



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

K. Hüsey^{1*}, H.-H. Hinrichsen², M. Eero¹, H. Mosegaard¹, J. Hemmer-Hansen¹, A. Lehmann², and L. S. Lundgaard¹

¹National Institute of Aquatic Resources, Technical University of Denmark, Jaegersborg Alle 1, 2920 Charlottenlund, Denmark

²GEOMAR Helmholtz Centre for Ocean Research Kiel, Düsterbrookweg 20, 24105 Kiel, Germany

*Corresponding author: tel: +45 3588 3458; fax: +45 3588 3333; e-mail: kh@aqua.dtu.dk

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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

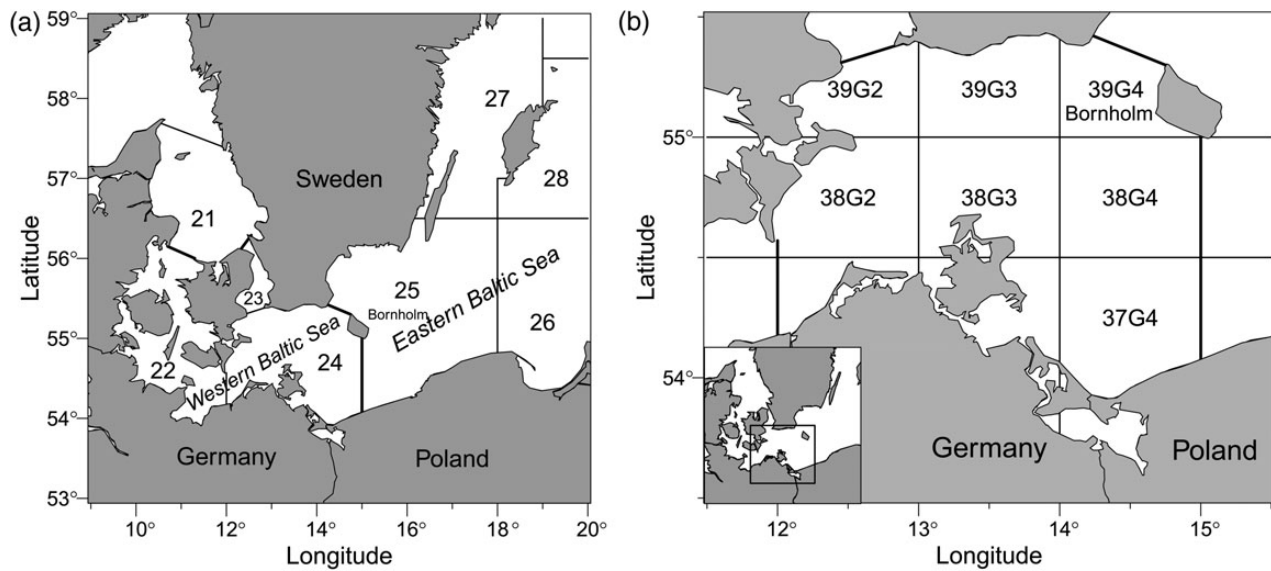


Figure 1. (a) Map of the Baltic Sea. Numbers indicate ICES SD, thin lines indicate SD boundaries, and solid lines the boundaries between the Kattegat, western and eastern Baltic Sea management areas. (b) Map of the Arkona Basin (SD24) in the western Baltic Sea. Lines indicate the statistical rectangles 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 (Hüßy, 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 (Hüßy, 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; Petereit 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 Hüßy 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

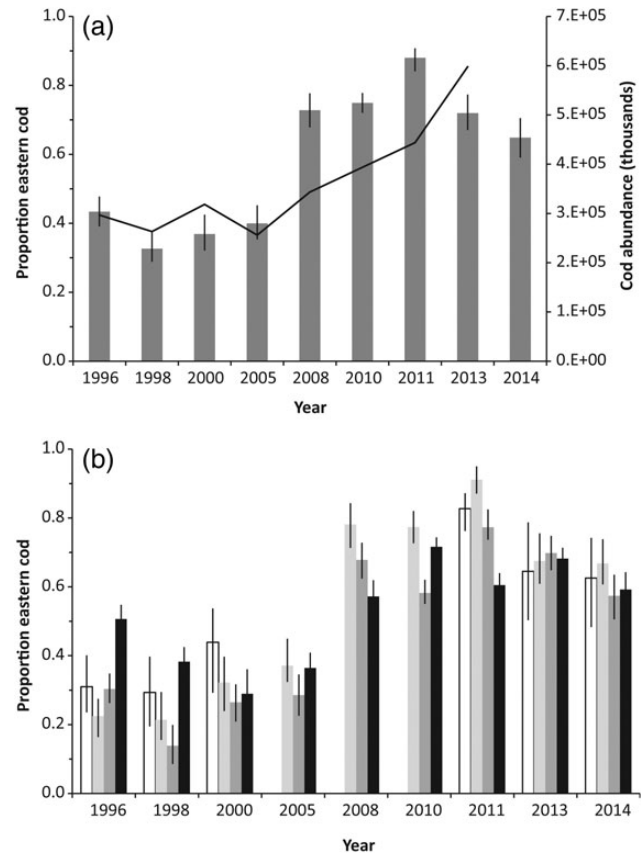


Figure 2. (a) Trends in proportion of eastern Baltic cod in the Arkona Basin (SD 24) over the years 1996–2014 (bars) with stock abundance of eastern Baltic cod during the same years (line; data from ICES, 2013), and (b) Proportion of eastern Baltic cod for each size group separately, where white $\leq 32\text{ cm}$, light grey = $32\text{--}39\text{ cm}$, dark grey = $40\text{--}47\text{ cm}$, 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

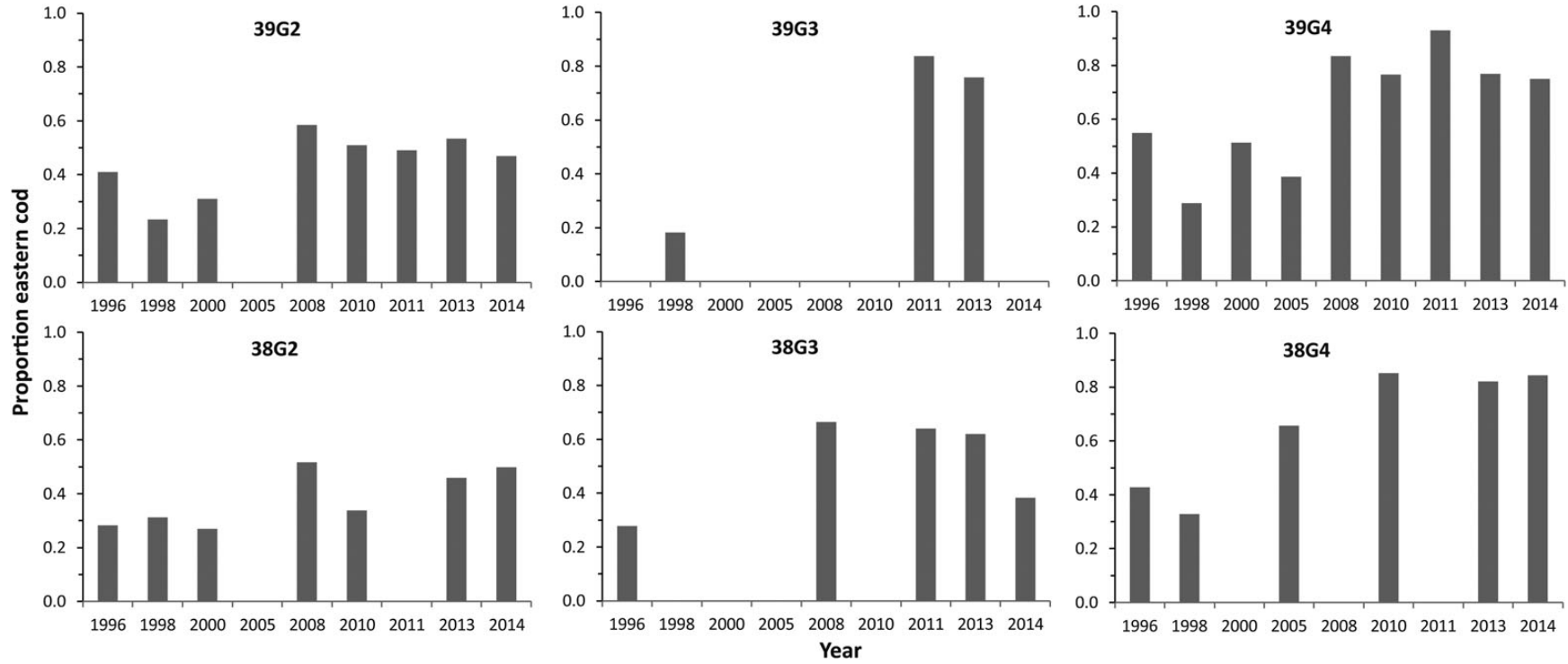


Figure 3. Proportion of eastern Baltic cod (> 20 cm) per year in the six ICES rectangles within the Arkona Basin (SD 24) for the years 1996–2014. Only years with > 10 fish per rectangle and year were used. Years without bars indicate lack of data. Rectangles are arranged to match their relative positions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

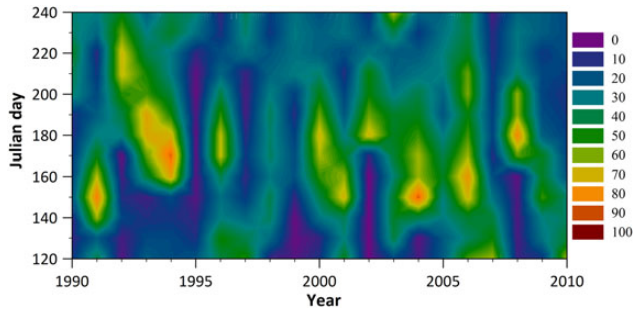


Figure 4. Habitat suitability in the Arkona Basin (SD 24) in relation to Julian day and year. Only data from eastern Baltic cod’s main spawning time May–August (Julian days 120–240) are shown. Values represent per cent of maximum possible habitat size.

Table 2. Relative probabilities (mean + 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 ± 0.216		
(2) Dead (bottom)	0.180 ± 0.105	0.114 ± 0.056	0.066 ± 0.061
(3) Dead (temperature)	0.002 ± 0.008	0.001 ± 0.007	0.001 ± 0.004
(4) Yolk-sac survivors	0.191 ± 0.151	0.165 ± 0.141	0.026 ± 0.033

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

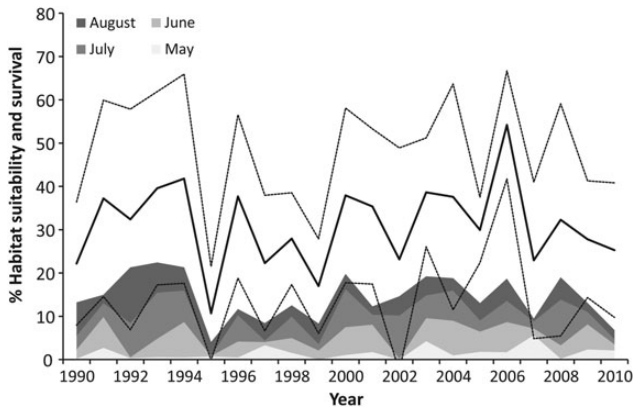


Figure 5. Average habitat suitability in May–August (average = solid black line, ± s.d. = broken lines) and relative larval survival probability (shaded area) in the Arkona Basin (SD 24) in relation to years and spawning month, where May: white, June: light grey, July: grey, and August: dark grey.

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

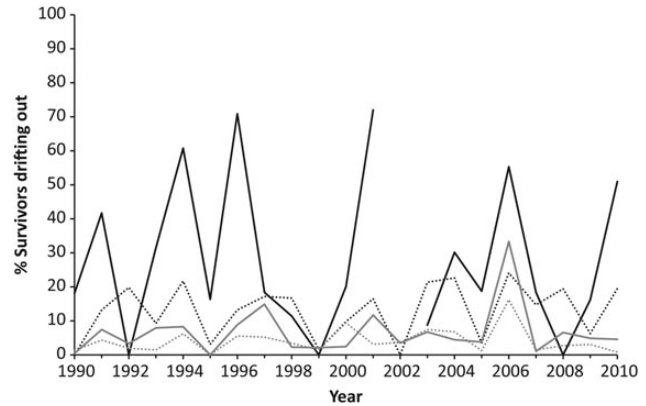


Figure 6. Percentage of surviving larvae drifting out of the Arkona Basin (SD 24) in relation to year for different months of hatch: May = solid black, June = dotted black, July = solid grey, and August = dotted grey. Missing values are the result of zero surviving larvae.

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 ± 23% (mean ± s.d.), June = 13 ± 8%, July = 7 ± 7%, and August = 4 ± 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 (Bernier, 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 (Cadrin 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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