sea islands may also be quantitatively
 9 restricted. For instance, comparing locality Mön (Belt Sea island Falster) with
 10 German coastline localities Warnemünde and Ahrenshoop, respectively, drifter
 11 endpoint clouds showed substantial overlap at low densities (10 drifter per unit) but
 12 no overlap at high densities (500 or 1000 drifters per unit) (Figure 3A, B, C).
 13 Accordingly, overlap coefficients between these localities range between 0.02 and
 14 0.07 (Table 2). A similar picture was seen for other regions within the Belt Sea
 15 area, e.g., the region around the Danish island Sealand, the Swedish coastline
 16 and the Öresund (Figure S1, Table S4). Overall, although Lagrangian particle
 17 tracking did not provide evidence for absolute barriers of passive larval drift along
 18 coastlines, the hydrodynamic conditions caused locality specific density
 19 distributions. Hence, regions exist where larval exchange between adjacent
 20 localities is particularly low as seen for i) the region around Rügen Island, ii) the
 21 Öresund, and iii) the Belt Sea area.

22

23 **Genotyping**

24 A total of 449 specimens from 25 localities (Table S1) were genotyped at a single
 25 locus of the maternally transmitted mtDNA (D-loop) and five single copy nuclear
 26 loci (Glu-5', EFbis, MAL-I, M7 lysin, mac-1) (Table S5). The application of four

1 nuclear markers (Glu-5', EFbis, MAL-I, M7 lysin) allowed allocating alleles to their
 2 phylogenetic origin and unambiguously identifying mixed individuals.
 3 Unexpectedly, the Glu-5' marker indicated the presence of *M. galloprovincialis*
 4 alleles in three specimens found at the locality Kiel Fjord (Hörn) (Table S5).
 5 Genotyping of these animals was therefore repeated by using an alternative
 6 primer pair targeting the Glu-5' marker (JH5/JH54) and by additionally applying the
 7 Glu-3' marker to test for recombination between species specific alleles in
 8 secondary contact zones. These additional analyses confirmed the existence of
 9 non-recombinant *M. galloprovincialis* alleles.

10

11 **Population structure**

12 Bayesian inference was performed to allocate specimens from Baltic populations
 13 to genetic clusters using genetically pure references from allopatric populations of
 14 *M. edulis* (Helgoland) and *M. trossulus* (Penn Cove). Furthermore, we estimated
 15 the hybrid character of each specimen in terms of Q values, i.e., proportion of the
 16 genome belonging to each genetic cluster. Bayesian inference was performed
 17 based on eight different model settings (STRUCTURE model assumption: STR1 to
 18 STR8) (Figure 4). Results of Bayesian inference with all eight model assumptions
 19 consistently showed that populations Tjärnö to Grömitz had the highest number of
 20 *M. edulis*-like specimens and the same result was obtained for Kiel Fjord
 21 populations (localities GEOMAR, Ship museum, Hörn, East shore). Populations
 22 from Usedom, Hel, and Askö were allocated as *M. trossulus*-like while populations
 23 Steinbeck, Gollwitz, Warnemünde, Ahrenshoop, Barhöft, and Dranske showed the
 24 highest proportion of interspecific admixture. By repeating Bayesian analyses
 25 using an alternative dataset excluding Kiel Fjord populations, we tested whether
 26 over-proportional sampling at this locality may have an effect on the inference

1 results. However, no substantial differences between both datasets were observed
2 (Figure 4 A, B).

3 Two *post-hoc* analyses to Bayesian inference were performed. First, genotypic
4 data obtained from all five nuclear markers were used to estimate genetic
5 divergence between localities based on a locus by locus AMOVA. The AMOVA
6 suggested considerable divergence between localities ($F_{ST} = 0.28$, $p < 0.0001$) and
7 each marker contributed differently to the divergence (mac-1: $F_{ST} = 0.11$,
8 $p < 0.0001$; Glu-5': $F_{ST} = 0.34$, $p < 0.0001$; EFbis: $F_{ST} = 0.28$, $p < 0.0001$; MAL-I: $F_{ST} =$
9 0.57 , $p < 0.0001$; M7 lysin: $F_{ST} = 0.38$, $p < 0.0001$). Pairwise F_{ST} -values (Table S6)
10 revealed remarkably high divergence between the reference populations
11 Helgoland (*M. edulis*) and Penn Cove (*M. trossulus*) ($F_{ST} = 0.83$, $p < 0.0001$) and
12 these two reference populations were also remarkably divergent to populations of
13 the Baltic Area (Tjärnö to Askö, Table S6). In contrast, pairwise F_{ST} -values of *M.*
14 *edulis*-like populations (Tjärnö to Grömitz) were between zero and 0.17 (in
15 exceptional cases) and pairwise F_{ST} -values of *M. trossulus*-like populations
16 (Usedom, Hel, Askö) ranged between zero and 0.02. However, pairwise F_{ST} -
17 values between these two groups ranged from 0.26 to 0.48.

18 Second, specimens were classified according to their hybrid index based on
19 counting the number of *M. edulis* specific alleles at loci Glu-5', EFbis, MAL-I, M7
20 lysin (0 = *M. trossulus*; 8 = *M. edulis*). The frequency distribution of hybrid indices
21 at each locality showed the presence of hybrid specimens in all Baltic populations
22 (Figure S2). In particular, genetically pure *M. edulis* specimens were only present
23 at low frequency at Aarhus, Flensburg, Gelting and Kiel Fjord (Hörn); genetically
24 pure *M. trossulus* specimens were absent from the Baltic. The hybrid character
25 changed in the area around Ahrenshoop, i.e., the frequency of *M. trossulus*
26 specific alleles was substantially higher in populations Barhöft, Dranske, Usedom,

1 Hel compared to all other Baltic populations analysed in this study including those
 2 from Kiel Fjord (Figure S2).

3

4 **Cline shape analyses**

5 Cline shape analyses were performed using genetic data from populations along a
 6 transect from localities Flensburg to Hel (Figure 1B, Table S1). These localities
 7 were chosen as a direct consequence of hydrodynamic modelling. This model
 8 explained larval dispersal by a stepping stone model over short distances (mainly
 9 between adjacent localities) without any absolute barrier. Consequently, clines
 10 could be fitted based on the absolute distance between localities measured along
 11 the coastlines. All other localities were excluded from cline shape analyses
 12 because of several reasons: non-Baltic reference populations Helgoland and Penn
 13 Cove as well as populations Aarhus, Tjärnö and Askö cannot be fitted in a transect
 14 representing a continuous stepping-stone like dispersal route with clearly
 15 predictable distances between localities. Furthermore, Kiel Fjord localities
 16 (GEOMAR, Ship museum, Hörn, East shore) were excluded as these localities are
 17 not covered by the hydrodynamic model and hence dispersal routes could not be
 18 predicted.

19 Cline shape analyses based on Q values from Bayesian inference (dataset
 20 excluding Kiel Fjord populations, Figure 4 A) predicted the cline centre between
 21 transect position 523 km and 546 km (corresponding roughly to an area between
 22 Ahrenshoop and Barhöft, Figure 1, Tables 1, S1). The cline width was estimated to
 23 span an area of 203 km to 418 km around the cline centre (corresponding roughly
 24 to an area between Steinbeck and Rügen Island, Figure 1, Tables 1, S1).
 25 Confidence intervals of these parameters were compared in a pairwise manner
 26 and considered to be significantly different from each other in cases where 2 log

1 likelihood confidence intervals did not overlap (Tables 1, S7). While cline centre
 2 estimates based on different STRUCTURE model assumptions were not
 3 significantly different, cline width estimates differed significantly between clines
 4 estimated based on model assumptions STR3 and STR8 as well as STR5 and
 5 STR8 (Tables 1, S7).

6 Cline shape analyses based on locus specific *M. edulis* allele frequencies (Table
 7 S5) predicted cline centres between transect positions 280 km (EFbis) and 623 km
 8 (MAL-I) (Table 1) which corresponds to an area between Grömitz and east of
 9 Rügen Island (Figure 1, Table S1). The position of locus specific cline centres
 10 between loci MAL-I and M7 lysin, MAL-I and EFbis, and Glu-5' and EFbis differed
 11 significantly given that 2 log likelihood confidence intervals did not overlap (Table
 12 1, Table S7). Locus specific cline widths ranged between 24 km (for maternally
 13 transmitted mtDNA) and 785 km around the cline centre but were not significantly
 14 different in pairwise comparisons.

15

16

17 **Discussion**

18 **Can current larval drift patterns maintain the structure of the Baltic *Mytilus*** 19 **transition zone?**

20

21 The overall goal of this study was to explore whether founder events
 22 shape/maintain the population structure of Baltic *Mytilus* species, i.e., whether or
 23 not long distance larval dispersal beyond the limits of the Baltic *Mytilus* transition
 24 zone explains discordances between allele frequency clines, pervasive gene flow,
 25 and hybrid swarm formation. In addition, it was tested whether complete or
 26 incomplete barriers to larval dispersal may causally maintain the phenotypic and

1 genotypic integrity of Baltic *Mytilus* species. Exploring these questions requires i)
2 predictions about larval drift routes and ii) identifying areas of major genetic shifts
3 between Baltic *Mytilus* species (*M. edulis* x *M. trossulus*).

4 In order to test these hypotheses, drift routes of Baltic *Mytilus* larvae were
5 predicted using hydrodynamic modelling combined with Lagrangian particle
6 tracking covering a recent time scale over one decade from 1997 to 2008.

7 Dispersal of *Mytilus* larvae can be described as follows: Larvae drift over short
8 distances along coastlines. The model shows that larvae cannot reach opposing
9 coastlines, i.e., larvae do not drift between West and East coast of the
10 Skagerrak/Kattegat or South and North coast of the Baltic Proper. However, the
11 drift model suggests that larvae can be step-wise exchanged over short distances
12 via Belt Sea Islands and hence, an indirect connection between these opposing
13 coastlines exist.

14 Although hydrodynamic modelling does not indicate the existence of absolute
15 barriers to gene flow, there is evidence for areas where the exchange of larvae
16 between adjacent localities is particularly low and acts as “quantitative barrier”.
17 The model data support the existence of at least three “quantitative barriers” which
18 are i) the region around Rügen Island, ii) the Öresund, and iii) the Belt Sea area.

19 A second precondition for testing the hypotheses above is the knowledge about
20 genetic structure, i.e. the position of the transition zone. Identifying the position
21 and structure of a southern Baltic *Mytilus* transition zone is generally challenging
22 because gene flow between populations is known to be pervasive (e.g., Kijewski et
23 al. 2006) and results in hybrid swarm formation (Riginos and Cunningham 2005).
24 This problem was solved by analysing multilocus nuclear genetic data using
25 Bayesian inference and using allopatric reference populations representing
26 genetically pure species. The method implemented in the software package

1 STRUCTURE was able to estimate admixture proportions. Consequently, the
 2 transition zone is defined as the area along the transect where the highest
 3 numbers of admixed specimens are found. This area was identified by analysing
 4 clinal variation of the population specific admixture proportion (average
 5 STRUCTURE Q-values) and the cline centre representing the transition zone was
 6 identified in an area west of Rügen Island comprising localities Steinbeck to
 7 Dranske (Figures 1, 4, 5). Consequently, populations from Tjärno to Grömitz were
 8 allocated as *M. edulis*-like and populations Usedom to Askö were classified as *M.*
 9 *trossulus*-like.

10 Conclusions about the impact of passive larval drift on the genetic structure of
 11 Baltic *Mytilus* populations were now possible by combining the i) predictions drawn
 12 from the hydrodynamic model and Lagrangian particle tracking with ii) results from
 13 genetic analyses, i.e., the position of the transition zone. First, there is no support
 14 to explain discordant clines as a result of current founder effects (Barton 1993),
 15 i.e., current long distance dispersal of larvae far beyond the limits of the transition
 16 zone. This is because the hydrodynamic model shows short distance dispersal (10
 17 to 30 km for the majority of drifters; Figure 2A). In addition, locality specific drifter
 18 endpoint clouds (e.g., Figures 2B, 3) did support short distance dispersal also in
 19 the area of major genetic transition which is found along a virtual line between the
 20 Öresund (Väinölä and Hvilson 1991), the Belt Sea Islands (Wennerström et al.
 21 2013) and the area west of Rügen Island (this study). Interestingly, although larval
 22 exchange between localities within zones of major genetic transition (Öresund -
 23 Belt Sea Islands - west of Rügen Island) was generally observed, larval exchange
 24 between adjacent localities can become quantitatively restricted. For instance,
 25 while larval exchange between southern coastline localities Warnemünde,
 26 Ahrenshoop, and Barhöft is substantial, exchange of drifters is much smaller

1 between Barhöft and Rügen (Table 2, Figure 3). Similarly, larval exchange can be
 2 substantially restricted in some areas of the Öresund (Table S4, Figure S1).
 3 Consequently, larval drift patterns at recent time scales may even partly contribute
 4 to the maintenance of phenotypic and genotypic integrities between Baltic *Mytilus*
 5 populations than promoting admixture and hybrid swarm formation. In contrast,
 6 Gilg and Hilbish (2003 a, b) showed that larval drift patterns causally shape the
 7 structure of the *M. edulis* x *M. galloprovincialis* secondary contact zone in south-
 8 western England. These authors found that the hybrid zone lies in between
 9 barriers to dispersal preventing pure species to enter the region of the contact
 10 zone. However, ocean currents allow long distance dispersal of hybrid mussel
 11 larvae out of the hybrid zone and into the distribution range of genetically pure *M.*
 12 *galloprovincialis* in North Cornwall.

13

14 **What processes shape Baltic *Mytilus* population structure?**

15 When analysing mechanisms explaining the extraordinary structure of Baltic
 16 *Mytilus* populations one has to deal with i) processes maintaining phenotypic and
 17 genotypic integrity and ii) processes allowing pervasive introgression. Although
 18 this study was designed to analyse the action of passive larval drift, the
 19 experimental and analytical results allow discussing more processes shaping the
 20 genetic constitution of Baltic *Mytilus* populations.

21 The analysis of allele frequency changes (single locus analysis) and admixture
 22 proportions (multilocus analysis using Bayesian inference) in the conceptual
 23 framework of cline shape analyses corroborated earlier findings by Stuckas et al.
 24 (2009). First, shapes of allele frequency clines show pronounced discordances
 25 particularly with respect to the position of their cline centres (MAL-I and M7 lysin,
 26 MAL-I and EFbis as well as Glu-5' and EFbis; Figure 5; Tables 1, S7). Mechanisms

1 causing discordant clines have been basically discussed by Stuckas et al. (2009)
 2 but some findings of this investigations demand particular attention. In contrast to
 3 the study by Stuckas et al. (2009), this study was successful in detecting
 4 divergences between populations at the D-loop of maternally transmitted mtDNA
 5 and showed clinal variation with a cline centre in the approximate region of
 6 Warnemünde (Figures 1, 5). Given that Stuckas et al (2009) predicted the cline
 7 centre of paternally transmitted DNA at approx. the same position, DUI of
 8 mitochondrial DNA may cause a pronounced pattern of nuclear-mitochondrial
 9 incompatibility resulting in postzygotic incompatibility as described by Saavedra et
 10 al. (1996). The observation that haplotype clines of both mtDNA types share the
 11 cline centre with M7 lysin supports previous conclusions that weak semi-
 12 permeable barriers to gene flow exist.

13 Bayesian inference of population structure using multilocus nuclear data
 14 suggested a transition zone between Baltic *Mytilus* species in an area west of
 15 Rügen Island. This zone marks a region where admixed genotypes are most
 16 frequent and cline shape analysis of admixture proportions showed strong clinal
 17 variation. Thus, genetic composition of genomes changes within relatively short
 18 spatial scales. The position of this transition zone is in an area where
 19 environmental conditions also change significantly. In fact, the transition zone west
 20 of Rügen Island is approximately at the position of the Darss Sill, an area where
 21 the salinity level drops below 10 PSU. The Darss Sill is a topographical barrier for
 22 dense and salty water in-flowing into the Baltic Proper. Consequently, the position
 23 of the transition zone west of Rügen Island can be better explained by the position
 24 of the Darss Sill (and environmental changes related to it) than by the position of a
 25 quantitatively restricted larval exchange around Rügen Island (compare Figure 3
 26 and arguments above). This statement underlines the potential role of salinity

1 driven selection to osmotic (salinity) stress. Low salinity has been shown to impact
2 mussel growth performance in the Baltic, with approx. 60% reductions in somatic
3 and shell growth observed between sites with salinities of 12 vs. 6 PSU (Kossak
4 2006). Transplantation experiments revealed that growth performance of
5 autochthonous populations from sites with salinities <10 is significantly higher (by
6 a factor of 2.6 - 26) than that of allochthonous populations transplanted to such
7 sites (Kossak 2006). Low salinity and the coupled low availability of inorganic
8 carbon for shell formation thus severely impact energy budgets of mussels and
9 constitute a strong selective force (Thomsen et al. 2015).

10 Processes discussed above (larval drift over only short distances, weak semi-
11 permeable barriers to gene flow, local adaptation) provide explanations to
12 understand the maintenance of morphological and genotypic integrities. There is,
13 however, also evidence for mechanisms allowing pervasive introgression.

14 Analyses of cline shapes based on allele frequencies of single genetic loci as well
15 as based on admixture proportion derived from multilocus Bayesian inference
16 suggest that cline widths are generally large. In fact, cline widths ranged between
17 393 km and 785 km among nuclear genetic loci (Table 1). This observation can be
18 interpreted as support for the existence of only weak barriers to gene flow allowing
19 many loci to cross the transition zone and to spread among populations in face of
20 weak postzygotic genetic incompatibility. This hypothesis supports the idea that
21 pairwise admixture is substantially driven by neutral mechanisms. Alternatively,
22 assuming that introgressive hybridization of certain alleles or allele combinations is
23 adaptive and increase fitness, hybridization can result in adaptive radiation
24 particularly when species invade new environments (Seehausen 2004a). If
25 populations of hybrids (hybrid swarm) invade new environments, recombinant
26 hybrid genotypes i) might guarantee superior adaptation to environmental

1 condition but ii) might also reduce fitness due to genome incompatibilities.
2 However, given that genome incompatibilities result from a complex interplay of
3 different non linked genetic loci, segregation of these loci will result in a broad
4 variation of recombinant genotypes (Schilthuizen et al. 2004; Seehausen 2004b).
5 Consequently, these authors suggest that the selection regime in hybrid swarms
6 will purge incompatible alleles and genetic loci linked to them; a process that might
7 lead to a complex shift of allele frequencies in the hybrid swarm compared to the
8 parental species. This concept by Seehausen (2004a, b) and Schilthuizen (2004)
9 provides not only a potential explanation for the existence of the hybrid swarm in
10 the Baltic but also for the observation of long introgression tails. Furthermore, it is
11 also compatible with earlier explanations that discordant cline shapes indicate the
12 movement of an ancient *Mytilus* hybrid zone that existed already before the
13 Littorina Sea evolved approx. 8000 years ago (Donner 1995). Under this
14 hypothesis, hybrid genotypes were the precondition to colonize the brackish Baltic
15 environment.

16

17 **Conclusions**

18 The study demonstrates that founder events do not explain the existence of
19 discordant allele frequency clines, pervasive gene flow, and hybrid swarm
20 formation. This is because hydrodynamic modelling and Lagrangian particle
21 tracking showed short distance dispersal patterns of *Mytilus* larvae rather than
22 long distance dispersal beyond the limits of the transition zone positioned west of
23 Rügen Island. Instead, genetic patterns are more consistent with functional
24 explanations, e.g., weak interspecific reproductive barriers in face of minor
25 genomic incompatibilities and/or adaptation to environmental conditions. Future
26 research is needed not only to experimentally prove these explanations but also to

1 link them to putative functional consequences of pervasive gene flow. In fact,
 2 although genetic identities of many populations outside the transition zone allow
 3 allocation to classical taxonomic categories, all Baltic populations are affected by
 4 introgression (hybrid indices larger than 0, Figure S2). In particular, populations
 5 from Tjärnö to Grömitz (including Kiel Fjord localities) were classified as *M. edulis*-
 6 like (Figure 4), but admixture of these populations results in substantial genetic
 7 divergence to North Sea *M. edulis* (pairwise F_{ST} ranging between 0.20 and 0.47,
 8 Table S6). Admixture may even include alleles from the Atlantic/Mediterranean *M.*
 9 *galloprovincialis*, as seen at Kiel Fjord localities. Baltic *M. edulis*-like populations
 10 are similarly diverse to North Sea mussels as to populations allocated as *M.*
 11 *trossulus*-like (Usedom, Hel, Askö; pairwise F_{ST} ranging between 0.26 and 0.48,
 12 table S6). Interestingly, Kossak (2006) demonstrated that *M. edulis*-like
 13 populations outside of the transition zone grow well over a wide range of different
 14 salinities while populations from the North Sea (e.g., Helgoland) and the Baltic
 15 Proper (e.g., Askö) show generally low growth rate outside their provenance
 16 habitats. Thus, our study supports that introgressive hybridization may be adaptive
 17 and all Baltic *Mytilus* species may represent locally evolving taxa which extends
 18 the view by Väinölä and Strelkov (2011) for Baltic *M. trossulus*. Anyway, the high
 19 admixture proportion found in Baltic mussels already demonstrates different
 20 evolutionary histories and, therefore, any comparisons between Baltic and non-
 21 Baltic *Mytilus edulis* and *M. trossulus* should be performed with caution.

22

1 **Acknowledgements**

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11

1 **References**

- 2 Bartel M, Hartmann S, Lehmann K, Postel K, Quesada H, Philipp E, Heilmann K,
3 Micheel B, Stuckas H (2012) Identification of proteins in *Mytilus edulis*
4 sperm: implications for analyses of reproductive traits. *Marine Biology*, **159**,
5 2195-2207.
- 6 Barton NH (1993) Why species and subspecies? *Current Biology*, **3**, 797-799.
- 7 Bierne N, Borsa P, Daguin C, Jollivet D, Viard F, Bonhomme F, David P (2003a)
8 Introgression patterns in a mosaic hybrid zone between *Mytilus edulis* and
9 *Mytilus galloprovincialis*. *Molecular Ecology*, **12**, 447-462.
- 10 Bierne N, Daguin C, Bonhomme F, David P, Borsa P (2003b) Direct selection on
11 allozymes is not required to explain heterogeneity among marker loci
12 across a *Mytilus* hybrid zone. *Molecular Ecology*, **12**, 2505-2510.
- 13 Bulnheim H-P, Gosling E (1988) Population genetic structure of mussels from the
14 Baltic Sea. *Helgoländer Meeresuntersuchungen*, **42**, 113-129.
- 15 Burzynski A, Zabwicka M, Skibinski DOF, Wenne R (2006) Doubly Uniparental
16 Inheritance Is Associated With High Polymorphism for Rearranged and
17 Recombinant Control Region Haplotypes in Baltic *Mytilus trossulus*.
18 *Genetics*, **174**, 1081–1094.
- 19 Derryberry EP, Derryberry GE, Maley JM, Brumfield RT (2014) HZAR: hybrid zone
20 analysis using an R software package. *Molecular Ecology Resources*, **14**, 652-
21 663.
- 22 Donner J (1995) The Quaternary History of Scandinavia, Cambridge University
23 Press: Cambridge.

- 1 Excoffier L, Laval G, Schneider S (2005) Arlequin ver 3.0: An integrated software
2 package for population genetics data analysis. *Evolutionary Bioinformatics*
3 *Online*, **1**, 47-50
- 4 Evanno G, Regnaut S, Goudet J (2005) Detecting the number of clusters of
5 individuals using the software STRUCTURE: a simulation study. *Molecular*
6 *Ecology*, **14**, 2611-2620.
- 7 Gilg MR, Hilbish TJ (2003a) The geography of marine larval dispersal: coupling
8 genetics with fine-scale physical oceanography. *Ecology*, **84**, 2989-2998.
- 9 Gilg MR, Hilbish TJ (2003b) Patterns of larval dispersal and their effect on the
10 maintenance of a blue mussel hybrid zone in South-eastern England.
11 *Evolution*, **57**, 1061-1077.
- 12 Heß A-K, Bartel M, Roth K, Messerschmidt K, Heilmann K, Kenchington E,
13 Micheel B, Stuckas H (2012) Expression M6 and M7 lysin in *Mytilus edulis*
14 is not restricted to sperm but occurs also in oocytes and somatic tissue of
15 males and females. *Molecular Reproduction and Development*, **79**, 517-
16 524.
- 17 Hinrichsen HH, Lehmann A, John M ST, Brügge B (1997) Modelling the cod larvae
18 drift in the Bornholm Basin in summer 1994. *Continental Shelf Research*,
19 **17**, 1765-1784.
- 20 Horn HS (1966) Measurement of 'overlap' in comparative ecological studies.
21 *American Naturalist*, **100**, 419-424.
- 22 Inoue K, Waite JH, Matsuoka M, Odo S, Harayama S (1995) Interspecific
23 Variations in Adhesive Protein Sequences of *Mytilus edulis*, *M.*
24 *galloprovincialis* and *M. trossulus*. *Biological Bulletin*, **189**, 370- 375.

- 1 Kijewski T, Zbawicka M, Väinölä R, Wenne R (2006) Introgression and
2 mitochondrial heteroplasmy in the Baltic populations of mussels *Mytilus*
3 *trossulus* and *M. edulis*. *Marine Biology*, **149**, 1371-1385.
- 4 Koehn KR (1991) The genetics and taxonomy of species in the genus *Mytilus*.
5 *Aquaculture*, **94**, 125-145.
- 6 Kossak U (2006) How climate change translates into ecological change: Impacts
7 of warming and desalination on prey properties and predator-prey
8 interactions in the Baltic Sea. *Ph.D. dissertation, IFM-GEOMAR, Christian-*
9 *Albrechts-Universität, Kiel*.
- 10 Kronsell J, Andersson P (2012) Total regional runoff to the Baltic Sea. HELCOM
11 Indicator Fact Sheets 2011. Online. (<http://www.helcom.fi/environment2/ifs>).
- 12 Lehmann A, Hinrichsen HH (2000) On the thermohaline variability of the Baltic
13 Sea. *Journal of Marine Systems*, **25**, 333-357.
- 14 Lehmann A, Krauss W, Hinrichsen HH (2002) Effects of remote and local
15 atmospheric forcing on circulation and upwelling in the Baltic Sea. *Tellus*
16 *Series A-Dynamic Meteorology and Oceanography*, **54**, 299-316.
- 17 Lehmann A, Hinrichsen HH, Getzlaff K, Myrberg K (2014) Quantifying the
18 heterogeneity of hypoxic and anoxic areas in the Baltic Sea by a simplified
19 coupled hydrodynamic-oxygen consumption model approach. *Journal of*
20 *Marine Systems*, **134**, 20-28.
- 21 Pritchard J, Stephens M, Donnelly P (2003) Inference of population structure using
22 multilocus genotype data. *Genetics*, **155**, 945-959.
- 23 Quesada H, Zapata C, Alvarez G (1995) A multilocus allozyme discontinuity in the

- 1 mussel *Mytilus galloprovincialis*: the interaction of ecological and life-history
2 factors. *Marine Ecology Progress Series*, **116**, 99-115.

- 3 Quesada H, Stuckas H, Skibinski DOF (2003) Heteroplasmy suggests paternal
4 cotransmission of multiple genomes and pervasive reversion of maternally
5 into paternally transmitted genomes of mussel (*Mytilus*) mitochondrial DNA.
6 *Journal of Molecular Evolution*, **57 (Suppl. 1)**, S138-147.

- 7 R Development Core Team (2012) *R: A language and environment for statistical*
8 *computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-
9 900051-07-0, URL <http://www.R-project.org/>.

- 10 Rawson PD, Secor CL, Hilbish TJ (1996a) The effects of natural hybridization on
11 the regulation of doubly uniparental mtDNA inheritance in the blue mussels
12 (*Mytilus* spp.). *Genetics*, **144**, 241-248.

- 13 Rawson PD, Joyner KL, Meetze K, Hilbish TJ (1996b) Evidence for intragenic
14 recombination within a novel genetic marker that distinguishes mussels in
15 the *Mytilus edulis* species complex. *Heredity*, **77**, 599- 607.

- 16 Rayssac N, Pernet F, Lacasse O, Tremblay R (2010) Temperature effect on
17 survival, growth, and triacylglycerol content during the early ontogeny of
18 *Mytilus edulis* and *M. trossulus*. *Marine Biology Progress Series*, **417**, 183-
19 191.

- 20 Rice WR (1989) Analyzing tables of statistical tests. *Evolution*, **43**, 223-225.

- 21 Riginos C, Sukhdeo K, Cunningham CW (2002) Evidence for selection at multiple
22 allozyme loci across a mussel hybrid zone. *Molecular Biology and*
23 *Evolution*, **19**, 347-351.

- 1 Riginos C, Cunningham CW (2005) Local adaptation and species segregation in
2 two mussel (*Mytilus edulis* x *Mytilus trossulus*) hybrid zones. *Molecular*
3 *Ecology*, **14**, 381-400.
- 4 Riginos C, Wang D, Abrams JA (2006) Geographic variation and positive selection
5 on M7 lysin, an acrosomal sperm protein in mussels (*Mytilus* spp.).
6 *Molecular Biology and Evolution*, **23**, 1952-1965.
- 7 Saavedra C, Stewart DT, Stanood RR, Zouros E (1996) Species-specific
8 segregation of gender-associated mitochondrial DNA types in an area
9 where two mussel species (*Mytilus edulis* and *M. trossulus*) hybridize.
10 *Genetics*, **143**, 1359-1367.
- 11 Schilthuizen M, Hoekstra RF, Gittenberger E (2004) Hybridization, rare alleles and
12 adaptive radiation. *Trends in Ecology and Evolution*, **19**, 404-405.
- 13 Seehausen O (2004a) Hybridization and adaptive radiation. *Trends in Ecology and*
14 *Evolution*, **19**, 198-207.
- 15 Seehausen O (2004b) Resposne to Schilthuizen et al.: Hybridization, rare alleles
16 and adaptive radiation. *Trends in Ecology and Evolution*, **19**, 405-406.
- 17 Skibinski DOF, Gallagher C, Beynon CM (1994) Sex-limited mitochondrial DNA
18 transmission in the marine mussel *Mytilus edulis*. *Genetics*, **138**, 801-809.
- 19 Stuckas H, Stoof K, Quesada H, Tiedemann R (2009) Evolutionary implications of
20 discordant clines across the Baltic *Mytilus* hybrid zone (*Mytilus edulis*,
21 *Mytilus trossulus*). *Heredity*, **103**, 146-156.
- 22 Thomsen J, Haynert K, Wegner KM, Melzner F (2015) Impact of seawater
23 carbonate chemistry on the calcification of marine bivalves. *Biogeosciences*

- 1 , **12**, 4209-4220.
- 2 Väinölä R, Hvilsum MM (1991) Genetic divergence and a hybrid zone between
3 Baltic and North Sea *Mytilus* populations (Mytilidae: Mollusca). *Biological*
4 *Journal of the Linnean Society*, **43**, 127-148.
- 5 Väinölä R, Strelkov P (2011) *Mytilus trossulus* in Northern Europe. *Marine Biology*,
6 **158**, 817-833.
- 7 Wennerström L, Laikre L, Ryman N, Utter FM, Ghani NIA, Andre C, DeFaveri J,
8 Johansson D, Kautsky L, Merilä J, Mikhailova N, Pereyra R, Sandström A,
9 Teacher AGF, Wenne R, Vasemägi A, Zbawicka M, Johannesson K,
10 Primmer CR (2013) Genetic biodiversity in the Baltic Sea: species-specific
11 patterns challenge management. *Biodiversity and Conservation*, **22**, 3045-
12 3065.
- 13 Zouros E, Ball AO, Saavedra C, Freemann KR (1994) An unusual type of
14 mitochondrial DNA inheritance in the blue mussel *Mytilus*. *Proceedings of*
15 *the National Academy of Science USA* , **91**, 7463-7467.
- 16

1 **Data accessibility**

2 Glu5' nucleotide sequences are submitted to Genbank (Accession numbers #####
3 - #####).

4

5 **Author's contribution**

6 **H.S.** designed the study, performed population genetic analyses and wrote the
7 manuscript; **L.K.** performed lab work, contributed to population genetic analysis
8 and prepared figures; **H. Sch.** performed lab work, quantified drifter distributions,
9 and sampling; **C.B.** performed lab work, contributed to population genetic analyses
10 and performed sampling; **H.-H. H.** designed and conducted hydrodynamic
11 modelling and Lagrangian particle tracking; **M.B.** performed lab work and
12 sampling; **K.L.** performed lab work; **F.M.** designed the study and performed
13 sampling. All authors contributed to manuscript revisions.

Tables

Table 1: Estimated cline shape parameters using the software package HZAR and the best model for cline fit (cline fit model) as selected by the software package HZAR based on the Akaike criterion. Clines were fitted into plots of average Q-values for each locality over the distance along the transect (Table 1) and Q-values are derived from Bayesian inference of population structure using the software package STRUCTURE using different model assumptions (STR1-STR8). Similarly, cline fitting was performed using *M. edulis* specific nuclear allele and mtDNA haplotype frequencies at each locality of the transect and 2 log likelihood confidence intervals are given in parentheses.

STRUCTURE-model*/single locus marker	Cline fit model	F _{West}	F _{East}	p _{min}	p _{max}	Cline centre (km)	Cline width (km)	lnL
STR 1	2	0.961	0.034	0.986	0.034	532 (487-589)	418 (288-588)	-3.80
STR 2	2	0.968	0.033	0.989	0.029	536 (493-592)	400 (273-563)	-3.81
STR 3	2	0.974	0.005	1.000	0.000	523 (483-573)	402 (307-534)	-5.85
STR 4	2	0.980	0.007	1.000	0.000	532 (492-583)	385 (290-517)	-5.36
STR 5	2	0.994	0.034	0.997	0.034	546 (501-604)	415 (304-567)	-3.30
STR 6	2	0.996	0.043	0.997	0.043	556 (510-615)	396 (283-549)	-2.88
STR 7	1	1.000	0.000	1.000	0.000	541 (514-578)	214 (148-314)	-4.46
STR 8	1	1.000	0.000	1.000	0.000	542 (515-578)	203 (140-302)	-3.87
MAL-I	2	1.000	0.306	1.000	0.306	623 (549-733)	393 (236-627)	-2.85
Glu-5'	2	0.975	0.722	1.000	0.632	566 (424-796)	785 (455-1176)	-5.10
M7 lysin	2	1.000	0.278	1.000	0.278	422 (360-499)	530 (378-785)	-5.80
EFbis	2	0.225	0	0.235	0	280 (130-418)	600 (305-1176)	-2.27
D-loop	3	0.950	0.611	0.96 (0.92-0.98)	0.74 (0.58-0.83)	454 (410-582)	24 (0-552)	-9.84

*STRUCTURE-model indicates model assumptions for Bayesian inference using the STRUCTURE software package (see Material and Methods): STR1: admixture, correlated allele frequencies; STR2: admixture, uncorrelated allele frequencies; STR3: no admixture, correlated allele frequencies; STR4: no admixture, uncorrelated allele frequencies; STR5: admixture, correlated allele frequencies, *locprior*; STR6: admixture, uncorrelated allele frequencies, *locprior*; STR7: no admixture, correlated allele frequencies, *locprior*; STR8: no admixture, uncorrelated allele frequencies, *locprior*.

Table 2: Pairwise overlap coefficients according to Horn (1966) for drifter distributions of selected localities (compare Figure 3). Note: 0 = no overlap between drifter distribution; 1 = complete overlap between drifter distribution.

Locality	1	2	3	4	5
1 Mön					
2 Warnemünde	0.02				
3 Ahrenshoop	0.07	0.66			
4 Barhöft	0.02	0.03	0.24		
5 Rügen	0	0	0	0.09	
6 Usedom	0	0	0	0	0.10

Legend to Figures

Figure 1 Sampling sites of populations analysed in this study. **(A)** Overview of the study area covering the North Sea (including sample site Helgoland; genetically pure *M. edulis* as reference), Skagerrak, Kattegat (including sample sites Tjörnö, Aarhus), the Belt Sea Islands (e.g., Fyn (F), Sealand (S)) and the Baltic Proper (including sample site Askö). **(B)** Localities covering the transect used for allele/haplotype frequency cline shape analyses: Flensburg (FL), Gelting (GE), Maasholm (MA), Kappeln (KA), Eckernförde (ECK), Wendtorf (W; near Kiel), Fehmarnsund (FS), Grömitz (GR), Steinbeck (S), Gollwitz (GP), Warnemünde (WM), Ahrenshoop (AH), Barhöft (B), Dranske (D), Usedom (U), Hel (H). **(C)** Sampling localities at Kiel Fjord: GEOMAR (G), Ship museum (M), Hörn (H), East shore (E). Locality Wendtorf (W) is shown as reference. (Note: Genetically pure reference specimens of *M. trossulus* were obtained from Penn Cove (North America, see Table S1 for details).

Figure 2 Results of Lagrangian particle tracking. **A)** Relative frequencies of drifters plotted over the distance travelled from their respective release point to the endpoint. The diagram shows that the majority of drifters move only 20 km or less indicating that that passive drift over long distance may not play a role for dispersal of *Mytilus spp.* in the Baltic area. **B)** Pictogram showing a qualitative analysis of drifter endpoints that were released at the locality Warnemünde. This example shows how an overall larvae drift patterns was derived based on qualitative analyses of drifter endpoint distributions of 72 localities around the Baltic.

Figure 3 Results of Lagrangian particle tracking at different localities: **(A)** Mön (Denmark), **(B)** Warnemünde (Germany), **(C)** Ahrenshoop (Germany), **(D)** Barhöft (Germany), **(E)**

Rügen Island (Germany), **(F)** Usedom (Germany) (compare also Figure 1). Densities of drifter endpoint are quantified: areas where more than 1000 (dark blue line), more than 500 (light blue line) or at least 10 (grey line) drifters per unit ($1^{\circ} \times 1^{\circ}$) were observed.

Figure 4 Results of populations structure using Bayesian inference (STRUCTURE software) and the model setting (out of eight) (ancestry model: admixture; allele frequency model: correlated; without *locprior* setting). **A)** Bayesian inference performed for 21 populations (excluding samples from Kiel-Fjord) and used as data basis for cline shape analyses. Bar Plot of Q-values indicating to what proportion the genome of each specimen is allocated to one of the two clusters (depicted as red and green), i.e., bars consisting of both colours represent hybrid genotypes. **B)** Bayesian inference performed for 25 populations (including samples from Kiel Fjord).

Figure 5 Selected results of cline shape analyses and cline shapes are plotted over the distances between localities of the transect (given in km, Table 1); approximate position of the sampling sites are indicated at the upper line of each picture. The fitted curve is depicted as continuous line and the respective 2 log likelihood confidence interval is depicted as grey area. Vertical lines represent cline centres and indicate the respective range of the cline centre confidence interval (compare also Table 1). **A)** Example of cline fitting to average Q-values derived from Bayesian inference using the STRUCTURE software package. This picture presents cline fitting using average Q-values of each locality from one model setting (out of eight) (ancestry model: admixture; allele frequency model: correlated; without *locprior* setting). **B-F)** Cline fitting was also performed using average *M. edulis* specific allele/haplotype frequencies at different loci (Table S5): **(B)** MAL-I, **(C)** Glu5', **(D)** M7Iysin, **(E)** EFbis, **(F)** mtDNA (D-loop).

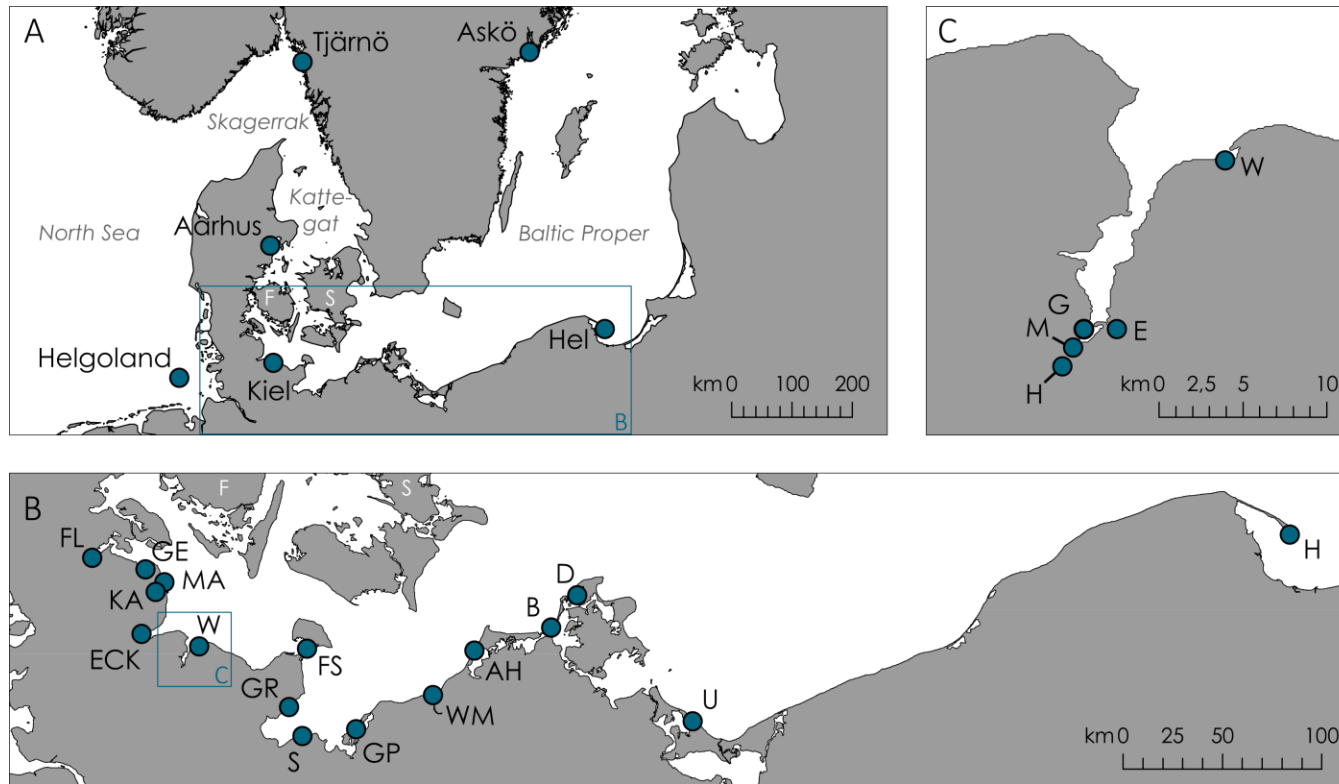


Figure 1

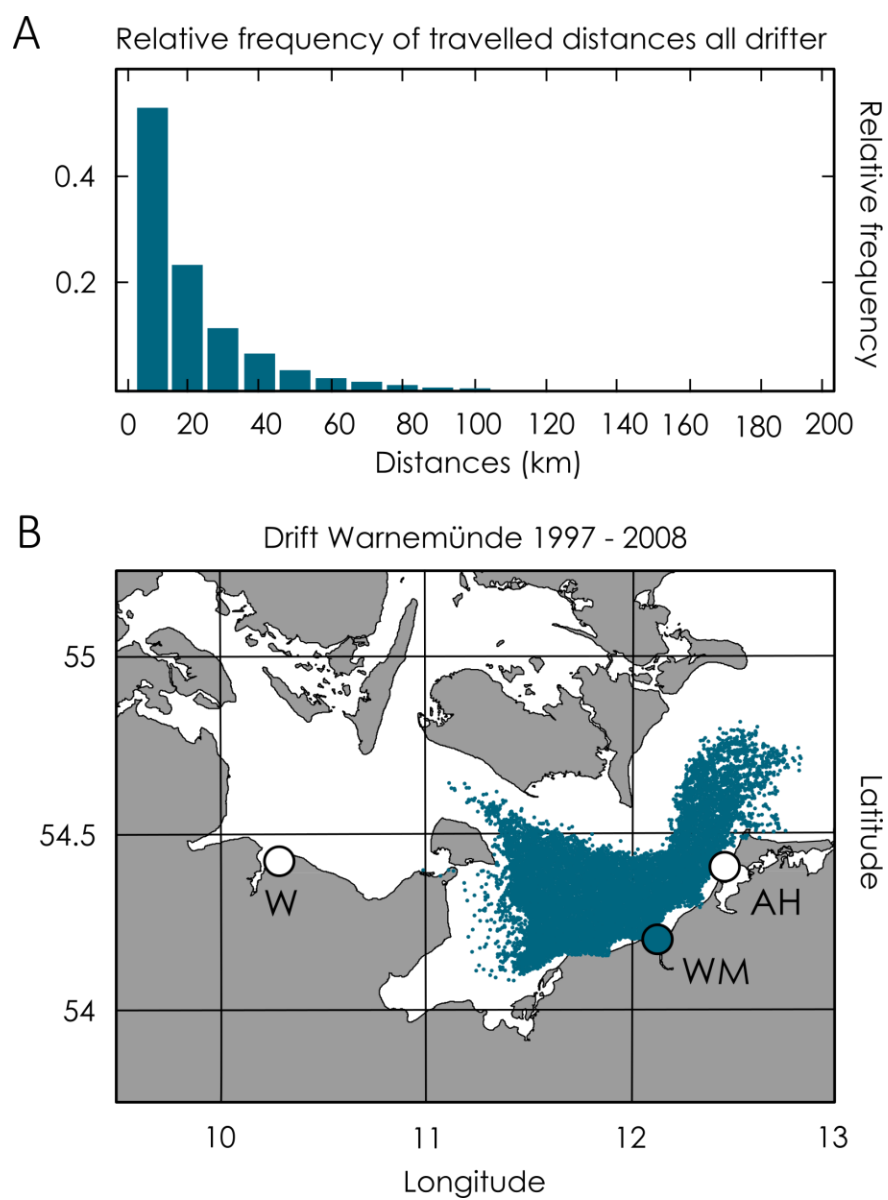


Figure 2

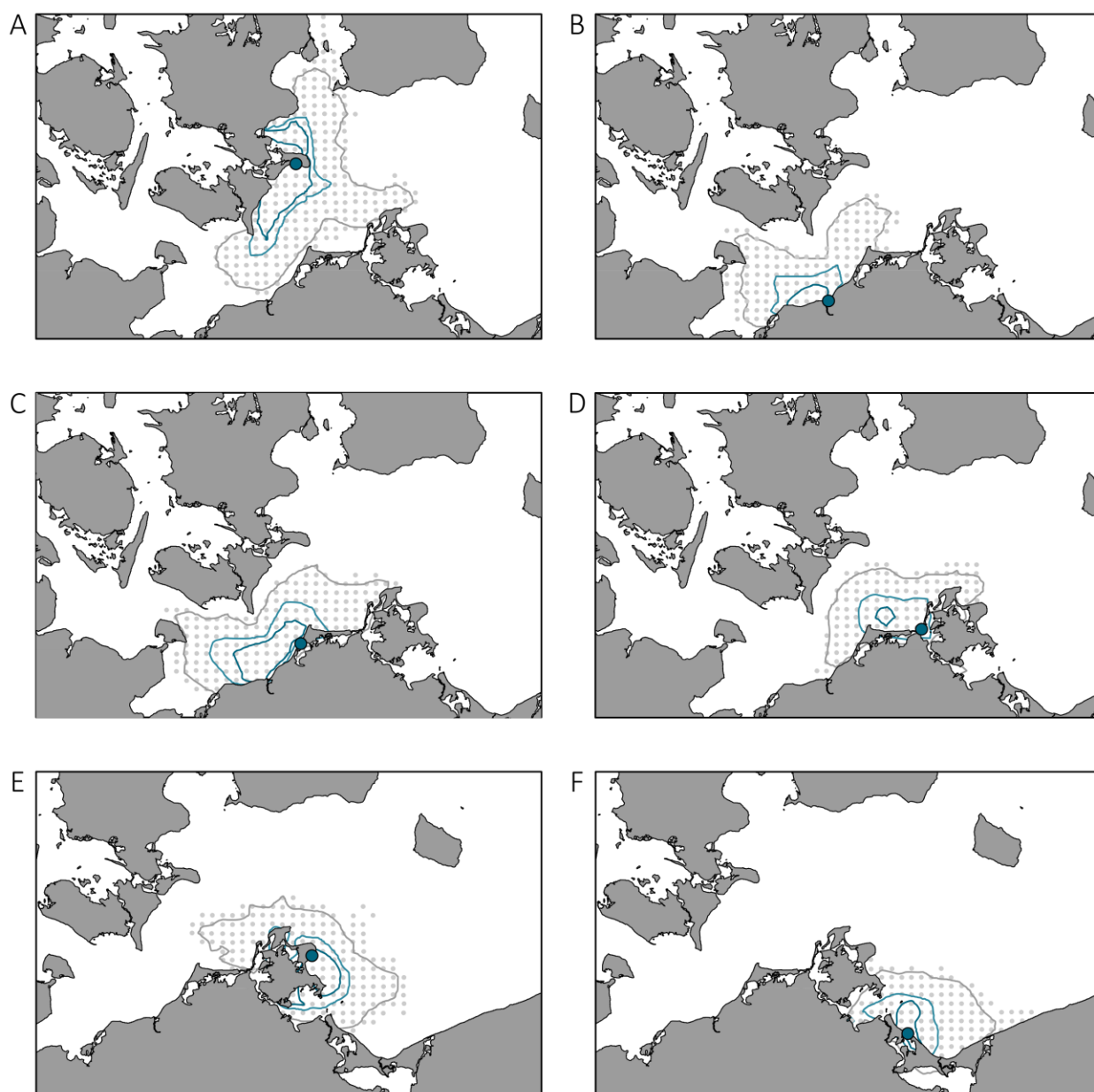


Figure 3

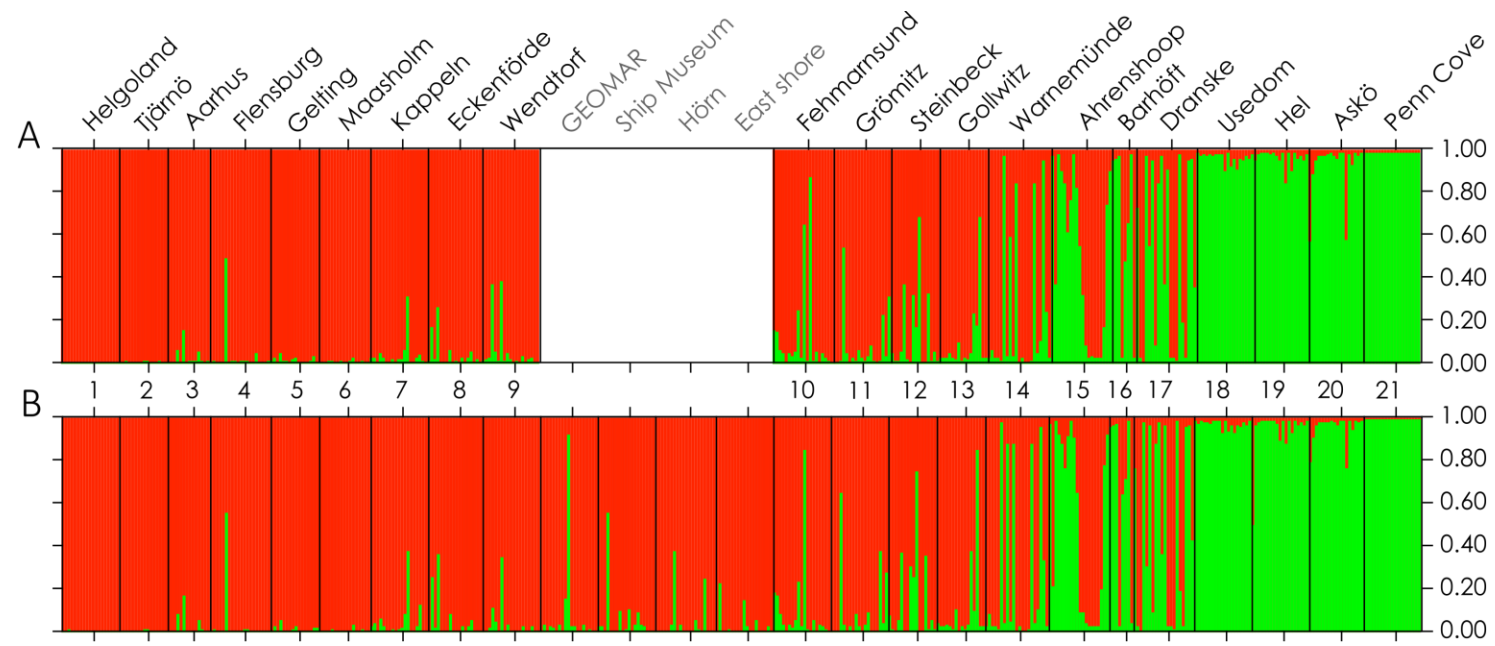


Figure 4

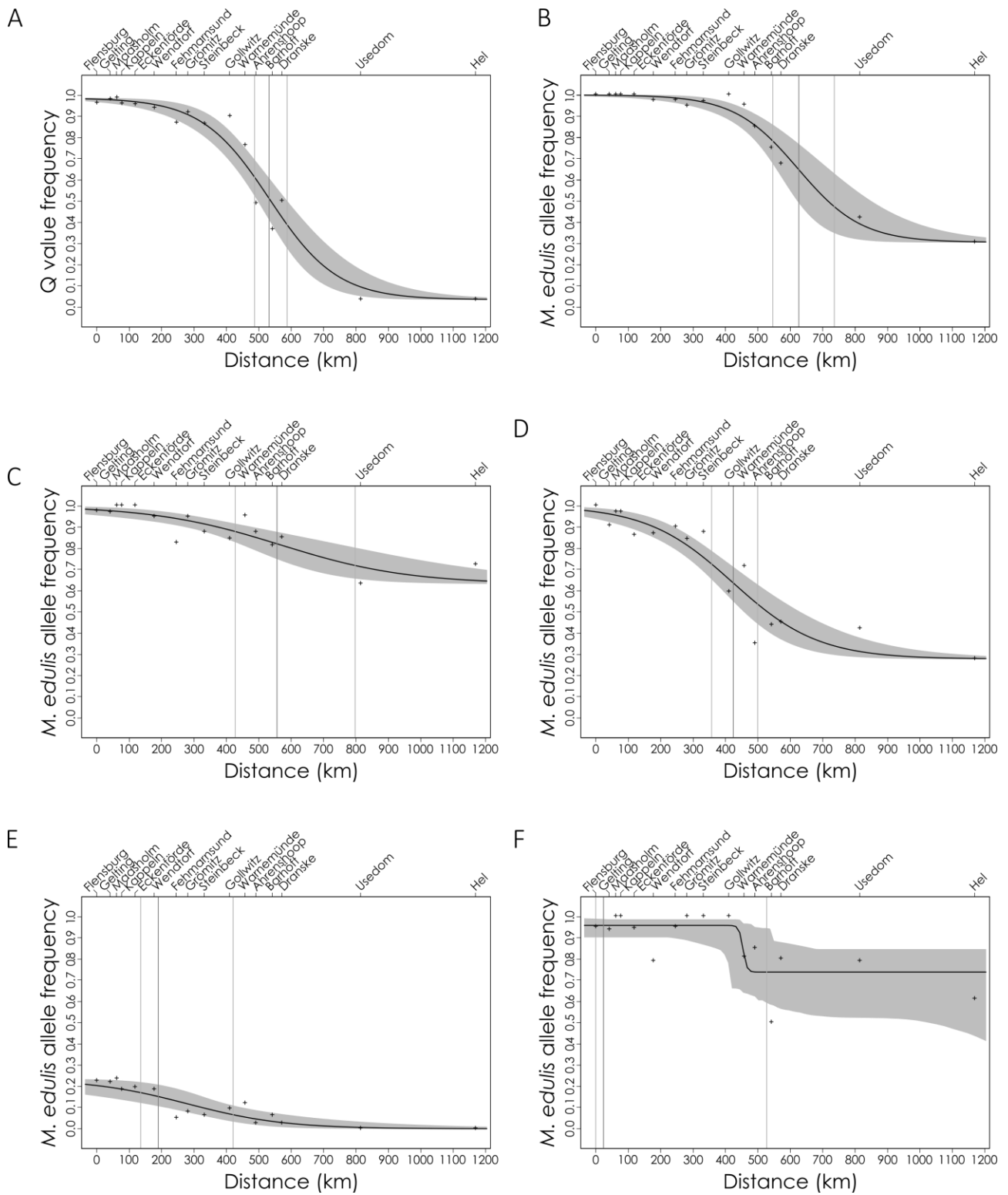
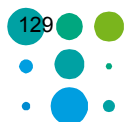


Figure 5



Cruise Report
FRV „Clupea” Cruise 279
10.02. – 21.02.2014

Hydroacoustic survey for the assessment of small pelagics in the Baltic Sea

Scientists in charge: Dr. Daniel Oesterwind (TI-OF) & Dr. Patrick Polte (TI-OF)

1. In a nutshell

The first part of the cruise was conducted to assess concentrations of ripe and running herring in the area of the outer coastal waters of the Pommeranian Bay by hydroacoustic means.

Distribution list:

BLE, Hamburg
Schiffsführung FFS „Clupea”
Deutsche Fischfang-Union
Sassnitzer Seefischerei e. G.
Landesverband der Kutter- u. Küstenfischer
DFFU Cuxhaven
BMEL, Ref. 614
Thünen-Institut - Pressestelle, Dr. Welling
Thünen-Institut - Präsidialbüro
Thünen-Institut - Fischereiökologie
Thünen-Institut - Seefischerei Hamburg
Thünen-Institut - Ostseefischerei
Thünen-Institut - FIZ-Fischerei

BFEL HH, FB Fischqualität
Reiseplanung Forschungsschiffe, Herr Dr. Rohlf
Fahrtteilnehmer
Bundesamt für Seeschifffahrt und Hydrographie, Hamburg
Mecklenburger Hochseefischerei Sassnitz
Doggerbank Seefischerei GmbH, Bremerhaven
Deutscher Fischerei-Verband e. V., Hamburg
Leibniz-Institut für Meereswissenschaften IFM-GEOMAR
BSH, Hamburg
Leibniz-Institut für Ostseeforschung Warnemünde
Institut für Fischerei der Landesforschungsanstalt
LA für Landwirtschaft, Lebensmittels. und Fischerei
Euro-Baltic Mukran

2. Cruise objectives

The following objectives were planned for CLU279:

5. Hydro-acoustic investigations of the abundance and distribution of adult herring around Rügen

3. Cruise narrative and preliminary results

3.1 Cruise narrative (Daniel Oesterwind & Patrick Polte)

FRV "Clupea" was equipped with all hydro-acoustic equipment and biological sampling gear for both cruise parts on February 10th. Due to the ice cover and wind conditions FRV "Clupea" left Marienehe port on February 12th with a delay of 2 days to Sassnitz port. Due to the weather and ice at the area of Rügen and Greifswalder Bodden, the first week of the cruise had to be cancelled. Scientists boarded FRV "Clupea" in the morning of February 17th and the acoustic cruise part started immediately. Due to a power blackout on FRV "Clupea" during the weekend the Doppler log had to be calibrated at first. The cruise continued with the first CTD-station to measure the hydrographic conditions to set the acoustic records. Afterwards, the hydro acoustic records started at the first transect (T3) at the Prorer Wiek. Generally, survey operations were conducted during daytime. At the end of the first day transect 3, transect 2 and a half of transect 1 were finished and FRV Clupea returned to Sassnitz port. Because of the rare acoustic signals, only one haul was performed at the first day. On the second day, FRV "Clupea" left Sassnitz port in the morning to continue the survey and finished the northern transect (T1). Afterwards FRV "Clupea" steamed to the southern transects (T4 & T5) and finished the last two transects in the afternoon. After transect 5 FRV "Clupea" shipped to the beam trawl position near Oderbank and performed a standard haul, before FRV "Clupea" shipped into the port of the Island of Rugen and the second day ended. On the second day a total of three hauls (2 OTM + 1 TBB) and eight CTD stations were performed. Due to the low herring abundance and therefore the low number of fishing hauls all transects were fulfilled within two days, and enough time remained for the ichthyoplankton survey. Therefore FRV "Clupea" left the port of Lauterbach Rügen and moved Stralsund to change the scientific crew and to start with the second part.

3.2 Hydroacoustic sampling (Matthias Schaber)

Hydroacoustic data were recorded with a Simrad EK60 scientific echosounder with hull-mounted 38 kHz and 120 kHz transducers. Post-processing and analysis were accomplished with Myriax Echoview 5.4 software. Data from the 38 kHz transducer were used for integration. Corresponding transducer settings were: Pulse duration 1024 μ s, ping interval 4 s⁻¹.

Data were recorded at a ship speed of 10 to 11 kn. Overall hydroacoustic transect length was 78 nm. Transects and NASC values (1 nm intervals) are depicted in Fig. 2.

Altogether, NASC values were zero in large parts of the surveyed area indicating absence of herring pre-spawning aggregations. However, in deeper parts of the section connecting transects T2 and T1 as well as on the northernmost transect T1 patches of several very large schools were detected leading to NASC values sometimes well exceeding 10 000 m²nm⁻² in the corresponding intervals. Trawl hauls targeting the schools yielded large herring in mostly pre-spawning condition indicating arrival of spawners. In the shallow southeastern part of the survey area (section connecting T4 and T5), also correspondingly large schools were detected. However, those were spatially restricted and occurred on a short transect section.

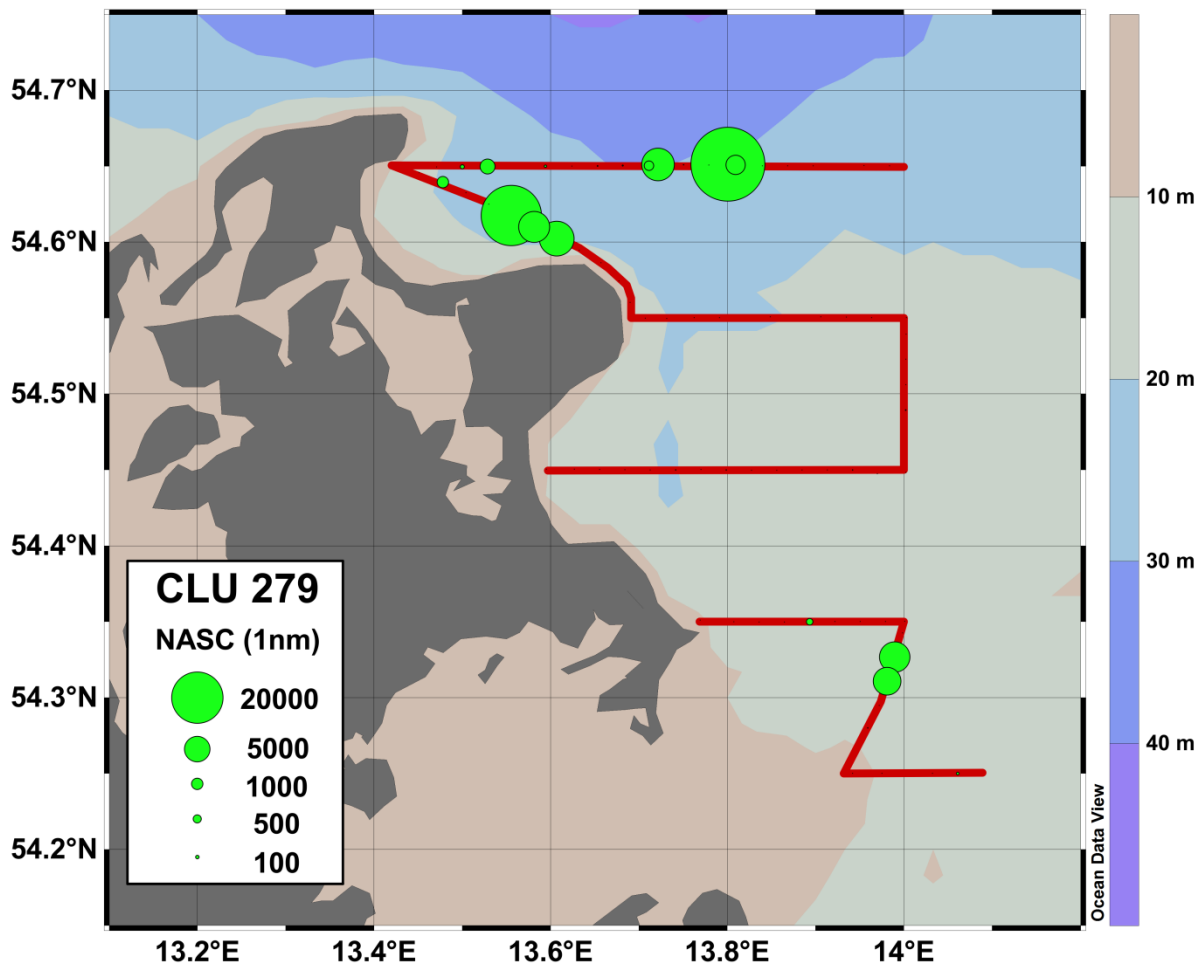


Figure 1: Clupea CLU279. Hydroacoustic transects (red line) and NASC values (Nautical Area Scattering Coefficient, m^2nm^{-2}). Water depths (m) are indicated in scale. The large schools identified mostly in the northern part of the survey area consisted almost exclusively of big, pre-spawning herring.

3.3 Biological sampling

To validate and allocate echorecordings, altogether 3 fishery hauls were performed (Figure XX with an OTM PSN 388 and fish were handled after the standard acoustic protocol. One additional haul were performed with a beam trawl near Oderbank. The total catch is listed in Table 1.

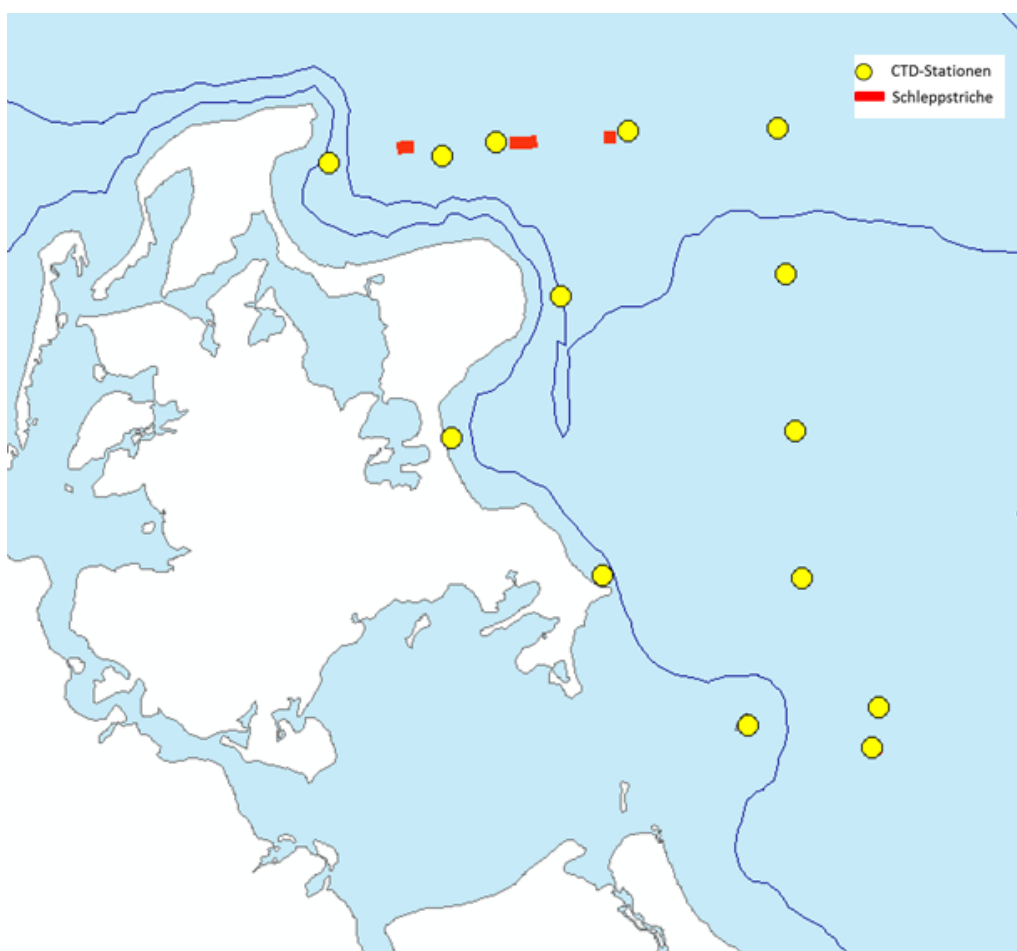


Figure 2. Overview about the performed CTD stations and fisheries hauls.

Table 1. Catch composition during FRV Clupea cruise 279.

Gear	transect	Haul	Species	Total wet weight
OTM PSN388	T1	1	<i>Cyclopterus lumpus</i>	0,267
OTM PSN388	T1	2	<i>Sprattus sprattus</i>	10,05
OTM PSN388	T1	2	<i>Clupea harengus</i>	52,37
OTM PSN388	T1	3	<i>Clupea harengus</i>	235,86
TBB 2m		4	<i>Platichthys flesus</i>	0,084

4. Cruise Participants

1. Part:

Dr. Daniel Oesterwind
Dr. Matthias Scharber
Mario Koth

scientist in charge
scientist (acoustic)
technician

TI-OF
TI-SF
TI-OF

5. Acknowledgments

We hereby thank all participants, the crew of FRV "Clupea" and Captain R. Singer for their outstanding cooperation and commitment.

Stationlist:

Cruise	Year	Station	Device	Datum	Zeit	Phase	Lat	Long
279	14	2992	CTD SBE19+ offline	17.02.14	09:49:01	Von Deck	54°27,029N	013°35,210E
279	14	2993	CTD SBE19+ offline	17.02.14	11:41:28	Von Deck	54°26,906N	014°00,217E
279	14	2994	CTD SBE19+ offline	17.02.14	12:23:16	Von Deck	54°33,022N	014°00,147E
279	14	2995	CTD SBE19+ offline	17.02.14	13:23:21	Von Deck	54°32,983N	013°43,908E
279	14	2996	CTD SBE19+ offline	17.02.14	14:50:18	Von Deck	54°38,961N	013°27,257E
279	14	2997	OTM Krake mit Rollen	17.02.14	15:19:53	Von Deck	54°39,046N	013°31,092E
279	14	2998	CTD SBE19+ offline	17.02.14	16:13:37	Von Deck	54°38,996N	013°35,768E
279	14	2999	OTM Krake mit Rollen	18.02.14	08:28:35	Von Deck	54°39,045N	013°43,624E
279	14	3000	CTD SBE19+ offline	18.02.14	09:21:24	Von Deck	54°39,129N	013°39,754E
279	14	3001	OTM Krake mit Rollen	18.02.14	09:59:05	Von Deck	54°39,052N	013°46,777E
279	14	3002	CTD SBE19+ offline	18.02.14	10:42:59	Von Deck	54°39,323N	013°49,234E
279	14	3003	CTD SBE19+ offline	18.02.14	11:32:18	Von Deck	54°39,011N	014°00,026E
279	14	3004	CTD SBE19+ offline	18.02.14	13:29:26	Von Deck	54°21,040N	013°45,931E
279	14	3005	CTD SBE19+ offline	18.02.14	14:22:31	Von Deck	54°21,015N	014°00,072E
279	14	3006	CTD SBE19+ offline	18.02.14	15:03:19	Von Deck	54°14,993N	013°55,979E
279	14	3007	CTD SBE19+ offline	18.02.14	15:37:42	Von Deck	54°14,998N	014°05,017E
279	14	3008	TBB 2m Kurre	18.02.14	15:54:31	Von Deck	54°13,382N	014°04,941E
279	14	3009	CTD SBE19+ offline	18.02.14	16:20:05	Von Deck	54°13,589N	014°04,994E

Cruise Report

FRV „Clupea” Cruise 280

Short daily description of activities, research locations and research done

The acoustic equipment was still on FRV Clupea from cruise number 279. On the first day (27.03.2014) the acoustic survey started at port Sassnitz. Eleven CTD station and 4 fishing hauls were performed on transects one, two and three (from the North). On the second day (28.03.2014) FRV Clupea continued the cruise on transect 3, 4 and 5, due to the low abundance of pelagic fish, only one fishing hauls and 8 CTD stations were conducted. Due to the remaining time, FRV Clupea steamed to a small port at the Island of Ruden in the south east of the Island of Rügen and shipped at the morning of the 29th of March to Stralsund (port Dänholm) to finish the survey and to change the scientific stuff.

The total biomass (in kg) of fished species is listed in the following table:

Cruise days:	Haul	Transect	<i>C. harengus</i>	<i>Ammodytes</i>	<i>Cyclopterus lumpus</i>	<i>S. sprattus</i>	total
27.03.2014: 1 day	1	2	7.66		0.17	4.18	12.01
	2	2	51.8		0.37	0.34	52.51
28.03.2014: 1 day	3	1	9.92			16.76	26.68
	4	1	8.02			0.16	8.18
Total 2 days	5	3	7.54	0.2		7.26	15
	total		84.94	0.2	0.54	28.7	114.38

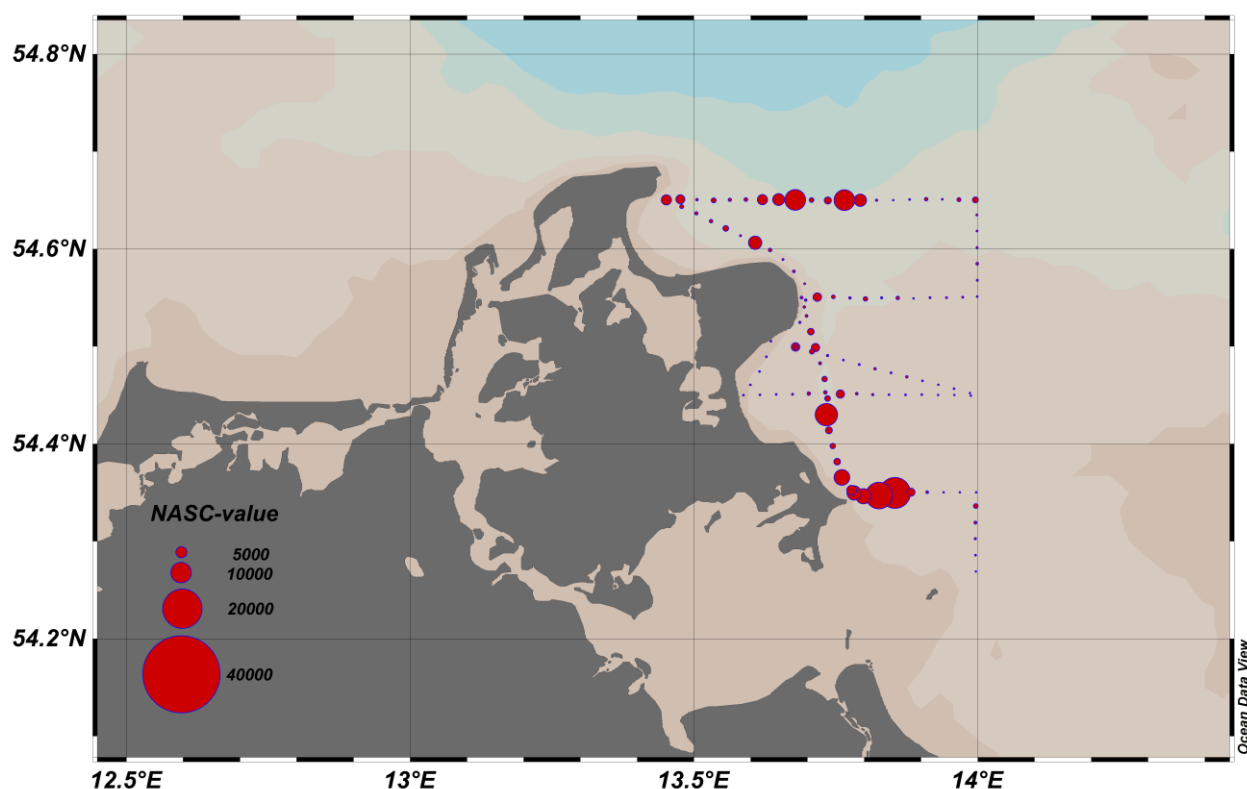


Figure 1. Preliminary NASC-values of Clupea Cruise 280 on the 27th and 28th of March 2014.

Stationlist:

Cruise numb	Year	StationNr	Bem. Gerät	Bem. Station	Datum	Zeit	Phase	Geog.Breite	Geog.Länge
280	14	3198	CTD SBE19+ offline	1	27.03.14	06:48:28	Von Deck	54°30,529N	013°39,648E
280	14	3199	CTD SBE19+ offline	2	27.03.14	07:14:48	Von Deck	54°33,027N	013°41,857E
280	14	3200	pelagic gear	3	27.03.14	07:31:28	Von Deck	54°33,040N	013°44,043E
280	14	3201	CTD SBE19+ offline	3	27.03.14	08:11:07	Von Deck	54°32,880N	013°46,810E
280	14	3202	pelagic gear	4	27.03.14	08:27:28	Von Deck	54°32,982N	013°50,300E
280	14	3203	CTD SBE19+ offline	4	27.03.14	09:10:47	Von Deck	54°32,960N	013°53,216E
280	14	3204	CTD SBE19+ offline	5	27.03.14	09:38:15	Von Deck	54°33,005N	013°59,978E
280	14	3205	CTD SBE19+ offline	6	27.03.14	10:16:54	Von Deck	54°38,976N	013°59,909E
280	14	3206	pelagic gear	7	27.03.14	11:12:35	Von Deck	54°39,004N	013°45,839E
280	14	3207	CTD SBE19+ offline	7	27.03.14	11:56:08	Von Deck	54°38,988N	013°42,644E
280	14	3208	pelagic gear	8	27.03.14	12:29:46	Von Deck	54°39,035N	013°34,708E
280	14	3209	CTD SBE19+ offline	8	27.03.14	13:07:15	Von Deck	54°39,020N	013°31,825E
280	14	3210	CTD SBE19+ offline	9	27.03.14	13:28:18	Von Deck	54°39,012N	013°27,002E
280	14	3211	CTD SBE19+ offline	10	27.03.14	15:14:29	Von Deck	54°27,170N	013°44,126E
280	14	3212	CTD SBE19+ offline	11	27.03.14	15:49:40	Von Deck	54°27,002N	013°34,995E
280	14	3213	CTD SBE19+ offline	12	28.03.14	05:33:28	Von Deck	54°26,985N	014°00,045E
280	14	3214	CTD SBE19+ offline	13	28.03.14	06:20:21	Von Deck	54°27,051N	013°47,342E
280	14	3215	pelagic gear	14	28.03.14	06:34:33	Von Deck	54°26,959N	013°44,197E
280	14	3216	CTD SBE19+ offline	14	28.03.14	07:27:49	Von Deck	54°25,005N	013°44,257E
280	14	3217	CTD SBE19+ offline	15	28.03.14	07:58:13	Von Deck	54°20,986N	013°46,971E
280	14	3218	CTD SBE19+ offline	16	28.03.14	08:22:32	Von Deck	54°21,011N	013°52,113E
280	14	3219	CTD SBE19+ offline	17	28.03.14	08:55:24	Von Deck	54°21,031N	013°59,979E
280	14	3220	CTD SBE19+ offline	18	28.03.14	09:35:29	Von Deck	54°14,986N	013°59,818E
280	14	3221	CTD SBE19+ offline	19	28.03.14	09:51:34	Von Deck	54°15,013N	013°55,983E

Short daily description of activities, research locations and research done

The acoustic equipment was already on board from the previous survey. To test different survey design, FRV Clupea shipped on the first day from port Sassnitz on transect one, two and partly on transect three. Three fishery hauls and 10 CTD stations were performed. On the second day a zig-zag course at the same area were shipped. During that day 9 CTD stations and 3 fishing hauls were conducted. The survey finished at the evening in Stralsund at port Dänholm.

08.05.2014: 1 day

09.05.2014: 1 day

Total 2 days

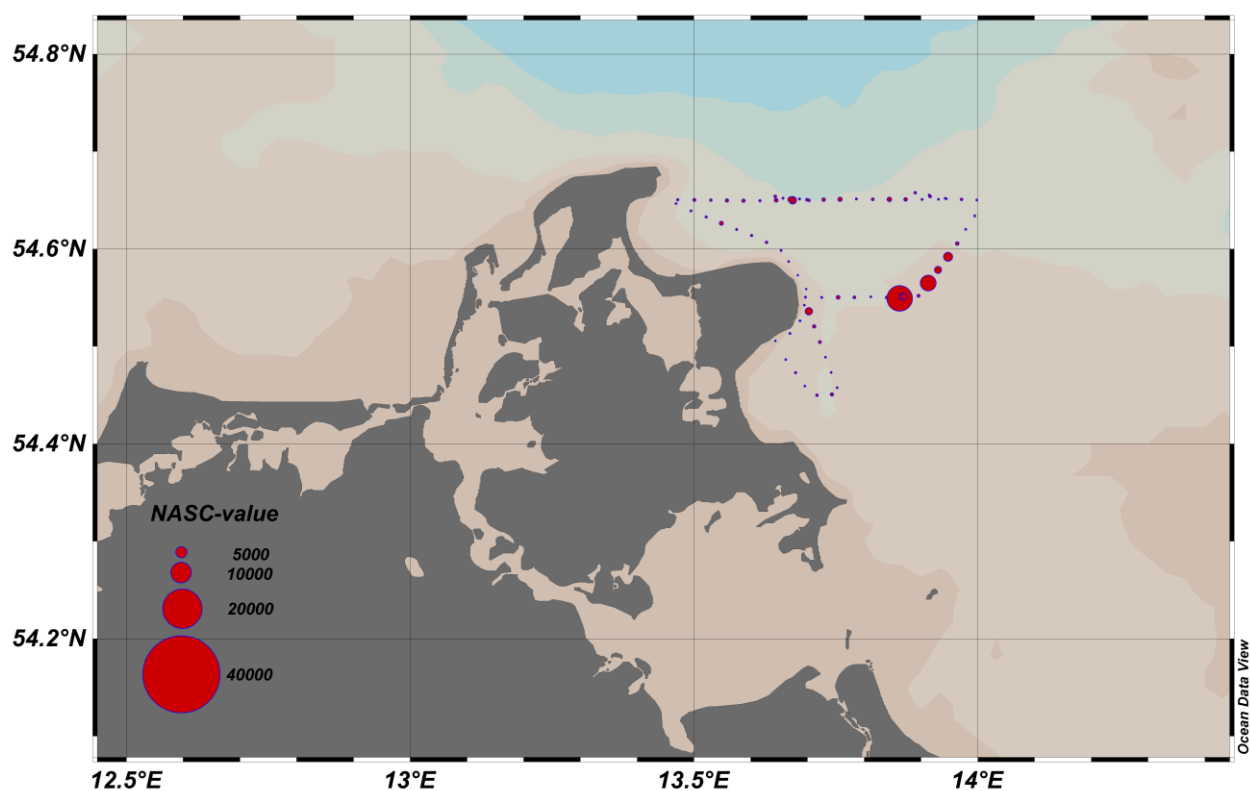


Figure 2. Preliminary NASC-values of FRV Clupea Cruise 280 on 8th of May.

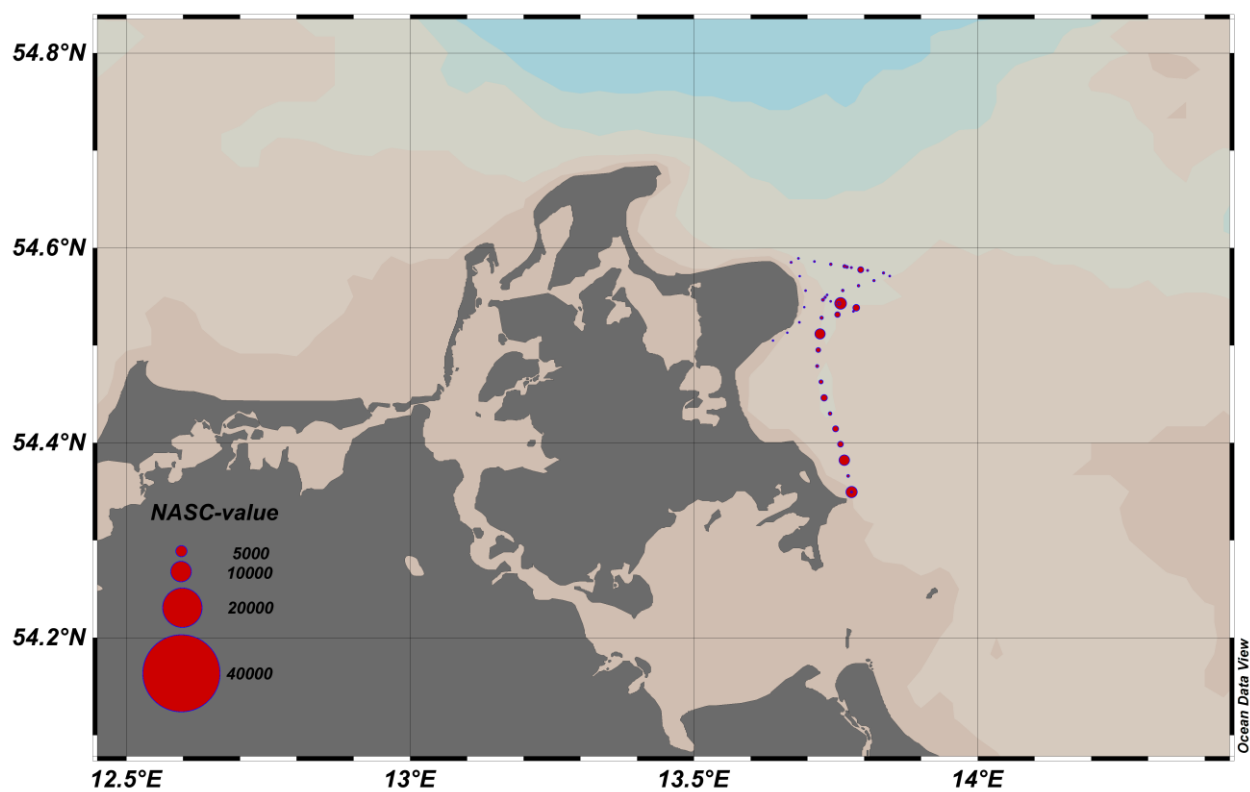


Figure 3. Preliminary NASC-values of FRV Clupea Cruise 280 on 9th of May.

The total amount of fished species in kg is listed in the following table:

Haul	1	2	3	4	5	6	total (kg)
<i>G. morhua</i>		100.84					100.84
<i>C. harengus</i>	11.88	60.72	21.22	0.62	0.87	1.31	96.62
<i>Belone belone</i>			0.32				0.32
<i>Ammodytidae</i>		0.90					0.90
<i>Cyclopterus lumpus</i>	0.24		0.19				0.43
<i>Myoxocephalus scorpius</i>		0.25					0.25
<i>S. sprattus</i>	194.18	79.47	189.08			91.54	554.26
<i>Merlangius merlangus</i>		0.56					0.56
Total (kg)	206.30	242.74	210.81	0.62	0.87	92.84	754.18

Stationlist:

Cruise numb	Year	Station No	Device	Datum	Zeit	Phase	Lat	Long
280	14	3517	CTD SBE19+ offline	08.05.14	06:24:18	Von Deck	54°35,865N	013°39,083E
280	14	3518	CTD SBE19+ offline	08.05.14	07:16:44	Von Deck	54°39,018N	013°27,451E
280	14	3519	pelagic gear	08.05.14	08:12:12	Von Deck	54°39,037N	013°42,441E
280	14	3520	CTD SBE19+ offline	08.05.14	09:22:07	Von Deck	54°39,303N	013°38,469E
280	14	3521	pelagic gear	08.05.14	10:29:14	Von Deck	54°39,043N	013°57,057E
280	14	3522	CTD SBE19+ offline	08.05.14	11:27:27	Von Deck	54°39,486N	013°53,278E
280	14	3523	CTD SBE19+ offline	08.05.14	11:55:04	Von Deck	54°38,991N	013°59,861E
280	14	3524	CTD SBE19+ offline	08.05.14	12:43:05	Von Deck	54°33,051N	013°53,706E
280	14	3525	pelagic gear	08.05.14	12:59:03	Von Deck	54°33,048N	013°51,214E
280	14	3526	CTD SBE19+ offline	08.05.14	13:57:30	Von Deck	54°33,029N	013°50,358E
280	14	3527	CTD SBE19+ offline	08.05.14	14:30:58	Von Deck	54°33,017N	013°41,637E
280	14	3528	CTD SBE19+ offline	08.05.14	15:11:26	Von Deck	54°27,070N	013°45,424E
280	14	3529	CTD SBE19+ offline	08.05.14	15:22:30	Von Deck	54°27,018N	013°43,398E
280	14	3530	CTD SBE19+ offline	09.05.14	04:39:56	Von Deck	54°35,448N	013°40,002E
280	14	3531	pelagic gear	09.05.14	05:12:07	Von Deck	54°34,642N	013°47,695E
280	14	3532	CTD SBE19+ offline	09.05.14	05:49:59	Von Deck	54°34,944N	013°45,453E
280	14	3533	CTD SBE19+ offline	09.05.14	06:13:49	Von Deck	54°34,354N	013°51,106E
280	14	3534	CTD SBE19+ offline	09.05.14	06:50:07	Von Deck	54°32,866N	013°43,058E
280	14	3535	pelagic gear	09.05.14	07:04:34	Von Deck	54°32,557N	013°45,675E
280	14	3536	CTD SBE19+ offline	09.05.14	07:41:54	Von Deck	54°33,014N	013°43,412E
280	14	3537	CTD SBE19+ offline	09.05.14	08:02:26	Von Deck	54°32,220N	013°47,796E
280	14	3538	CTD SBE19+ offline	09.05.14	08:21:54	Von Deck	54°31,687N	013°43,511E
280	14	3539	pelagic gear	09.05.14	09:03:46	Von Deck	54°28,092N	013°43,279E
280	14	3540	CTD SBE19+ offline	09.05.14	09:43:24	Von Deck	54°26,768N	013°43,768E
280	14	3541	CTD SBE19+ offline	09.05.14	10:09:54	Von Deck	54°22,855N	013°45,941E

Cruise Report FRV „Clupea” Cruise 286

Short daily description of activities, research locations and research done

A third possibility of survey design was tested.

FRV Clupea was equipped in Rostock at port Marienehe. At Day 1 (29.10.14) FRV Clupea steamed from Rostock port to the study area at the Island of Rügen to port Sassnitz. On day 2 (30.10.14) the acoustic survey started at port Sassnitz. Due to problems with the CTD, it was not possible to record hydrographic data on the first day. However, 2 fishing stations were performed on the west side of Rügen Island and FRV Clupea returned back to port Sassnitz. On day 3 (31.10.14), the CTD were fixed and 7 CTD stations and 3 fishing stations in the northeastern area of the Island were performed and FRV Clupea steamed back into port Sassnitz. On the fourth day (01.11.14), the sampling continued and 15 CTD and 3 fishing hauls were conducted and FRV Clupea returned into port Sassnitz. On the last day (02.11.14) the cruise was finished with 11 CTD stations and 3 fishing hauls and FRV Clupea shipped to Stralsund into port Dänholm.

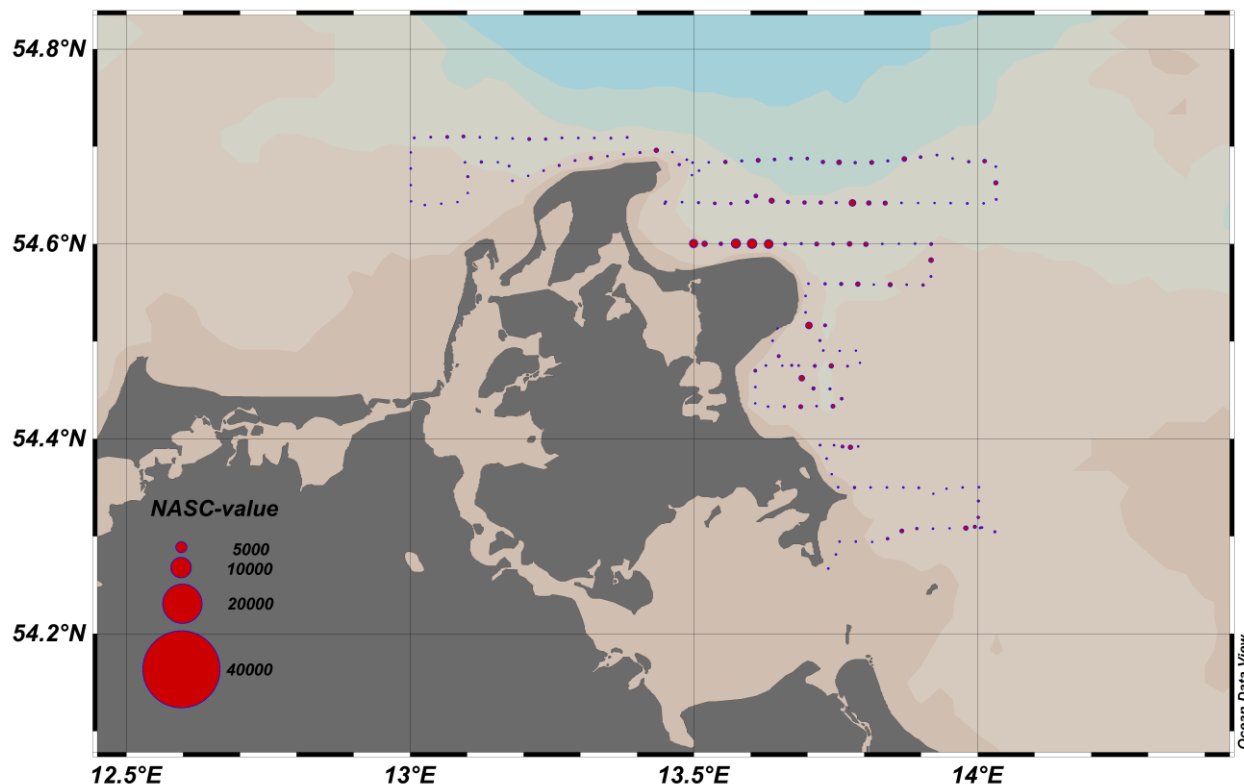


Figure 1. Preliminary NASC-values of Clupea Cruise 286.

The total amount of fished species in kg
is listed in the following table:

species	total (kg)
<i>G. morhua</i>	68.14
<i>P. flesus</i>	0.68
<i>C. harengus</i>	203.01
<i>B. belone</i>	0.06
<i>L. limanda</i>	0.40
<i>Ammodytidae</i>	13.14
<i>E. encrasicolus</i>	0.62
<i>P. platessa</i>	4.82
<i>C. lumpus</i>	1.16
<i>S. sprattus</i>	189.30
<i>S. maximus</i>	1.42
Total	482.7

Stationlist:

Cruise	Year	Stations-Jahr	Device	S-Nr	Datum	Zeit	Phase	Lat	Long
286	14	4607	OTM PSN388 Krake		1 30.10.14	10:10:15	Von Deck	54°42,515N	013°18,217E
286	14	4608	OTM PSN388 Krake		2 30.10.14	13:00:51	Von Deck	54°41,024N	013°05,758E
286	14	4609	CTD SBE19+ offline		3 31.10.14	07:57:28	Von Deck	54°38,561N	013°26,842E
286	14	4610	OTM PSN388 Krake		4 31.10.14	08:25:44	Von Deck	54°38,489N	013°33,641E
286	14	4611	CTD SBE19+ offline		5 31.10.14	09:09:42	Von Deck	54°38,955N	013°36,282E
286	14	4612	CTD SBE19+ offline		6 31.10.14	09:48:12	Von Deck	54°38,519N	013°45,061E
286	14	4613	CTD SBE19+ offline		7 31.10.14	10:54:37	Von Deck	54°38,506N	014°01,932E
286	14	4614	CTD SBE19+ offline		8 31.10.14	11:12:33	Von Deck	54°41,039N	014°01,910E
286	14	4615	OTM PSN388 Krake		9 31.10.14	11:25:37	Von Deck	54°41,060N	013°59,227E
286	14	4616	OTM PSN388 Krake		10 31.10.14	12:39:57	Von Deck	54°41,018N	013°46,033E
286	14	4617	CTD SBE19+ offline		11 31.10.14	13:20:05	Von Deck	54°41,175N	013°43,205E
286	14	4618	CTD SBE19+ offline		12 31.10.14	14:16:39	Von Deck	54°40,859N	013°28,402E
286	14	4619	CTD SBE19+ offline		13 01.11.14	06:56:32	Von Deck	54°36,004N	013°29,989E
286	14	4620	OTM PSN388 Krake		14 01.11.14	07:04:45	Von Deck	54°36,013N	013°31,301E
286	14	4621	CTD SBE19+ offline		15 01.11.14	07:47:26	Von Deck	54°36,024N	013°33,890E
286	14	4622	CTD SBE19+ offline		16 01.11.14	08:23:08	Von Deck	54°35,982N	013°42,693E
286	14	4623	CTD SBE19+ offline		17 01.11.14	09:12:17	Von Deck	54°35,996N	013°55,080E
286	14	4624	CTD SBE19+ offline		18 01.11.14	09:31:30	Von Deck	54°33,476N	013°55,013E
286	14	4625	CTD SBE19+ offline		19 01.11.14	09:58:02	Von Deck	54°33,511N	013°48,362E
286	14	4626	CTD SBE19+ offline		20 01.11.14	10:24:47	Von Deck	54°33,503N	013°41,782E
286	14	4627	CTD SBE19+ offline		21 01.11.14	10:44:53	Von Deck	54°30,981N	013°41,840E
286	14	4628	OTM PSN388 Krake		22 01.11.14	10:57:25	Von Deck	54°30,887N	013°43,831E
286	14	4629	CTD SBE19+ offline		23 01.11.14	11:37:57	Von Deck	54°29,418N	013°43,178E
286	14	4630	CTD SBE19+ offline		24 01.11.14	11:57:36	Von Deck	54°29,400N	013°47,571E
286	14	4631	CTD SBE19+ offline		25 01.11.14	12:07:40	Von Deck	54°28,464N	013°47,561E
286	14	4632	CTD SBE19+ offline		26 01.11.14	12:30:39	Von Deck	54°28,506N	013°41,982E
286	14	4633	CTD SBE19+ offline		27 01.11.14	12:54:45	Von Deck	54°28,503N	013°36,468E
286	14	4634	CTD SBE19+ offline		28 01.11.14	13:13:00	Von Deck	54°25,980N	013°36,490E
286	14	4635	OTM PSN388 Krake		29 01.11.14	13:37:21	Von Deck	54°25,983N	013°42,497E
286	14	4636	CTD SBE19+ offline		30 01.11.14	14:26:07	Von Deck	54°26,206N	013°45,789E
286	14	4637	CTD SBE19+ offline		31 02.11.14	07:17:01	Von Deck	54°23,514N	013°49,020E
286	14	4638	OTM PSN388 Krake		32 02.11.14	07:39:31	Von Deck	54°23,452N	013°46,897E
286	14	4639	CTD SBE19+ offline		33 02.11.14	08:17:20	Von Deck	54°23,744N	013°44,462E
286	14	4640	CTD SBE19+ offline		34 02.11.14	08:26:39	Von Deck	54°23,590N	013°43,294E
286	14	4641	CTD SBE19+ offline		35 02.11.14	08:47:55	Von Deck	54°21,004N	013°45,029E
286	14	4642	CTD SBE19+ offline		36 02.11.14	09:17:07	Von Deck	54°20,987N	013°52,446E
286	14	4643	OTM PSN388 Krake		37 02.11.14	09:21:32	Von Deck	54°21,031N	013°52,603E
286	14	4644	CTD SBE19+ offline		38 02.11.14	10:14:10	Von Deck	54°20,810N	013°56,201E
286	14	4645	CTD SBE19+ offline		39 02.11.14	10:32:53	Von Deck	54°20,997N	014°00,109E
286	14	4646	CTD SBE19+ offline		40 02.11.14	10:53:32	Von Deck	54°18,468N	014°00,048E
286	14	4647	OTM PSN388 Krake		41 02.11.14	11:14:31	Von Deck	54°18,701N	013°59,281E
286	14	4648	CTD SBE19+ offline		42 02.11.14	11:59:28	Von Deck	54°18,473N	014°01,627E
286	14	4649	CTD SBE19+ offline		43 02.11.14	12:36:13	Von Deck	54°18,478N	013°52,571E
286	14	4650	CTD SBE19+ offline		44 02.11.14	13:08:28	Von Deck	54°17,646N	013°45,027E

**Federal Research Institute for Rural Areas,
Forestry and Fisheries**



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Cruise report FRV Solea, Cruise 699 03.02.2015 to 18.02.2015

Ichthyoplankton and fish in the western Baltic

Person in charge: Dr. Daniel Oesterwind

Cruise leaders: Dr. Daniel Oesterwind / Dr. Matthias Schaber (part 1), Dr. Helmut Winkler (part 2)

Background

In the frame of the ICES-coordinated “Baltic International Acoustic Survey”, Germany annually conducts a hydroacoustic survey in September and October to assess the clupeid stocks in the Baltic Sea. The aim of the cruise SO 699 is to complement these existing monitoring programmes with an additional investigation during the spring spawning migration period to reveal migration and pre-spawning aggregation patterns of spring-spawning herring in the Western Baltic Sea. The research is performed within the EU-Project BIO-C³, where herring biology and migration patterns are one important task to cover. Furthermore, we intend to perform an ichthyoplankton sampling focussing on the distribution of herring larvae in the western Baltic Sea. Data from these investigations will be compared with investigations performed by RV Clupea which will investigate herring larvae abundances in important inshore spawning grounds (Greifswalder Bodden) at the same time.

Verteiler:

BLE, Hamburg
Schiffsführung FFS „Solea”
BMELV, Ref. 614
Thünen-Institut, Präsidialbüro
Thünen-Institut, Pressestelle (M. Welling)
Thünen-Institut für Seefischerei
Thünen-Institut für Fischereiökologie
Thünen-Institut für Ostseefischerei
Thünen-Institut, FIZ-Fischerei
Fahrtteilnehmer
Verantw. Seeinsatzplanung, Herr Dr. Rohlf
BFEL Hamburg, FB Fischqualität
IFM-GEOMAR, Kiel
Institut für Fischerei der Landesforschungsanstalt
LA für Landwirtschaft, Lebensmittels. u. Fischerei
BSH, Hamburg

Deutscher Fischerei-Verband e. V., Hamburg
Leibniz-Institut für Ostseeforschung
Doggerbank GmbH
Mecklenburger Hochseefischerei Sassnitz
Kutter- und Küstenfisch Sassnitz
Landesverband der Kutter- und Küstenfischer
Sassnitzer Seefischer
Deutsche Fischfang Union Cuxhaven
Eurobaltic Mukran

The second cruise part was performed to register the biodiversity of the demersal fish fauna around the Island of Rügen within the Bio-C³ frame, therefore fishing with two different gears were conducted at the same stations.

Cruise schedule and preliminary results

Part 1 (03.02.2015 – 13.02.2015)

On the 3th of February FRV Solea was loaded with the scientific equipment at Port Marienehe and steamed North West to the Island of Fehmarn to calibrate the acoustic sensors. Due to problems with the trawl gear sensors a technician was on board to fix the sensors. At the evening FRV Solea shipped back to port Warnemünde to drop off the technician. On the next day, FRV Solea left port Warnemünde in the morning and shipped immediately to the first acoustic transects in SD 24 to start with the acoustic recordings (Fig. 1 & Fig. 2). At the beginning of the transect FRV Solea tried to fish with a Bongo gear, but due to a cable failure no communication between the gear and the vessel was possible. Another try with a gear sensor did not work as well. Therefore the cruise leader decided to cancel the plankton fishing due to the missing Bongo depth information during fishing. At the same day a total of 5 CTD stations and 3 fishing hauls were conducted. From the next day till the 10th of February FRV Solea continued recording along the hydroacoustic transects in SD 24 with the exception of the 8th of February where fishing was interrupted due to bad weather conditions (wind: 18 m/s, wave high 2.5 m) and FRV Solea weathered close to the Island of Møn. Altogether, FRV Solea performed a total of 13 fishing hauls and a total 35 CTD stations in SD 24. At the afternoon of the 10th of February FRV Solea finished the survey in SD 24 and arrived port Warnemünde in the evening, to change some of the scientific personal.

On the next morning FRV Solea started survey work in SD 22 and steamed eastwards with Dr. Matthias Schaber as cruise leader. Within the next 3 days FRV Solea performed 9 fishing hauls and 15 CTD stations. At the afternoon of the 13th of February, the Cruise leader Matthias Schaber was brought to Kiel and FRV Solea shipped eastwards and reached port Marienehe at night.

On the next day the scientific equipment was unload and the next part of the cruise was prepared. A total of eleven different fish species were caught during the acoustic cruise resulting in a total caught biomass of 1046 kg (Tab. 1).

NASC (Nautical Area Scattering Coefficient) values indicating clupeid aggregations were highest in the Arkona Sea (SD 24) with highest measurements north of Rügen Island as well as in the central Arkona Sea. Noteable NASC values were also measured in inshore areas of the western Arkona Sea (Fig. 2). In SD 22, NASC levels were highest in the Mecklenburg Bight and to a lesser degree in southeastern parts of Kiel Bight.

Table 1. Wet weight of the fished species during cruise part one (acoustics).

Species	kg
<i>Aphia minuta</i>	0.029
<i>Clupea harengus</i>	341.763
<i>Cyclopterus lumpus</i>	19.359
<i>Engraulis encrasicolus</i>	3.540
<i>Gadus morhua</i>	33.238
<i>Gasterosteus aculeatus</i>	0.020
<i>Merlangius merlangus</i>	3.930
<i>Platichthys flesus</i>	0.586
<i>Pleuronectes platessa</i>	1.219
<i>Sprattus sprattus</i>	642.700
<i>Syngnathus typhle</i>	0.001
total	1046,385

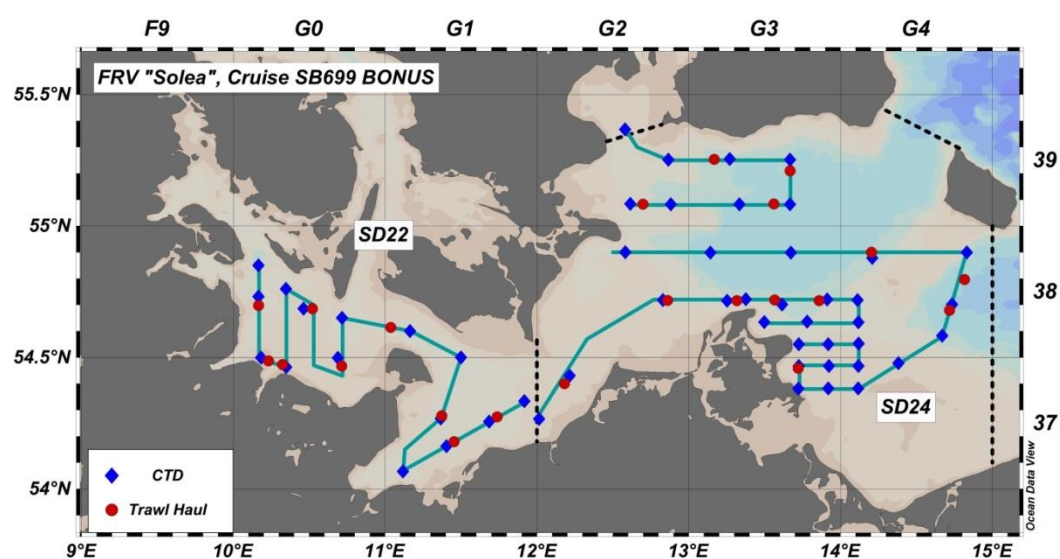


Figure 1. Cruise track with conducted CTD and haul stations.

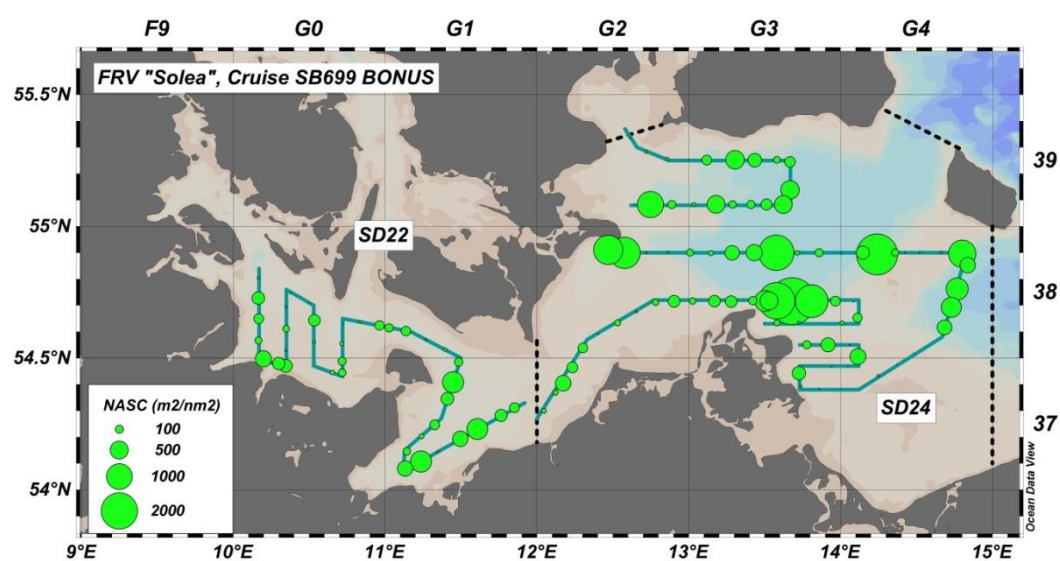


Figure 2. Cruise track and preliminary NASC values.

Part 2 (16.02.2015 – 18.02.2015)

On the 16th of February, the second part of the cruise starts with Dr. Helmut Winkler as cruise leader. FRV Solea left port Marienehe in the morning and steamed eastwards to the fishing area.

During the three cruise days, FRV Solea conducted a total of 12 fishing hauls with a bottom trawl (TV3-520/40-10). In addition to each haul a 20 minute beam trawl and a CTD station were performed resulting in a total of 12 CTD and 12 beam trawl stations. The catch of the bottom trawl was immediately handled while the small fish community in the beam trawl was fixed in alcohol and species will be identified in the lab. A total of 25 different fish species were identified in the bottom trawl. While the number of individuals was dominated by sprat and herring, followed by flounder and cod, the biomass was dominated by cod, followed by herring and flounder (Table 2).

Concerning the round goby, only two individuals could be observed in the beam trawl in the Pomeranian Bay, while close to the Island of Rügen no round goby was caught.

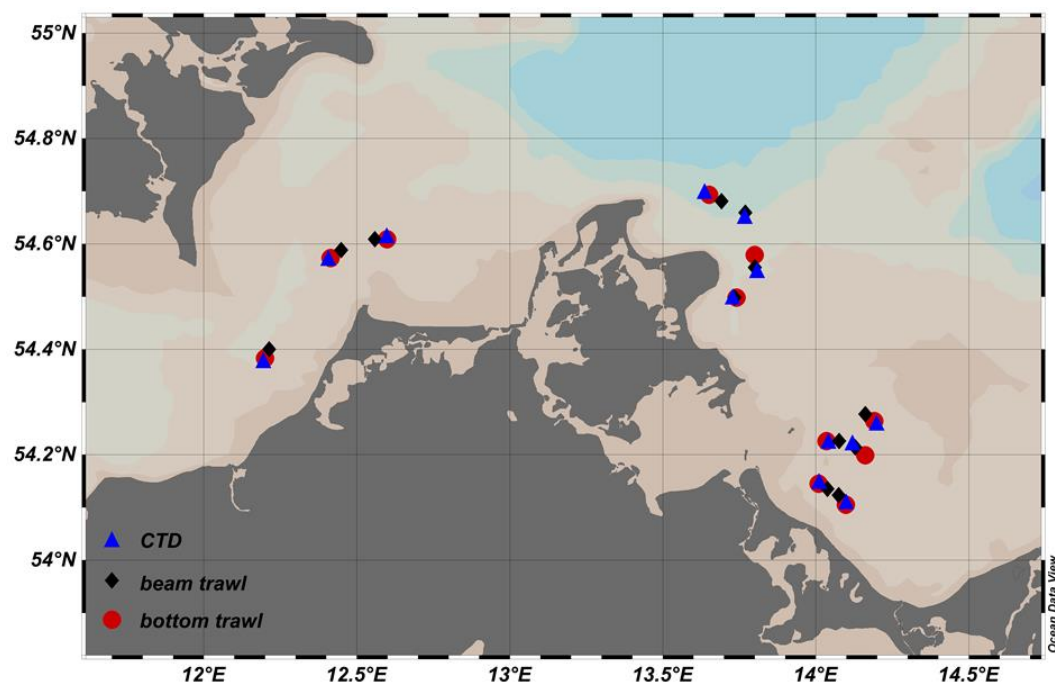


Figure 3. Fishing and CTD stations of the second cruise part.

Table 2. Wet weight of the fished species during cruise part two (bottom trawl).

Species	kg
<i>Clupea harengus</i>	244.472
<i>Gadus morhua</i>	467.010
<i>Perch</i>	122.160
<i>Platichthys flesus</i>	152.650
<i>Pleuronectes platessa</i>	19.847
<i>Limanda limanda</i>	107.362
<i>Sprattus sprattus</i>	46.038
others	51.700
total	1211.239

Concerning the species presence in the bottom trawls *S. sprattus*, *C. harengus* and *P. flesus* were common in every haul, while other species for example *C. maraena*, *G. cernua* and *S. rhombus* could be identified only in single hauls (Annex 2).

Cruise participants

- | | | |
|----------------|-------------------------|---|
| 1. Cruise part | Dr. Daniel Oesterwind | Senior Scientist (TI-OF, 03.02. – 10.02.15) |
| | Dr. Matthias Schaber | Senior Scientist (TI-SF, 03.02. – 13.02.15) |
| | Ina Hennings | Technician (TI-OF, 03.02. – 13.02.15) |
| | Nadja Schneider | Technician (TI-OF, 03.02. – 13.02.15) |
| | Peter Schael | Technician (TI-OF, 10.02. – 13.02.15) |
| | Tim Kirchner | Student (03.02. – 13.02.15) |
| | Vincent Siebert | Student (10.02. – 13.02.15) |
| | Farina Reif | Student (03.02. – 10.02.15) |
| | Ulf Böttcher | Technician (03.02.2015) |
| 2. Cruise part | Dr. Helmut Winkler | Senior Scientist (University of Rostock) |
| | Dennis Wittmann | Student |
| | Robert Rölling | Student |
| | Frederik Kaiser | Student |
| | Christian Küchenmeister | Student |

I hereby thank all participants, the captain and the crew of FRV Clupea for their cooperation and support.

Rostock, 27.04.2015

Dr. Daniel Oesterwind
(Scientist in charge)

Annex 1

A1. Stationsinformation

Equipment	Operation	Station number	Datum	time	Geog.Breite	Geog.Länge
CTD Seabird	139	78	03.02.15	14:33	54°21,360N	011°16,315E
CTD Seabird	140	79	03.02.15	14:39	54°21,333N	011°16,330E
CTD Seabird	141	80	04.02.15	7:53	54°15,919N	012°00,884E
Bongo	142	1	04.02.15	8:03	54°16,055N	012°00,757E
Bongo	143	2	04.02.15	8:10	54°16,280N	012°00,785E
Pelagic Trawl 'Krake'	144	1	04.02.15	9:43	54°24,026N	012°10,894E
CTD Seabird	145	81	04.02.15	10:30	54°25,804N	012°12,945E
CTD Seabird	146	82	04.02.15	13:35	54°43,037N	012°49,743E
Pelagic Trawl 'Krake'	147	2	04.02.15	13:56	54°42,996N	012°51,675E
CTD Seabird	148	83	04.02.15	15:51	54°42,848N	013°15,097E
Pelagic Trawl 'Krake'	149	3	04.02.15	16:20	54°42,968N	013°19,049E
CTD Seabird	150	84	04.02.15	17:09	54°43,221N	013°22,618E
Pelagic Trawl 'Krake'	151	4	05.02.15	8:10	54°43,155N	013°34,024E
CTD Seabird	152	85	05.02.15	9:04	54°42,047N	013°36,810E
Pelagic Trawl 'Krake'	153	5	05.02.15	10:29	54°42,984N	013°51,527E
CTD Seabird	154	86	05.02.15	11:16	54°43,213N	013°54,593E
CTD Seabird	155	87	05.02.15	12:08	54°43,098N	014°06,711E
CTD Seabird	156	88	05.02.15	12:48	54°38,015N	014°07,030E
CTD Seabird	157	89	05.02.15	14:06	54°38,218N	013°46,811E
CTD Seabird	158	90	05.02.15	15:10	54°38,020N	013°29,846E
CTD Seabird	159	91	05.02.15	16:17	54°33,038N	013°43,446E
CTD Seabird	160	92	05.02.15	17:05	54°32,998N	013°55,194E
CTD Seabird	161	93	05.02.15	17:53	54°33,123N	014°07,123E
CTD Seabird	162	94	05.02.15	18:33	54°28,007N	014°07,003E
CTD Seabird	163	95	05.02.15	19:19	54°28,029N	013°55,357E
CTD Seabird	164	96	06.02.15	8:39	54°27,954N	013°43,472E
Pelagic Trawl 'Krake'	165	6	06.02.15	8:55	54°27,540N	013°43,311E
CTD Seabird	166	97	06.02.15	10:25	54°22,863N	013°43,383E
CTD Seabird	167	98	06.02.15	11:13	54°22,901N	013°55,183E
CTD Seabird	168	99	06.02.15	12:03	54°22,882N	014°06,963E
CTD Seabird	169	100	06.02.15	13:16	54°28,627N	014°22,920E
CTD Seabird	170	101	06.02.15	14:36	54°34,895N	014°40,263E
Pelagic Trawl 'Krake'	171	7	06.02.15	15:22	54°40,741N	014°43,057E
Pelagic Trawl 'Krake'	171	7	06.02.15	15:22	54°40,746N	014°43,059E
CTD Seabird	172	102	06.02.15	16:04	54°42,001N	014°44,160E
Pelagic Trawl 'Krake'	173	8	06.02.15	16:48	54°47,738N	014°47,380E
Pelagic Trawl 'Krake'	175	10	07.02.15	8:19	54°53,978N	014°14,420E
CTD Seabird	176	103	07.02.15	9:10	54°52,602N	014°12,712E
CTD Seabird	177	104	07.02.15	12:03	54°53,788N	013°40,365E
CTD Seabird	178	105	07.02.15	14:44	54°53,803N	013°08,697E

CTD Seabird	179	106	07.02.15	17:51	54°53,942N	012°34,964E
CTD Seabird	180	107	09.02.15	7:40	55°22,021N	012°34,990E
CTD Seabird	181	108	09.02.15	9:07	55°15,058N	012°52,047E
Pelagic Trawl 'Krake'	182	11	09.02.15	10:16	55°15,154N	013°10,053E
CTD Seabird	183	109	09.02.15	11:29	55°15,202N	013°16,278E
CTD Seabird	184	110	09.02.15	13:00	55°15,140N	013°40,149E
Pelagic Trawl 'Krake'	185	12	09.02.15	13:26	55°12,607N	013°40,109E
CTD Seabird	186	111	09.02.15	14:47	55°04,847N	013°40,132E
Pelagic Trawl 'Krake'	187	13	09.02.15	15:26	55°05,062N	013°33,651E
CTD Seabird	188	112	09.02.15	17:40	55°04,891N	013°20,084E
CTD Seabird	189	113	10.02.15	8:51	55°04,934N	012°52,964E
CTD Seabird	190	114	10.02.15	9:52	55°05,046N	012°37,016E
Pelagic Trawl 'Krake'	191	14	10.02.15	10:17	55°04,995N	012°41,936E
CTD Seabird	192	115	11.02.15	7:34	54°19,955N	011°55,067E
Pelagic Trawl 'Krake'	193	15	11.02.15	8:27	54°16,435N	011°44,362E
CTD Seabird	194	116	11.02.15	9:12	54°15,317N	011°41,239E
Pelagic Trawl 'Krake'	195	16	11.02.15	10:13	54°10,781N	011°27,303E
CTD Seabird	196	117	11.02.15	10:57	54°09,698N	011°24,305E
CTD Seabird	197	118	11.02.15	12:13	54°03,952N	011°07,090E
CTD Seabird	198	119	11.02.15	13:54	54°15,986N	011°22,119E
Pelagic Trawl 'Krake'	199	17	11.02.15	14:07	54°16,656N	011°22,419E
CTD Seabird	200	120	11.02.15	16:01	54°30,001N	011°29,912E
CTD Seabird	201	121	11.02.15	17:28	54°36,039N	011°09,852E
Pelagic Trawl 'Krake'	202	18	12.02.15	7:36	54°36,844N	011°02,221E
CTD Seabird	203	122	12.02.15	9:43	54°38,977N	010°43,019E
Pelagic Trawl 'Krake'	204	19	12.02.15	11:01	54°28,029N	010°42,829E
CTD Seabird	205	123	12.02.15	11:45	54°29,905N	010°41,352E
Pelagic Trawl 'Krake'	206	20	12.02.15	14:20	54°41,072N	010°31,263E
CTD Seabird	207	124	12.02.15	15:05	54°41,139N	010°27,787E
CTD Seabird	208	125	12.02.15	16:16	54°45,565N	010°20,913E
CTD Seabird	209	126	12.02.15	18:08	54°27,748N	010°20,928E
CTD Seabird	210	127	13.02.15	7:33	54°51,061N	010°10,045E
Pelagic Trawl 'Krake'	211	21	13.02.15	8:45	54°41,875N	010°09,966E
CTD Seabird	212	128	13.02.15	9:30	54°43,911N	010°10,050E
Pelagic Trawl 'Krake'	213	22	13.02.15	11:21	54°29,246N	010°13,907E
CTD Seabird	214	129	13.02.15	12:11	54°29,986N	010°11,005E
Pelagic Trawl 'Krake'	215	23	13.02.15	12:52	54°28,408N	010°19,517E
CTD Seabird	216	130	16.02.15	10:02	54°22,583N	012°11,718E
Bottom Trawl 'TV3/520'	217	62	16.02.15	10:10	54°22,974N	012°12,012E
Beam Trawl 2 m	218	1	16.02.15	11:07	54°24,021N	012°12,858E
Beam Trawl 2 m	218	1	16.02.15	11:27	54°23,372N	012°12,330E
CTD Seabird	219	131	16.02.15	14:01	54°34,218N	012°24,443E
Bottom Trawl 'TV3/520'	220	63	16.02.15	14:09	54°34,391N	012°24,843E
Beam Trawl 2 m	221	2	16.02.15	15:01	54°35,285N	012°26,948E

Beam Trawl 2 m	221	2	16.02.15	15:21	54°34,753N	012°26,000E
CTD Seabird	222	132	16.02.15	16:12	54°36,784N	012°35,854E
Beam Trawl 2 m	223	3	16.02.15	16:19	54°36,537N	012°35,950E
Beam Trawl 2 m	223	3	16.02.15	16:39	54°35,671N	012°35,979E
Bottom Trawl 'TV3/520'	224	64	16.02.15	16:58	54°36,553N	012°35,951E
Bottom Trawl 'TV3/520'	225	65	17.02.15	7:31	54°08,706N	014°00,563E
Beam Trawl 2 m	226	4	17.02.15	8:20	54°08,123N	014°02,301E
Beam Trawl 2 m	226	4	17.02.15	8:40	54°08,589N	014°00,902E
CTD Seabird	227	133	17.02.15	8:58	54°08,846N	014°00,642E
Beam Trawl 2 m	228	5	17.02.15	9:15	54°07,374N	014°04,518E
Beam Trawl 2 m	228	5	17.02.15	9:35	54°06,854N	014°05,486E
CTD Seabird	229	134	17.02.15	9:46	54°06,487N	014°05,925E
Bottom Trawl 'TV3/520'	230	66	17.02.15	9:57	54°06,321N	014°05,853E
CTD Seabird	231	135	17.02.15	11:12	54°13,364N	014°02,455E
Bottom Trawl 'TV3/520'	232	67	17.02.15	12:01	54°13,547N	014°02,127E
Beam Trawl 2 m	233	6	17.02.15	12:48	54°13,567N	014°04,533E
Beam Trawl 2 m	233	6	17.02.15	13:08	54°13,595N	014°03,320E
Beam Trawl 2 m	234	7	17.02.15	13:44	54°12,835N	014°07,768E
Beam Trawl 2 m	234	7	17.02.15	14:04	54°12,316N	014°08,944E
Bottom Trawl 'TV3/520'	235	68	17.02.15	14:20	54°11,966N	014°09,657E
CTD Seabird	236	136	17.02.15	15:02	54°13,203N	014°07,189E
CTD Seabird	237	137	17.02.15	15:28	54°15,573N	014°11,927E
Bottom Trawl 'TV3/520'	238	69	17.02.15	15:36	54°15,839N	014°11,485E
Beam Trawl 2 m	239	8	17.02.15	16:24	54°16,601N	014°09,738E
Beam Trawl 2 m	239	8	17.02.15	16:44	54°16,027N	014°11,031E
Beam Trawl 2 m	240	9	18.02.15	7:32	54°29,876N	013°44,075E
Beam Trawl 2 m	240	9	18.02.15	7:52	54°29,852N	013°45,869E
CTD Seabird	241	138	18.02.15	8:11	54°29,836N	013°43,705E
Bottom Trawl 'TV3/520'	242	70	18.02.15	8:19	54°29,852N	013°44,449E
Bottom Trawl 'TV3/520'	243	71	18.02.15	9:49	54°34,731N	013°47,993E
CTD Seabird	244	139	18.02.15	10:34	54°32,830N	013°48,457E
Beam Trawl 2 m	245	10	18.02.15	10:43	54°33,281N	013°48,082E
Beam Trawl 2 m	245	10	18.02.15	11:03	54°34,223N	013°48,043E
CTD Seabird	246	140	18.02.15	11:57	54°39,007N	013°46,107E
Beam Trawl 2 m	247	11	18.02.15	12:06	54°39,565N	013°46,210E
Beam Trawl 2 m	247	11	18.02.15	12:26	54°40,440N	013°46,737E
Bottom Trawl 'TV3/520'	248	72	18.02.15	12:48	54°39,773N	013°46,385E
CTD Seabird	249	141	18.02.15	14:05	54°41,815N	013°38,218E
Bottom Trawl 'TV3/520'	250	73	18.02.15	14:14	54°41,580N	013°39,051E
Beam Trawl 2 m	251	12	18.02.15	15:05	54°40,834N	013°41,500E
Beam Trawl 2 m	251	12	18.02.15	15:25	54°41,276N	013°40,116E

Annex 2

A2. Presence (P) and Frenquence (F) for each species in the bottom trawls. Presence: number of total hauls (12); Frenquence: percentage of all individuals (13 474)

Species	P	F (%)
marine		
<i>Zoarces viviparus</i>	6	0,1
<i>Hippoglossoides platessoides</i>	2	0
<i>Gadus morhua</i>	11	8,7
<i>Platichthys flesus</i>	12	11,3
<i>Scophthalmus rhombus</i>	1	0
<i>Aphia minuta</i>	1	0,2
<i>Clupea harengus</i>	12	37,7
<i>Limanda limanda</i>	9	4,9
<i>Hyperoplus lanceolatus</i>	1	0
<i>Ammodytes tobianus</i>	3	0
<i>Pomatoschistus minutus</i>	3	0,4
<i>Pleuronectes platessa</i>	11	0,9
<i>Neogobius melanostomus</i>	2	0
<i>Cyclopterus lumpus</i>	2	0,1
<i>Syngnathus typhle</i>	1	0
<i>Myoxocephalus scorpius</i>	7	0,2
<i>Sprattus sprattus</i>	12	35,2
<i>Psetta maxima</i>	7	0,2
<i>Agonus cataphractus</i>	2	0
<i>Merlangius merlangius</i>	4	0,2
diadromous		
<i>Coregonus maraena</i>	1	0
<i>Osmerus eperlanus</i>	6	0,2
limnic		
<i>Perca fluviatilis</i>	5	3,6
<i>Gymnocephalus cernua</i>	1	0
<i>Sander lucioperca</i>	5	0,3

Cruise Report

FRV Clupea Cruise No. 290, 10.03.2015 – 26.06.2015

BIO-C³ herring migration

Research Area & Methods

Compared to the last year, the acoustic transects were fixed (Fig 1) and 5 cruise parts with a trip duration between 3 and 4 days were performed between the 10th of March and the 26th of June within the framework of the FRV Clupea Cruise Number 290.

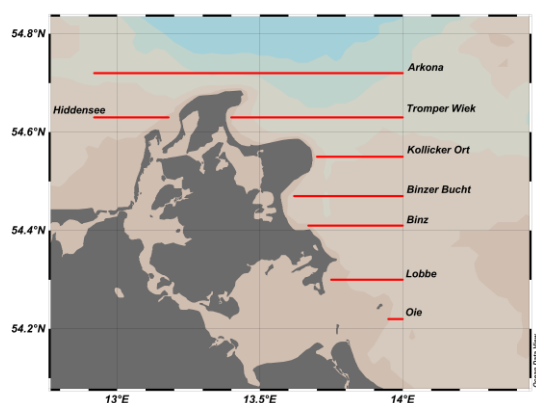


Figure 1. Planned acoustic transects for Clupea Cruise 290.

On each transect acoustic records were performed with an EK60 and fishing stations were conducted with a modified pelagic trawl called 'Krake'. At the beginning and at the end of each transect a CTD station with a Seabird CTD was done. Additional CTD data were recorded at least in the middle of the transect and / or at every fishing station. All fish were weight, individual length of a group of subsamples was measured and for a subsample of herring individual fish data (age, maturity, gonad weight etc.) were noticed.

Verteiler:

BLE, Hamburg
 Schiffsführung FFS „Clupea“
 BMEL Ref. 614
 TI, Präsidialbüro (M. Welling)
 TI, Verwaltung Hamburg
 TI, FI
 TI, OF
 TI, SF
 TI, FIZ-Fischerei
 TI, PR
 BFEL Hamburg, FB Fischqualität
 IFM-GEOMAR, Kiel
 Institut für Fischerei der Landesforschungsanstalt
 LA für Landwirtschaft, Lebensmittels. u. Fischerei
 BSH, Hamburg

Deutscher Fischerei-Verband e. V., Hamburg
 Leibniz Institut für Ostseeforschung
 Doggerbank GmbH
 Mecklenburger Hochseefischerei Sassnitz
 Kutter- und Küstenfisch Sassnitz
 Landesverband der Kutter- und Küstenfischer
 Sassnitzer Seefischer
 Deutsche Fischfang Union Cuxhaven
 Fahrtteilnehmer
 Schiffseinsatzplanung, Herr Dr. Rohlf

Cruise objectives

In the frame of the ICES-coordinated “Baltic International Acoustic Survey”, Germany annually conducts a hydroacoustic survey in September and October to assess the clupeid stocks in the Baltic Sea. The aim of the cruise CLU290 was to complement these existing monitoring programmes with an additional investigation during the spring spawning migration period to reveal migration and pre-spawning aggregation patterns of spring-spawning herring in the Western Baltic Sea at the Island of Rügen. The research is performed within the EU-Project BIO-C³, where herring biology and migration patterns are an important task to cover.

Preliminary Results

The first cruise started on the 10th of March and ended at the 13th of March (Fig. 2). A total of six fishery hauls and 24 CTD stations were performed. Herring was the dominant fish species with respect to the total catch composition and dominated the catch biomass in the eastern area of the Island of Rügen. During the cruise we had some problems with the CTD and the DATADIS recordings. Therefore DATADIS data are incomplete (see Annex).

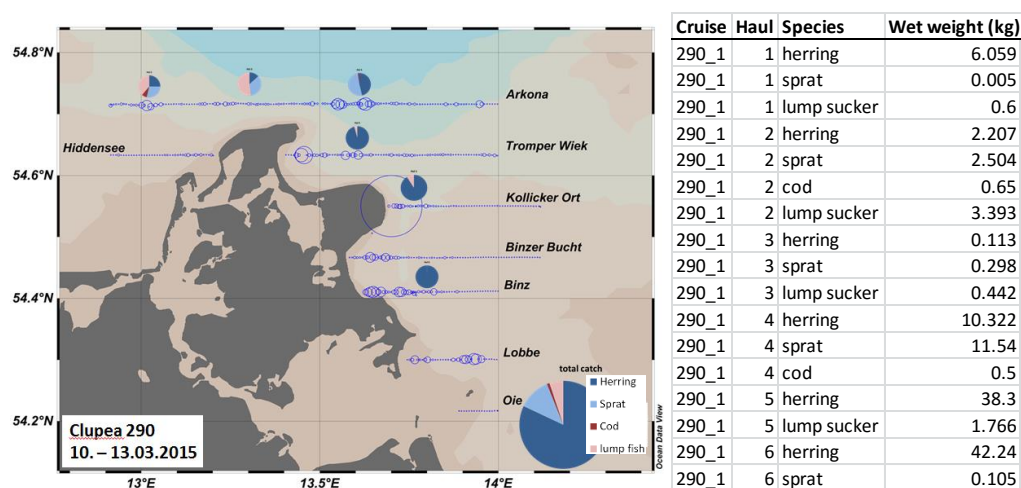


Figure 2. Recorded acoustic transects during the first cruise. NASC-values (blue circles) and catch composition (pie charts) as well as catch weights (right).

The second cruise part was performed between the 26th of March and 28th of March. Due the low acoustic signals (NASC values) the cruise lasts three days and a total of 6 fishery hauls were performed. In addition 22 CTD stations were completed. The total catch was dominated by sprat followed by herring, while three of six hauls were dominated by each species. A clear distribution pattern of herring is not visible on the first view. Further analyses have to be performed (Fig. 3).

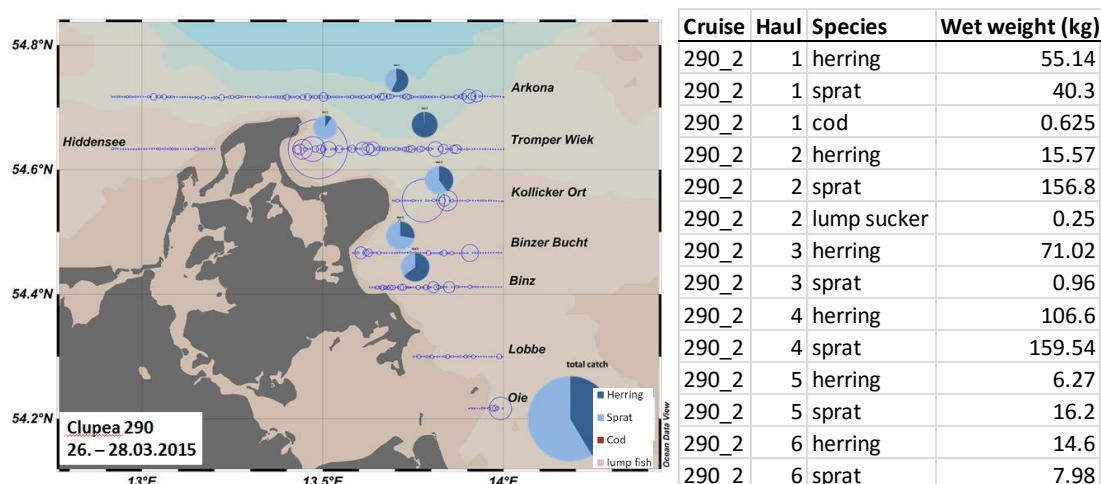


Figure 3. Recorded acoustic transects during the second cruise. NASC-values (blue circles) and catch composition (pie charts) as well as catch weights (right).

The third cruise part took place between the 10th and 12th of April. During the cruise 7 fishery hauls were performed and 23 CTD station conducted. The total catch composition was dominated by herring followed by sprat. This is reflected by the number of hauls dominated by herring (Fig. 4).

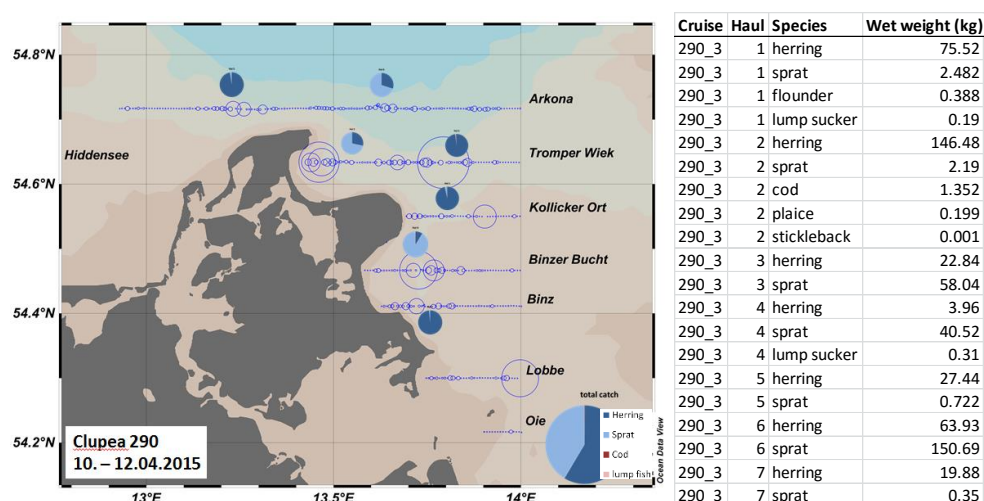


Figure 4. Recorded acoustic transects during the third cruise. NASC-values (blue circles) and catch composition (pie charts) as well as catch weights (right).

The fourth cruise part started at the end of April (24.04 – 26.04). A total of seven hauls and 21 CTD stations were conducted. The total catch composition was dominated by sprat but three hauls were dominated by herring (Fig. 5).

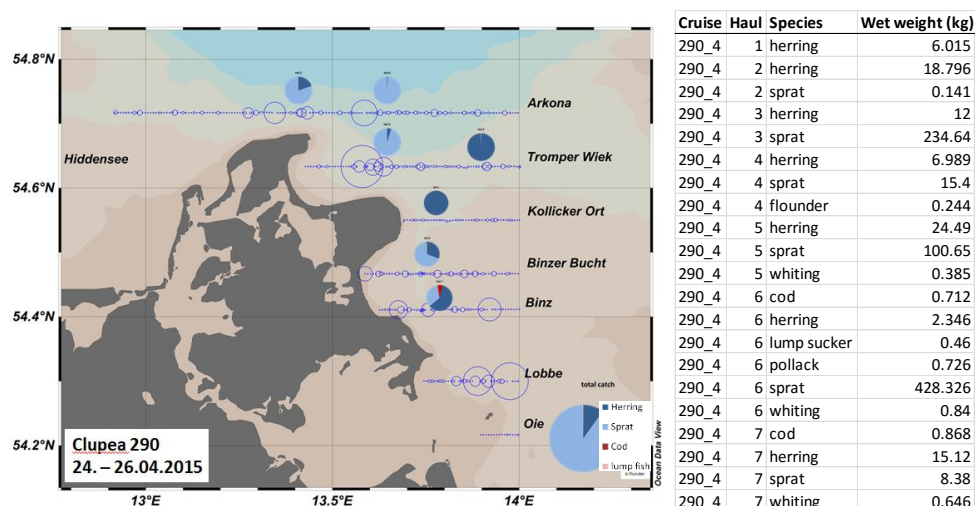


Figure 5. Recorded acoustic transects during the fourth cruise. NASC-values (blue circles) and catch composition (pie charts) as well as catch weights (right).

The last cruise part was performed during the 7th and 10th of May. Eight hauls and 25 CTD stations were completed. The total catch was dominated by sprat while herring dominated two hauls in the north western part of the investigation area (Fig. 6).

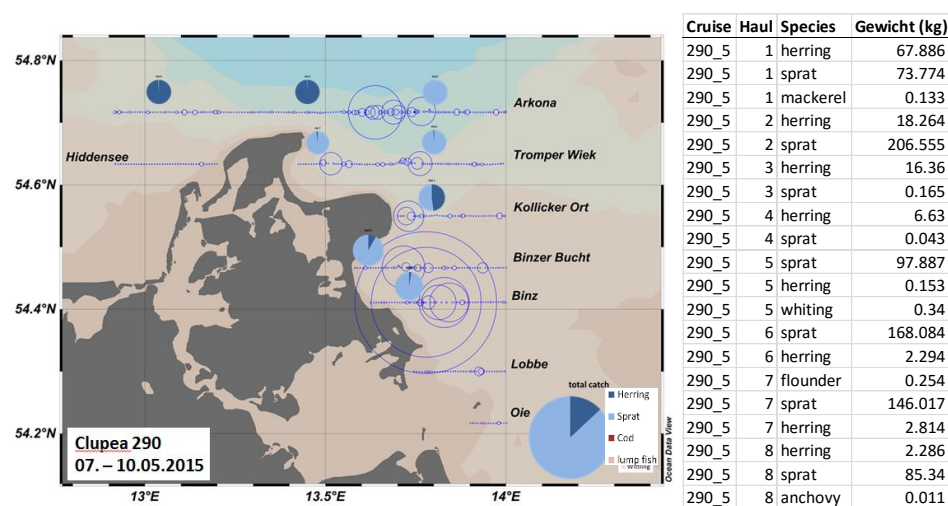


Figure 6. Recorded acoustic transects during the fifth cruise. NASC-values (blue circles) and catch composition (pie charts) as well as catch weights (right).

Metadata 290_1

Station	Device	Date	Starting Time	Starting Position	
8	CTD SBE19+	11.03.15	09:34:08	54°37,948N	013°12,064E
9	CTD SBE19+	11.03.15	10:40:06	54°37,971N	012°54,839E
10	CTD SBE19+	11.03.15	11:15:58	54°42,918N	012°54,832E
11	OTM Krake	11.03.15	11:31:07	54°42,979N	012°57,279E
11	CTD SBE19+	11.03.15	12:26:54	54°42,715N	013°01,385E
13	OTM Krake	11.03.15	13:21:23	54°42,998N	013°15,208E
13	CTD SBE19+	11.03.15	14:08:50	54°42,897N	013°19,322E
15	CTD SBE19+	11.03.15	14:51:11	54°43,007N	013°29,986E
16	OTM Krake	12.03.15	08:26:09	54°42,955N	013°33,251E
16	CTD SBE19+	12.03.15	09:19:13	54°42,935N	013°37,081E
18	CTD SBE19+	12.03.15	10:51:59	54°43,004N	013°59,982E

19	CTD SBE19+	12.03.15	11:25:22	54°37,966N	013°59,925E
20	CTD SBE19+	12.03.15	12:41:41	54°38,016N	013°38,547E
21	OTM Krake	12.03.15	12:46:18	54°37,984N	013°38,391E
22	CTD SBE19+	12.03.15	14:16:37	54°38,030N	013°23,929E
23	CTD SBE19+	13.03.15	05:43:14	54°24,638N	013°37,570E
24	OTM Krake	13.03.15	06:15:13	54°24,614N	013°44,166E
24	CTD SBE19+	13.03.15	06:57:09	54°24,567N	013°45,481E
26	CTD SBE19+	13.03.15	07:53:17	54°24,737N	013°59,964E
27	CTD SBE19+	13.03.15	08:37:06	54°18,010N	014°00,004E
28	CTD SBE19+	13.03.15	09:33:49	54°18,014N	013°44,516E
29	CTD SBE19+	13.03.15	10:39:40	54°13,034N	013°59,929E
30	CTD SBE19+	13.03.15	11:05:36	54°13,015N	013°53,342E

Metadata 290_2

Station	Device	Date	Starting Time	Starting Position	
1	CTD SBE19+	26.03.15	08:32:52	54°43,000N	013°59,981E
2	CTD SBE19+	26.03.15	09:23:15	54°43,010N	013°46,983E
2	OTM Krake	26.03.15	09:33:59	54°43,014N	013°46,062E
3	CTD SBE19+	26.03.15	10:19:53	54°43,100N	013°42,655E
4	CTD SBE19+	26.03.15	13:07:07	54°43,028N	012°55,053E
5	CTD SBE19+	26.03.15	13:41:43	54°38,061N	012°55,097E
6	CTD SBE19+	26.03.15	14:43:14	54°38,038N	013°12,426E
1	CTD SBE19+	27.03.15	08:06:23	54°37,968N	013°25,641E
2	OTM Krake	27.03.15	08:20:58	54°38,000N	013°28,386E
3	CTD SBE19+	27.03.15	09:36:31	54°37,980N	013°41,996E
4	OTM Krake	27.03.15	09:48:33	54°37,981N	013°44,064E
5	CTD SBE19+	27.03.15	11:12:04	54°37,990N	014°00,042E
6	CTD SBE19+	27.03.15	11:47:55	54°32,997N	013°59,961E
7	OTM Krake	27.03.15	12:20:52	54°33,005N	013°51,524E
8	CTD SBE19+	27.03.15	13:20:52	54°33,014N	013°41,630E
9	CTD SBE19+	27.03.15	14:03:59	54°28,001N	013°34,867E
10	OTM Krake	27.03.15	14:31:58	54°27,988N	013°42,090E
11	CTD SBE19+	27.03.15	15:11:16	54°28,002N	013°43,583E
1	CTD SBE19+	28.03.15	06:53:42	54°28,035N	013°43,950E
2	CTD SBE19+	28.03.15	07:52:47	54°27,991N	014°00,054E
3	CTD SBE19+	28.03.15	08:14:32	54°24,728N	013°59,988E
4	OTM Krake	28.03.15	09:03:27	54°24,666N	013°46,705E
5	CTD SBE19+	28.03.15	09:41:05	54°24,674N	013°44,562E
6	CTD SBE19+	28.03.15	10:10:56	54°24,664N	013°37,492E
7	CTD SBE19+	28.03.15	11:10:40	54°18,001N	013°44,660E
8	CTD SBE19+	28.03.15	12:06:49	54°17,994N	013°59,986E
9	CTD SBE19+	28.03.15	12:38:47	54°12,969N	013°59,996E
10	CTD SBE19+	28.03.15	13:05:20	54°13,012N	013°53,418E

Metadata 290_3

Station	Device	Date	Starting Time	Starting Position	
1	CTD SBE19+	10.04.15	06:42:38	54°33,037N	013°41,419E
2	OTM Krake	10.04.15	07:29:24	54°33,006N	013°46,228E

3	CTD SBE19+	10.04.15	08:11:59	54°33,035N	013°49,087E
4	CTD SBE19+	10.04.15	08:53:24	54°33,019N	014°00,011E
5	CTD SBE19+	10.04.15	09:25:58	54°37,970N	014°00,010E
6	OTM Krake	10.04.15	10:02:48	54°38,001N	013°50,675E
7	CTD SBE19+	10.04.15	10:39:01	54°37,986N	013°47,940E
8	OTM Krake	10.04.15	11:27:08	54°38,006N	013°34,870E
9	CTD SBE19+	10.04.15	12:02:33	54°38,056N	013°32,121E
10	CTD SBE19+	10.04.15	12:29:02	54°38,000N	013°25,636E
11	CTD SBE19+	10.04.15	14:14:07	54°27,995N	013°34,867E
12	OTM Krake	10.04.15	14:41:29	54°27,974N	013°41,719E
13	CTD SBE19+	10.04.15	15:18:30	54°28,084N	013°43,807E
1	CTD SBE19+	11.04.15	08:50:36	54°42,984N	012°55,076E
2	OTM Krake	11.04.15	10:25:49	54°42,998N	013°14,206E
3	CTD SBE19+	11.04.15	11:14:52	54°42,900N	013°17,886E
4	CTD SBE19+	11.04.15	11:49:06	54°43,015N	013°26,340E
5	OTM Krake	11.04.15	12:22:07	54°43,003N	013°34,498E
6	CTD SBE19+	11.04.15	13:04:53	54°43,378N	013°37,094E
7	CTD SBE19+	11.04.15	14:30:55	54°43,001N	014°00,055E
1	CTD SBE19+	12.04.15	06:04:52	54°28,004N	013°44,028E
2	CTD SBE19+	12.04.15	07:04:21	54°27,987N	014°00,050E
3	CTD SBE19+	12.04.15	07:27:36	54°24,682N	014°00,010E
4	OTM Krake	12.04.15	08:17:28	54°24,667N	013°46,770E
5	CTD SBE19+	12.04.15	08:55:30	54°24,834N	013°44,466E
6	CTD SBE19+	12.04.15	09:25:09	54°24,658N	013°37,453E
7	CTD SBE19+	12.04.15	10:25:45	54°17,992N	013°44,772E
7	CTD SBE19+	12.04.15	11:21:51	54°17,976N	014°00,110E
8	CTD SBE19+	12.04.15	11:53:58	54°12,992N	013°59,995E
10	CTD SBE19+	12.04.15	12:22:32	54°13,001N	013°53,331E

Metadata 290_4

Station	Device	Date	Starting Time	Starting Position	
1	CTD SBE19+	24.04.15	06:00:29	54°33,026N	013°41,459E
2	OTM Krake	24.04.15	06:16:27	54°32,998N	013°44,926E
3	CTD SBE19+	24.04.15	07:38:58	54°32,986N	013°59,906E
4	CTD SBE19+	24.04.15	08:11:39	54°37,950N	014°00,044E
5	OTM Krake	24.04.15	08:36:48	54°37,993N	013°54,227E
6	CTD SBE19+	24.04.15	09:17:40	54°37,886N	013°51,488E
7	CTD SBE19+	24.04.15	10:02:16	54°37,987N	013°39,691E
8	OTM Krake	24.04.15	10:11:12	54°37,980N	013°38,584E
9	CTD SBE19+	24.04.15	11:24:57	54°37,994N	013°25,630E
10	OTM Krake	24.04.15	12:59:32	54°28,027N	013°44,763E
11	CTD SBE19+	24.04.15	13:31:37	54°27,937N	013°42,449E
12	CTD SBE19+	24.04.15	14:02:17	54°28,003N	013°34,894E
1	CTD SBE19+	25.04.15	08:50:12	54°42,985N	012°55,009E
2	OTM Krake	25.04.15	10:25:21	54°43,028N	013°18,327E
3	CTD SBE19+	25.04.15	11:24:56	54°43,023N	013°22,704E
4	OTM Krake	25.04.15	12:15:55	54°42,995N	013°36,304E
5	CTD SBE19+	25.04.15	13:03:06	54°43,025N	013°39,900E

6	CTD SBE19+	25.04.15	14:18:45	54°42,996N	014°00,096E
1	CTD SBE19+	26.04.15	04:58:07	54°27,983N	013°44,148E
2	CTD SBE19+	26.04.15	05:56:47	54°28,006N	014°00,029E
3	CTD SBE19+	26.04.15	06:19:28	54°24,679N	014°00,028E
4	OTM Krake	26.04.15	07:08:55	54°24,660N	013°46,704E
5	CTD SBE19+	26.04.15	07:50:43	54°24,630N	013°44,659E
6	CTD SBE19+	26.04.15	08:19:43	54°24,627N	013°37,475E
7	CTD SBE19+	26.04.15	09:20:33	54°18,011N	013°44,703E
8	CTD SBE19+	26.04.15	10:16:37	54°17,999N	014°00,054E
9	CTD SBE19+	26.04.15	10:48:41	54°13,018N	014°00,004E
10	CTD SBE19+	26.04.15	11:15:31	54°12,992N	013°53,277E

Metadata 290_5

Station	Bem. Gerät	Date	Starting Time	Starting Position	
1	CTD SBE19+	07.05.15	07:06:08	54°32,977N	013°41,653E
2	OTM Krake	07.05.15	07:18:21	54°32,983N	013°43,970E
3	CTD SBE19+	07.05.15	08:18:27	54°33,065N	013°48,388E
4	CTD SBE19+	07.05.15	09:03:02	54°33,010N	013°59,985E
5	CTD SBE19+	07.05.15	09:37:17	54°28,017N	014°00,017E
6	CTD SBE19+	07.05.15	10:37:15	54°28,010N	013°43,952E
7	OTM Krake	07.05.15	10:43:56	54°27,981N	013°44,152E
8	CTD SBE19+	07.05.15	11:52:11	54°27,993N	013°34,901E
9	CTD SBE19+	07.05.15	12:18:15	54°24,646N	013°37,458E
1	CTD SBE19+	08.05.15	08:12:53	54°38,030N	013°12,442E
2	CTD SBE19+	08.05.15	09:16:39	54°38,009N	012°55,000E
3	CTD SBE19+	08.05.15	09:51:31	54°43,006N	012°54,987E
4	OTM Krake	08.05.15	10:11:07	54°43,009N	012°59,393E
5	CTD SBE19+	08.05.15	11:01:02	54°43,016N	013°03,487E
6	OTM Krake	08.05.15	12:17:08	54°43,006N	013°24,364E
7	CTD SBE19+	08.05.15	13:06:01	54°42,969N	013°28,573E
8	CTD SBE19+	08.05.15	14:07:46	54°43,025N	013°45,054E
1	CTD SBE19+	09.05.15	06:55:51	54°42,998N	013°44,972E
2	OTM Krake	09.05.15	07:05:22	54°43,052N	013°45,437E
3	CTD SBE19+	09.05.15	08:34:10	54°43,026N	013°59,984E
4	CTD SBE19+	09.05.15	09:12:32	54°38,011N	014°00,062E
5	OTM Krake	09.05.15	10:04:40	54°38,017N	013°46,706E
6	CTD SBE19+	09.05.15	10:46:01	54°38,185N	013°43,738E
7	OTM Krake	09.05.15	11:34:11	54°38,000N	013°32,275E
8	CTD SBE19+	09.05.15	12:15:24	54°38,144N	013°29,567E
9	CTD SBE19+	09.05.15	12:35:39	54°37,987N	013°25,433E
1	OTM Krake	10.05.15	05:05:15	54°24,687N	013°43,853E
2	CTD SBE19+	10.05.15	05:50:37	54°24,644N	013°45,869E
3	CTD SBE19+	10.05.15	06:44:19	54°24,653N	014°00,038E
4	CTD SBE19+	10.05.15	07:54:06	54°17,987N	013°44,693E
5	CTD SBE19+	10.05.15	08:51:05	54°18,007N	014°00,011E
6	CTD SBE19+	10.05.15	09:24:12	54°13,039N	014°00,013E
7	CTD SBE19+	10.05.15	09:53:15	54°12,992N	013°53,267E

Thünen-Institute of Baltic Sea Fisheries

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12.09.2016

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Cruise Report

for the FRV Solea cruise number 715 , from 25.01.2016 to 12.02.2016

Person in charge:

Dr. Daniel Oesterwind

Cruise leader:

Part B: Dr. Oesterwind (03.02. – 07.02.2016)

Part B

Purpose of the cruise part B

In the frame of the ICES-coordinated “Baltic International Acoustic Survey”, Germany annually conducts a hydroacoustic survey in September and October to assess the clupeid stocks in the Baltic Sea.

The aim of the cruise SO 715 Part B was to complement these existing monitoring programmes with an additional investigation during the spring spawning migration period to reveal migration and pre-spawning aggregation patterns of spring-spawning herring in the Western Baltic Sea. The research was performed within the EU-Project BIO-C³, where herring biology and migration patterns are an important task to cover. Our major focus was to observe the spawning aggregation and migration at the area of the Öresund and the Island of Rügen.

In addition genetic samples were retrieved from lumpsucker for a master thesis at the University of Copenhagen.

Verteiler:

BLE, Hamburg
Schiffsführung FFS „Clupea“
BMEL, Ref. 614
Thünen-Institut - Präsidialbüro (M. Welling)
Thünen-Institut - Fischereiökologie
Thünen-Institut - Seefischerei
Thünen-Institut - Ostseefischerei
Thünen-Institut - FIZ
Thünen-Institut – Einsatzplanung, Forschungsschiffe
BSH Hamburg
BFEL Hamburg, FB Fischqualität
IFM-GEOMAR, Kiel
Institut für Fischerei der Landesforschungsanstalt
LA für Landwirtschaft, Lebensmittels. u. Fischerei

Deutscher Fischerei-Verband e. V., Hamburg
Leibniz Institut für Ostseeforschung
Doggerbank GmbH
Mecklenburger Hochseefischerei Sassnitz
Kutter- und Küstenfisch Sassnitz
Landesverband der Kutter- und Küstenfischer
Sassnitzer Seefischer
Deutsche Fischfang Union Cuxhaven
Fahrtteilnehmer
Eurobaltic Mukran

Area of investigation

The area of the investigation was ICES SD 24. Recorded transects were similar to the transects of the hydroacoustic survey in September and October. However, small modifications were done (Fig. 3).

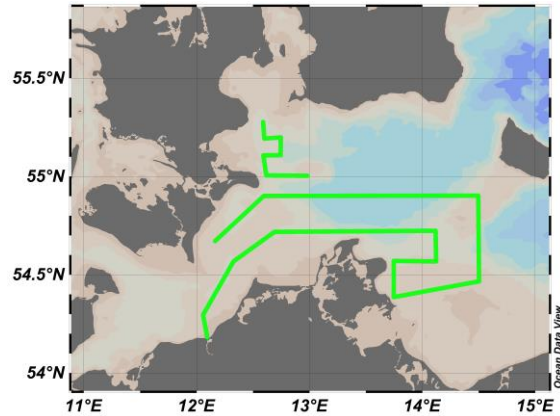


Figure 1. Cruise track of SO 715 part B

Cruise schedule and preliminary results

FRV Solea left port Marienehe on the 3rd of February to steam to the first acoustic transect. On the first day approximately 35 nautical miles were recorded and 3 CTD measurements were performed (Fig. 4). On the second day FRV shipped eastwards to continue hydroacoustic records on the transect and a total of 3 fishery and 5 CTD stations were realized. Weather conditions were stable and FRV Solea carried on the survey and performed 3 fishery and 6 CTD stations in the eastern area of the island of Rügen on the 5th of February. On the next day the FRV Solea shipped western and conducted 3 fishery and 5 CTD hauls. During the following night FRV Solea steamed northern to start hydroacoustic records close to the Öresund on the next morning and performed 2 fishery hauls and 7 CTD stations. Afterwards, FRV Solea shipped back to Warnemünde where part B finished at the evening of the 7th of February and the scientific personnel changed.

Preliminary results show relative low NASC values during the survey. Highest NASC values were measured close to the Island of Rügen and close to the Öresund (Fig. 4). A total of 1300kg of fish were caught. Fish composition consists of 10 different species; most abundant were *S. sprattus* and *C. harengus*, followed by *G. morhua* (Table 1).

Table 1. Caught fish (in kg) by station and in total for Solea cruise 715b.

Species	Fishery Stations										Total
	1	3	4	5	6	7	8	9	10	11	
<i>Clupea harengus</i>	19.864	21.188	85.17	57.02	33.98	24.6	53.352	26.81	91.051	127.818	540.853
<i>Cyclopterus lumpus</i>		0.421		0.254		0.433	0.909	0.458			2.475
<i>Engraulis encrasicolus</i>					0.026						0.026
<i>Gadus morhua</i>		2.417		10.56			6.859		0.378		20.214
<i>Gasterosteus aculeatus</i>	0.004										0.004
<i>Merlangius merlangus</i>						0.235			0.053		0.288
<i>Osmerus eperlanus</i>			0.373								0.373
<i>Platichthys flesus</i>			0.086		0.257		0.799				1.142
<i>Salmo salar</i>					3.088						3.088
<i>Sprattus sprattus</i>	514.131	4.004	31.03	0.479	7.635		110.108	53.14	15.799	26.532	762.858
Total	533.999	28.03	116.659	68.313	44.986	25.268	172.027	80.408	107.281	154.35	1331.321

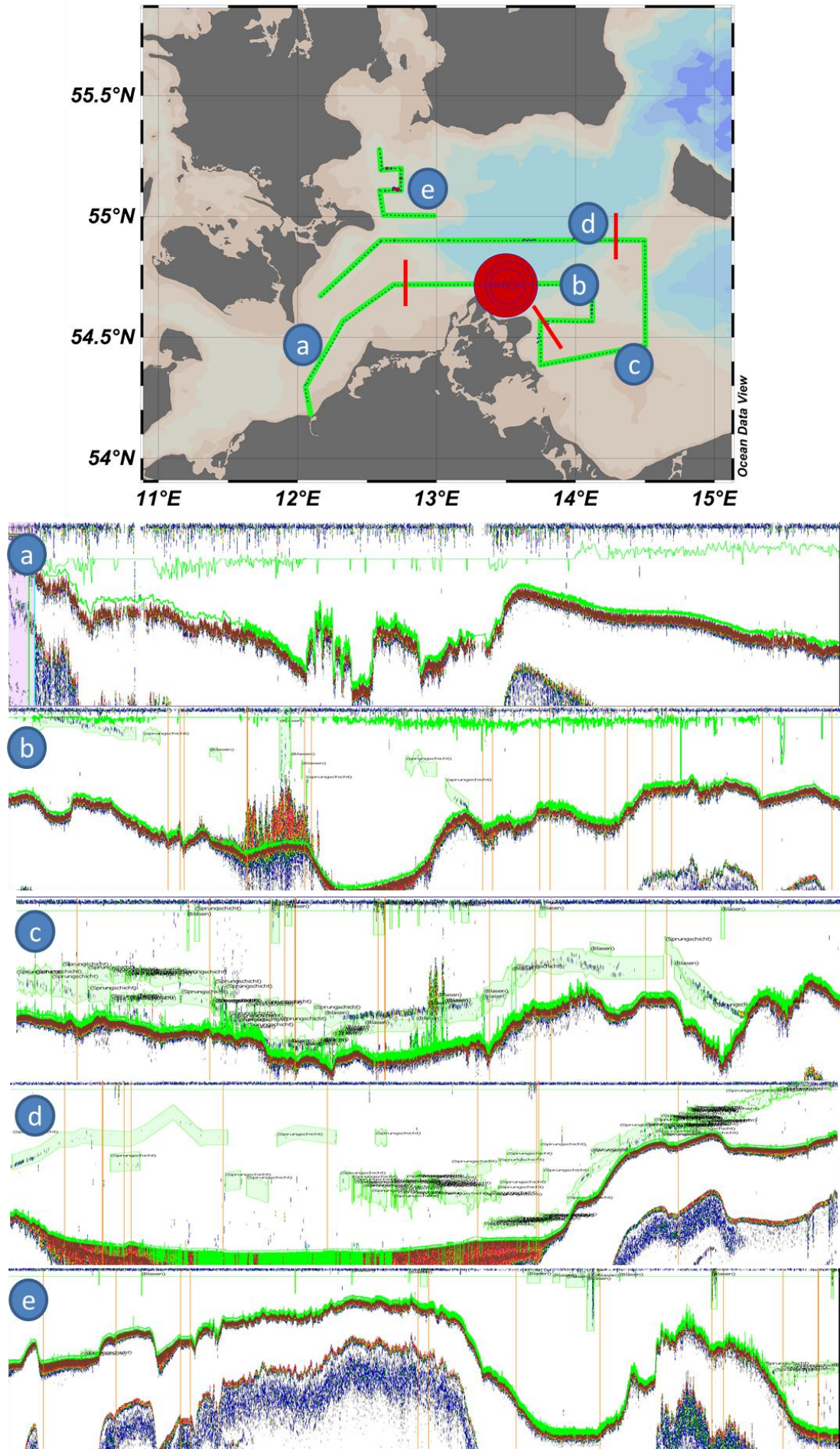


Figure 2. Upper chart: cruise track and preliminary relative NASC values. Lower charts: acoustic transects per day (a: 03.02.; b: 04.02.; c: 05.02.; d: 06.02.; e: 07.02.2016).

Participants

03.02.2015 – 08.02.2015

Dr. Daniel Oesterwind	TI-OF	Cruise leader
Kerstin Schöps	TI-OF	technician
Mario Koth	TI-OF	technician
Christian Schmidt		apprentice
Lea Wietrzynski		apprentice

Rostock 05.01.2016

Daniel Oesterwind
(scientist in charge)

Appendix

Table 2. Station information Solea Cruise 715 part B.

Cruise	station no.	station-year	Device	Bem. Gebiet	Date	time	start long.	start Lat.
715	120	2	CTD	SD 24 Darßer Schwelle	03.02.16	13:31:51	54°18,186N	012°03,497E
715	121	3	CTD	SD 24 Darßer Schwelle	03.02.16	15:25:33	54°33,948N	012°19,948E
715	122	4	CTD	SD 24 Darßer Schwelle	03.02.16	17:09:55	54°42,998N	012°41,930E
715	123	5	CTD	SD 24 Arkonasee	04.02.16	09:27:27	54°42,910N	013°18,595E
715	124	6	pelagic gear	SD 24 Arkonasee	04.02.16	10:22:10	54°42,929N	013°31,501E
715	125	7	CTD	SD 24 Arkonasee	04.02.16	10:50:23	54°42,776N	013°29,999E
715	126	8	CTD	SD 24 Arkonasee	04.02.16	13:11:36	54°42,964N	014°06,898E
715	127	9	pelagic gear	SD 24 Arkonasee	04.02.16	13:57:45	54°36,554N	014°07,121E
715	128	10	CTD	SD 24 Arkonasee	04.02.16	15:17:11	54°33,948N	014°07,090E
715	129	11	pelagic gear	SD 24 Arkonasee	04.02.16	16:35:58	54°33,641N	013°48,160E
715	130	12	CTD	SD 24 Arkonasee	04.02.16	17:32:15	54°33,976N	013°44,998E
715	131	13	pelagic gear	SD 24 Arkonasee	05.02.16	08:11:05	54°30,210N	013°43,733E
715	132	14	CTD	SD 24 Arkonasee	05.02.16	08:43:03	54°28,494N	013°43,642E
715	133	15	CTD	SD 24 E-lich Rügen	05.02.16	09:48:44	54°22,960N	013°45,083E
715	134	16	CTD	SD 24 E-lich Rügen	05.02.16	12:34:22	54°27,933N	014°30,010E
715	135	17	pelagic gear	SD 24 Arkonasee	05.02.16	13:41:07	54°38,340N	014°30,074E
715	136	18	CTD	SD 24 Arkonasee	05.02.16	14:30:10	54°40,739N	014°30,461E
715	137	19	CTD	SD 24 Arkonasee	05.02.16	15:57:22	54°53,862N	014°29,877E
715	138	20	pelagic gear	SD 24 Arkonasee	05.02.16	16:43:21	54°53,977N	014°19,141E
715	139	21	CTD	SD 24 Arkonasee	05.02.16	17:20:10	54°54,042N	014°15,550E
715	140	22	pelagic gear	SD 24 Arkonasee	06.02.16	08:11:56	54°54,013N	014°02,968E
715	141	23	CTD	SD 24 Arkonasee	06.02.16	08:50:21	54°54,464N	013°59,263E
715	142	24	pelagic gear	SD 24 Arkonasee	06.02.16	10:33:28	54°54,339N	013°37,366E
715	143	25	CTD	SD 24 Arkonasee	06.02.16	11:20:22	54°54,271N	013°42,203E
715	144	26	pelagic gear	SD 24 Arkonasee	06.02.16	13:31:55	54°54,021N	013°08,234E
715	145	27	CTD	SD 24 Arkonasee	06.02.16	14:06:29	54°54,113N	013°05,100E
715	146	28	CTD	SD 24 Arkonasee	06.02.16	15:55:48	54°53,988N	012°36,212E
715	147	29	CTD	SD 24 Arkonasee	06.02.16	18:04:19	54°40,000N	012°10,201E
715	148	30	CTD	SD 24 Arkonasee	07.02.16	07:29:20	55°16,782N	012°35,033E
715	149	31	pelagic gear	SD 24 Arkonasee	07.02.16	08:04:35	55°13,480N	012°36,209E
715	150	32	CTD	SD 24 Arkonasee	07.02.16	08:45:29	55°11,423N	012°36,002E
715	151	33	CTD	SD 24 Arkonasee	07.02.16	09:20:45	55°11,954N	012°44,051E
715	152	34	CTD	SD 24 Arkonasee	07.02.16	10:01:40	55°06,400N	012°44,671E
715	153	35	pelagic gear	SD 24 Arkonasee	07.02.16	10:07:34	55°06,537N	012°44,428E
715	154	36	CTD	SD 24 Arkonasee	07.02.16	11:09:03	55°06,373N	012°35,228E
715	155	37	CTD	SD 24 Arkonasee	07.02.16	11:56:22	55°00,290N	012°37,233E
715	156	38	CTD	SD 24 Arkonasee	07.02.16	13:16:42	55°00,148N	012°59,743E