EGG BUOYANCY AND SURVIVAL PROBABILITIES OF BALTIC FLOUNDER (PLATICHTHYS FLESUS)

DIFFERENCES BETWEEN SPAWNING AREAS AND INTER-ANNUAL VARIATION IN CONDITIONS FOR REPRODUCTION

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ABSTRACT

The reproductive success for pelagic spawning Baltic flounders is strongly linked to the hydrodynamics in the spawning areas. Egg survival is dependent upon the ability to achieve neutral buoyancy at a depth interval where temperature and oxygen concentrations are favourable for egg development. The main focus of this thesis was to compare egg survival probabilities of pelagic eggs from Baltic flounder in the Bornholm, Gdansk and Gotland basins, prior to and after the saline water inflow in December 2014. The results showed greatly enhanced survival probabilities in Bornholm basin 2015 (p<0.01), as egg survival increased from 47% in 2014 to 100% the following year. In Gdansk basin the situation was similar, and survival probability increased from 13% to 100% (p<0.01). In Gotland basin no difference in survival probability was identified, although the dominant cause of mortality shifted from sedimentation, i.e. due to low salinity conditions in 2014, to oxygen deficiency in 2015 (p<0.01).
INTRODUCTION

European flounder (*Platichthys flesus*) is a marine flatfish that has adapted well to the brackish conditions in the Baltic Sea, and it is found in less saline water further north than other pleuronectid species (Bagge, 1981). Inhabiting the Baltic Sea, the largest brackish water area in the world has forced species to evolve adaptations to the spatial and temporal variability in environmental conditions that constitute the Baltic waterbody. Hence, differences have been identified between the Baltic flounder and its marine counterparts (Nissling et al., 2002).

The complicated morphometry of the Baltic Sea, an almost land-locked water area with several deep basins separated by shallow sills, has given different regions characteristic hydrographic features. The only connection to the North Sea is represented by the narrow and shallow straits, the Sound and the Belt Seas (Matthäus and Franck, 1992), and the restricted water exchange is crucial for the environmental conditions in the different sub-basins, affecting salinity and oxygen conditions. Salinity is maintained by irregularly occurring saline water inflows from the North Sea (Mohrholz et al., 2015). Consequently there is a surface water salinity gradient from the south to the north and from the west to the east, ranging between 8 and 3 psu. There is also a vertical layer stratification with a salinity gradient in the Baltic Proper deeper basins, and the formation of a halocline at about 50-70 metres that prevents deeper water from mixing with the oxygenated water in upper layers. Below the halocline the water can reach salinities of about 10 to 22 psu, with the most saline water in the Arkona- and Bornholm basins compared to the Gdansk- and Gotland basins (Nissling et al., 2002). Renewal of salinity in the bottom water is driven exclusively by lateral advection during the irregularly occurring major saline water inflow events. Thus, stagnant water with decreasing salinity and oxygen levels, or even anoxic conditions, can prevail for years.

The oxygen content of inflowing water has a seasonal dependency, and mainly, only the inflows occurring between October and March supply oxygen to the deep basins. Oxygenation of the deeper layers below the halocline is also reliant on the inflowing volume, as smaller inflows get diluted before reaching the deep basin areas. These are barotropic inflows, which are forced by special large scale atmospheric conditions, with wind and air pressure causing sea level differences between the Kattegat and the Arkona Basin. The barotropic inflows are also the ones normally responsible for the salinity increase in the deep basin areas. Major Baltic inflows are rare and the frequency has dropped since the early 80s, when they occurred 5 to 7 times per decade. During the following decades only 3 inflows were of the magnitude to be considered major, with one occurring in 1993, one in 2003 and the last one occurring in 2014. The basins located closer to the narrow straits, may however get supplied even during minor inflows, and hence they are generally more oxygen rich and have a higher salinity throughout the water column than is the situation in the more eastern and northern basins (Mohrholz et al., 2015).

Understanding of the varying hydrographic conditions in the different basins is of great need, as it is the main factor regulating flounder abundance and distribution, which are related to the reproduction success due to varying salinity and oxygen conditions in the spawning areas (Petereit et al., 2014).

There are two sympatric flounder populations with different spawning strategies in the Baltic Sea. One with demersal eggs spawning in coastal areas as well as on offshore banks, and reproductive success has been documented as far north as in the Bothnian Sea and the Gulf of
Finland. The other ecotype produces pelagic eggs, thus spawning occurs below the halocline in the Baltic Sea deep basins, where eggs have to avoid the oxygen-depleted waters in deeper layers (Nissling et al., 1994), by achieving neutral buoyancy at depths with favourable oxygen conditions. Successful reproduction in the deep basin areas, i.e. the Arkona, Bornholm as well as in the Sound occurs regularly, while it, in the Gdansk and Gotland basins is thought to be more dependent on the irregularly occurring saline water inflow events (Nissling et al, 2002).

Several authors have suggested that the brackish water salinity has acted as a major evolutionary force on Baltic Sea teleosts, with selection for development of larger eggs with higher water content (Craik & Harvey, 1987), thus exhibiting lower egg specific gravity than their marine counterparts (Thorsen et al, 1996; Nissling et al., 2002). The adaption to low salinity can occur either through phenotypic plasticity or through genetic selection, but transference experiments have confirmed the latter to be of substantial importance as transfer of flounders from brackish to marine conditions, and vice versa, has resulted in only minor buoyancy changes (Solemdal, 1970; 1971; 1973). This is also true for transfer experiments regarding cod (Nissling & Westin, 1997), suggesting that salinity requirements for neutral egg buoyancy is a result of genetic selection, and may thus be used as a tool for stock discrimination.

Today, fishery for flounder in the Baltic Sea exists on mixed stocks, and increased knowledge of population structure, migration patterns as well as of spatial distribution is of great need to achieve a future sustainable management. In 1989, Bagge and Steffensen argued that the pelagic spawning flounders in the Baltic proper consisted of three distinct populations. One in the Arkona basin, one in the Bornholm basin and the last one distributed in both the Belt Sea and the Sound. This is in accordance with later findings (e.g. Nissling et al., 2002). Contrary to this, Florin and Höglund (2008), using microsatellite studies, suggested that the Baltic flounder should be divided into three management units; one demersal spawning flounder population in the northern Baltic, and two pelagic spawning populations, one in the southern Baltic and the other in Skagerrak, Kattegat and the North Sea.

The main focus of this thesis was to evaluate egg survival probabilities of flounder prior to, as well as after an inflow event, i.e. the potential for reproductive success of pelagic spawning flounder. In December 2014 the third largest inflow ever observed since the beginning of Matthäus and Francks’ (1992) retrospect perspective analysis from 1880 and onwards, occurred. The total volume amounted 320 km$^3$, with about 198 km$^3$ of highly saline and well oxygenated water, which have the potential to oxygenate even the anoxic environments prevailing in the Gdansk and Gotland basins (Mohrholz et al. 2015). By studying the ability of egg batches from different females to obtain neutral buoyancy within the reproductive layer, the part of the waterbody where conditions meet the criteria for successful reproduction (e.g. 10.6 psu, based on minimum requirements for neutral buoyancy, $\geq 2$ °C and 1.5 ml O$_2$·l$^{-1}$) in the spring of 2015, after the recent inflow event (SMHI, 2015), and compare this with conditions before the inflow, i.e. at stagnant conditions prevailing in 2014, it may be possible to demonstrate the importance of saline water inflows for increased egg survival probabilities in the spawning areas.

Another objective of the thesis is to evaluate the occurrence of subpopulations within the pelagic spawning flounder ecotype in the deep-basins of the Baltic Sea by analysing potential differences in egg specific gravity and egg size between areas. In addition, otoliths and tissue have been sampled and forwarded to the BONUS INSPIRE-project for genetic analysis and
analysis of otolith chemistry with the aim to identify spatial distribution patterns and connectivity.

Specifically, the aim of this thesis was to answer the questions (1) Does major saline water inflow events affect egg survival probabilities for deep-basin spawning flounders in the Baltic? (2) Does the pelagic spawning flounder ecotype exist in different subpopulations within the deep basins of the Baltic Sea?

MATERIAL AND METHODS

Sampling areas

The study includes measurements of egg specific gravity on fish collected during April of 2014 and 2015 in the Bornholm, Gdansk and Eastern Gotland Basins respectively (Figure 1). Fish were caught during trawl surveys by R/V Alkor in April 2014 and 2015. In addition both demersal and pelagic spawning flounders caught with gill-nets in the Hanö bight (Nogersund) and Eastern Gotland (Herrvik) were used to reveal differences in egg characteristics for population identification.

![Figure 1. Sampling stations in the Bornholm-, Gdansk and Gotland basins (trawling) and of Nogersund and Herrvik (gill-netting). CTD profiles were acquired at trawl stations BB25, GD60 and GB90. Division into sub-basins follow the HELCOM sub-basin classification. (ICES, 2015-05-25).](image)

- Demersal flounder
- Pelagic flounder
Trawling was performed at 50-90 meters depth, a depth that ensured flounders to belong to the offshore spawning populations. According to Molander (1954; see Nissling et al., 2010) coastal spawning flounder has a depth limit at about 30-40 meters. In total, 45 pelagic spawning flounders were used, whereof 15 were caught in the Bornholm Basin, 4 in the Gdansk deep and 26 in the Gotland Basin and 26 demersal spawning flounder of which 1 was caught of Nogersund (Bornholm basin) and 25 off Herrvik in the Eastern Gotland Basin. Coordinates for sampling locations are found in Table 1.

Table 1. Coordinates for sampling locations stated in decimal degrees. For Nogersund and Herrvik coordinates represent the sampling location situated in the centre.

<table>
<thead>
<tr>
<th>Station ID</th>
<th>Longitude</th>
<th>Latitude</th>
<th>Station ID</th>
<th>Longitude</th>
<th>Latitude</th>
</tr>
</thead>
<tbody>
<tr>
<td>BB24</td>
<td>15.9698</td>
<td>55.2785</td>
<td>GB79</td>
<td>19.0637</td>
<td>55.9940</td>
</tr>
<tr>
<td>BB25</td>
<td>16.2502</td>
<td>55.2918</td>
<td>GB80</td>
<td>18.7118</td>
<td>55.9493</td>
</tr>
<tr>
<td>BB31</td>
<td>15.5897</td>
<td>55.1100</td>
<td>GB82a</td>
<td>19.1600</td>
<td>56.0922</td>
</tr>
<tr>
<td>GD58</td>
<td>19.1182</td>
<td>54.9707</td>
<td>GB84</td>
<td>19.0013</td>
<td>56.2485</td>
</tr>
<tr>
<td>GD59</td>
<td>18.9188</td>
<td>54.9040</td>
<td>GB90</td>
<td>18.9980</td>
<td>56.5327</td>
</tr>
<tr>
<td>GD60</td>
<td>19.1343</td>
<td>54.8173</td>
<td>Nogersund</td>
<td>14.6526</td>
<td>55.7347</td>
</tr>
<tr>
<td>GD60a</td>
<td>19.2823</td>
<td>54.7160</td>
<td>Herrvik</td>
<td>18.9740</td>
<td>57.4453</td>
</tr>
</tbody>
</table>

Experiment setup

By stripping the flounder caught, semen and eggs were obtained and fertilization was conducted artificially in 7°C seawater with a salinity of 20 psu. This salinity allow successfully fertilized eggs to float, while the unfertilized eggs sink to the bottom, about 30 minutes after fertilization. Successfully fertilized eggs were incubated in 20 psu salinity at 7°C until measurements. The fertilization of a batch from one female involved stripping of 1-3 male flounders caught in the same haul.

Neutral egg buoyancy of ca 30 eggs per batch was determined 24 hours after fertilization at 7°C using a density gradient column, where positions of eggs were compared to the positions of 9-10 density floats of known specific gravity. The regression lines of the density floats ($r^2=0.995, p<0.01$) were used to estimate the exact specific gravity of eggs in each column. As density floats were calibrated to 23°C, 0.000028 g/cm$^3$ was added for each degree below, to adjust to density variability according to different temperatures at measurements. Egg diameter was measured under a stereomicroscope at 16x magnification, using a micrometer scale, before they were put into the density gradient columns. 8-9 eggs were rinsed and frozen to allow for measurements of dry weight, but these measurements are out of the scope for this study.

Depth, salinity, temperature and oxygen concentration were measured by CTD-casts at each sampling station. One station from each basin (BB25, GD60 and GB90) was used for comparison of egg survival probabilities between basins and years. By comparing the mean egg specific gravity of sampled egg batches from each basin with the water density from the corresponding CTD data of the same basin in 2014 and 2015 respectively, the depths where the eggs obtain neutral buoyancy were determined. Survival probability was judged based on threshold levels of oxygen concentration above or below 1.5 ml·l$^{-1}$ and temperature above or below 2°C.
Statistical analysis

Variability in egg specific gravity and egg size
The correlation between egg specific gravity and diameter of both pelagic and demersal eggs were tested using an ANOVA regression analysis. Data from eggs obtained in Nogersund and Herrvik were originally expressed as salinity of neutral buoyancy. Hence, values were converted to g/cm$^3$ using a Water Density Calculator with a temperature adjustment to 7°C. The calculator was calibrated according to the Unesco definition ‘The One International Equation of State of Seawater’ stated in 1980 (Unesco, 1981). Likewise, salinity of neutral buoyancy for egg batches sampled during the Alkor cruise were converted from the specific gravity measurements (expressed as g/cm$^3$) using the same calculator.

Occurrence of sub-populations
To reveal if egg specific gravity co-varied with female size, correlation between egg diameter and female length was analysed using a regression analyses. The analyses yielded no relation, thus female size could be excluded in further analysis. Hence, egg specific gravity of batches from different areas were compared using a single factor ANOVA. Further, to reveal potential differences in egg specific gravity between the Gdansk and the Gotland basins, an independent sample t-test with different means was used. If significant differences in egg specific gravity occurred between basins, flounders were considered to belong to different sub-populations.

Inter-annual survival probability
Environmental threshold levels for egg survival were defined according to earlier published literature (Hinrichsen et al., personal communication). Critical threshold levels in this study were a salinity of 10.6 psu based on minimum requirements for neutral buoyancy, a temperature of 2 °C and 1.5 ml O$_2$∙1$^{-1}$ (2.14 mg O$_2$∙1$^{-1}$) for oxygen. Egg development are temperature dependent, and may be affected by both too high and too low temperatures, and the most favourable temperatures for successful reproduction range between 2 °C and 10 °C. Oxygen levels below 1.5 ml O$_2$∙1$^{-1}$ also affect egg development, resulting in mortality. Eggs displaying buoyancy at levels exceeding bottom salinity will most likely die because of sedimentation. Further, a salinity of circa 10 psu are needed for spermatozoa activation, thus at lower salinities fertilization may be unsuccessful.

By comparing egg specific gravity for batches sampled in the Bornholm Basin (n=15) with the water density measured by a CTD-cast at station BB25, oxygen concentration, salinity and temperature was acquired for the respective depths where studied egg batches obtained neutral buoyancy. All eggs displaying neutral buoyancy at values exceeding the threshold values were considered surviving, while eggs buoyant at lower values were considered dying either due to unfavourable temperatures for successful reproduction or oxygen deficiency. Further, eggs with a specific gravity exceeding density in the bottom water were considered dying from sedimentation. In the same way egg specific gravity for egg batches obtained in stations located in Gotland Basin (n=26) were analysed together with the eggs obtained in Gdansk Basin (n=4), and compared with the CTD measurements from both station (GB90 and GD60).

The number of eggs considered surviving were counted separately for each basin and year, and the differences in survival probabilities between 2014 and 2015 were analysed using Fishers’ Exact Test. All statistical analysis were performed in the statistical software R studio.
RESULTS

Egg specific gravity and diameter

Egg specific gravity of both pelagic and demersal eggs was approximately normally distributed, and was strongly negative correlated to egg diameter ($r^2 = 0.8506$, df = 68, $p<0.01$, Figure 2), which also displayed normal distribution.

![Figure 2](image)

**Figure 2.** Egg specific gravity (g cm$^{-3}$) and salinity of neutral buoyancy (psu) of demersal (n=26) and pelagic (n=43) eggs obtained in the Bornholm, Gdansk and Gotland basins in relation to diameter (mm). The solid line represent the linear relationship between diameter and egg specific gravity for both pelagic and demersal eggs.

The smallest eggs displayed highest egg specific gravity, hence they achieved neutral buoyancy at higher salinities, than did the larger ones. Neutral buoyancy for pelagic eggs were achieved at ca 3.0 ± 0.3 (SE) psu while the smaller demersal eggs achieve neutral buoyancy at ca 20.5 ± 0.2 (SE) psu (Table 2). To learn if the female size should be taken into account when analysing differences in egg specific gravity between areas, female size was plotted against diameter of pelagic eggs. No significant relationship ($r^2 = 0.0013$, df = 42, $p>0.05$, Figure 3) was however found and female size was excluded in further analysis.

**Table 2.** Diameter (mm), egg specific gravity (g cm$^{-3}$) and salinity of neutral buoyancy (psu) of demersal and pelagic eggs from the Bornholm, Gdansk and Gotland basins, stated in mean ± standard error.

<table>
<thead>
<tr>
<th></th>
<th>Diameter</th>
<th>Egg specific gravity</th>
<th>Buoyancy</th>
<th>No. of observations</th>
</tr>
</thead>
<tbody>
<tr>
<td>Demersal</td>
<td>1.03 ± 0.01</td>
<td>1.016 ± 0.000</td>
<td>20.5 ± 0.2</td>
<td>26</td>
</tr>
<tr>
<td>Pelagic</td>
<td>1.22 ± 0.01</td>
<td>1.010 ± 0.000</td>
<td>13.0 ± 0.3</td>
<td>43</td>
</tr>
</tbody>
</table>
Figure 3. Mean egg diameter (mm) of batches in relation to female size (cm) for egg batches from the pelagic spawning ecotype in the Bornholm, Gdansk and Gotland basins (n=43).

**Differences in egg specific gravity between areas**

The salinity at which eggs achieve neutral buoyancy differed between the Bornholm, Gdansk and Gotland basins ($F_{2;42} = 39.12, p<0.01$, ANOVA), indicating that there are at least two different pelagic spawning populations in the three different regions. Means and standard deviations are given in Table 3. Specific gravity of flounder eggs from the Bornholm basin were higher (1.012 ± 0.001) than for eggs obtained in the Gdansk (1.010 ± 0.005) and Gotland (1.001 ± 0.001) basins, thus they achieve neutral buoyancy at higher salinities (Table 3).

<table>
<thead>
<tr>
<th>Area</th>
<th>Diameter</th>
<th>Egg specific gravity</th>
<th>Buoyancy</th>
<th>No. of observations</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bornholm basin</td>
<td>1.15 ± 0.06</td>
<td>1.012 ± 0.001</td>
<td>14.9 ± 1.4</td>
<td>15</td>
</tr>
<tr>
<td></td>
<td>1.03 - 1.25</td>
<td>1.009 - 1.013</td>
<td>11.5 - 16.6</td>
<td></td>
</tr>
<tr>
<td>Gdansk basin</td>
<td>1.19 ± 0.03</td>
<td>1.010 ± 0.001</td>
<td>12.7 ± 0.6</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>1.15 - 1.21</td>
<td>1.010 - 1.011</td>
<td>11.9 - 13.3</td>
<td></td>
</tr>
<tr>
<td>Gotland basin</td>
<td>1.26 ± 0.05</td>
<td>1.010 ± 0.001</td>
<td>11.9 ± 0.9</td>
<td>26</td>
</tr>
<tr>
<td></td>
<td>1.18 - 1.40</td>
<td>1.009 - 1.011</td>
<td>10.5 - 13.9</td>
<td></td>
</tr>
</tbody>
</table>

The majority of the eggs obtained in Bornholm basin achieved neutral buoyancy in a salinity range of 14.5-16.5 PSU, while the salinity range for neutral buoyancy for most of the eggs in Gotland basin occurred at about 11.0-13.0 PSU (Table 4). This is also clearly demonstrated in Figure 2.

The differences in egg specific gravity between the areas are shown in Figure 4. The lack of overlap between the confidence interval between eggs from the Bornholm basin and the other areas indicates that the eggs obtained in Bornholm basin represent one distinct population,
while the eggs from Gdansk and Gotland basins are derived from individuals belonging to the same spawning population ($t_{28} = 0.575$, $p>0.05$, t-test).

**Table 4.** Salinity range (psu) at which egg batches (number) of flounder from the Bornholm, Gdansk and Gotland basins achieved neutral buoyancy.

<table>
<thead>
<tr>
<th>Salinity</th>
<th>Bornholm</th>
<th>Gdansk</th>
<th>Gotland</th>
</tr>
</thead>
<tbody>
<tr>
<td>10.5-11</td>
<td>3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>11-11.5</td>
<td></td>
<td>5</td>
<td></td>
</tr>
<tr>
<td>11.5-12</td>
<td>1</td>
<td>1</td>
<td>10</td>
</tr>
<tr>
<td>12-12.5</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>12.5-13</td>
<td>2</td>
<td></td>
<td>3</td>
</tr>
<tr>
<td>13-13.5</td>
<td>1</td>
<td></td>
<td>2</td>
</tr>
<tr>
<td>13.5-14</td>
<td></td>
<td></td>
<td>2</td>
</tr>
<tr>
<td>14-14.5</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>14.5-15</td>
<td>2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>15-15.5</td>
<td>4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>15.5-16</td>
<td>3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>16-16.5</td>
<td>2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>16.5-17</td>
<td>1</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Figure 4.** Specific gravity of the egg batches obtained in the Bornholm, Gdansk and Gotland basins when a) treated as three distinct populations and b) Gdansk and Gotland are considered belonging to the same population. The bars show mean egg specific gravity (g cm$^{-3}$) from all batches obtained in the different areas, and the error bars represent the 95% confidence interval.

**Survival probabilities following varying environmental conditions**

Environmental factors, such as oxygen concentration and salinity prevailing prior to the major Baltic inflow in 2014 differed to those prevailing in 2015, after the inflow event. Mean and standard deviation of temperature, salinity and oxygen concentration within the depth range at which eggs achieved neutral buoyancy are given in Table 5.

In Bornholm basin, the highly saline inflowing water caused an increase in bottom water salinity, as the average salinity below the halocline increased from $13.7 \pm 2.0$ (sd) in 2014 to $15.5 \pm 2.6$ (sd) psu in 2015, thus the depth range at which eggs achieve neutral buoyancy shifted to smaller depths ($t_{26} = 3.97$, $p<0.01$, t-test). The inflowing water also caused an
increase in oxygen concentrations within the depth range for neutral egg buoyancy (t_{26}=3.02, p<0.01, t-test).

In Gdansk basin, the major inflow caused a mean salinity increase in the water below the halocline, from 10.6 ± 1.0 (sd) psu in 2014 to 14.0 ± 1.5 (sd) psu. The salinity increase of 2015, made it possible for eggs to achieve neutral buoyancy at smaller depths, and the depth range for neutral egg buoyancy is therefore found higher up in the water column (t_{48} = 21.17, p<0.01, t-test). Oxygen concentrations within the depth range for neutral egg buoyancy increased in 2015 compared to 2014 (t_{48} = 12.52, p<0.01, t-test).

After the major inflow in 2014, bottom water salinity in the Gotland basin displayed the same trend as seen in the other basins. Prior to the inflow, in April 2014 mean salinity below the halocline was 9.4 ± 1.0 (sd) but it increased to 11.1 ± 1.3 (sd) in April 2015. Accordingly the depth range for neutral egg buoyancy shifted at ca 118 m depth in 2014 to 84 m in 2015 (t_{24} = 7.67, p<0.01, t-test). There were also a notable difference in oxygen concentrations within the depth range of neutral buoyancy (t_{24} = 3.54, p<0.01, t-test), although still below 1.5 ml O₂∙l⁻¹ in most of the water column below the halocline. Only one of the egg batches, comprising low specific gravity managed to stay buoyant at a depth with favourable oxygen concentration, and hence survive the severe conditions in April 2015. In May 2015, mean salinity decreased to 10.1 ± 1.1 below the halocline, resulting, again, in a deeper depth range for neutral egg buoyancy, at ca 90-111 meters (Figure 7). Oxygen concentrations decreased within the depth range for neutral egg buoyancy compared to in April 2015 (t_{27} = 2.29, p<0.05, t-test), but were still higher than in April 2014 (t_{0} = 2.26, p<0.01, t-test).

Salinity in all basins increased in 2015 compared to 2014, and accordingly survival probability were higher in 2015, as eggs achieved neutral buoyancy less deep where conditions were more favourable for egg development. The uplift of the depth range for neutral egg buoyancy is shown in Figure 5 and the spawning conditions in May are displayed in Figure 6.

In 2014, 40% of the egg batches in Bornholm basin were considered dying because of oxygen deficiency (<1.5 ml O₂∙l⁻¹, 2.14 mg O₂∙l⁻¹), while 13% of the egg batches displayed too high specific gravity to achieve neutral buoyancy and hence they were considered dying from sedimentation. Survival probability in the Bornholm basin in 2014 thus amounted to 47%. The improved environmental conditions the year after the major inflow event resulted in significant higher survival probabilities as it increased to 100% (p<0.01, Fisher’s exact test, Figure 7 and Table 6).

**Table 5.** In average depth and depth range for studied flounder egg batches obtaining neutral buoyancy within the water column, and the in average temperature, salinity and oxygen concentration experienced by these egg batches in the Bornholm, Gdansk and Gotland basin respectively. Values are given in mean ± standard deviation.
The situation was similar in the Gdansk basin, where 53% of the egg batches would have died in the oxygen depleted waters in 2014, and the egg specific gravity of 33% of the egg batches involved dying from sedimentation. Only 13% would have managed to survive in the severe conditions prevailing in 2014. Notable changes in oxygen concentrations and salinity in 2015 lead to 100% survival probability, a significant difference to the previous year (p<0.01, Fisher’s exact test).

Environmental conditions in the Gotland basin differed from those displayed in the Bornholm and Gdansk basins. Even though the oxygen concentration increased in 2015, it was still not enough to support egg survival and development within the depth range for neutral egg buoyancy. In 2014 salinities were too low for eggs to achieve neutral buoyancy, and 87% of the egg batches investigated (n=30) were considered dying because of sedimentation. The rest of the egg batches, exhibiting lower specific gravity, would have died from oxygen deficiency. Hence none of the eggs investigated would have survived during the severe conditions prevailing in 2014.

Seemingly, in 2015, the summer following the big inflow, bottom water salinity increased, and 73% of the eggs managed to stay buoyant, but only one of the egg batches achieved neutral buoyancy at a depth with favourable oxygen concentration (10.54 psu and 2.3 mg O₂·l⁻¹). About 27% exhibited too high specific gravity for achieving neutral buoyancy in the water column, i.e. died from sedimentation. Although there was no difference in survival probabilities between the two years, there was still a significant difference in the cause of mortality (p<0.01, Fisher’s exact test).

The salinity decrease in the bottom water in May 2015 resulted in a deeper depth range for neutral egg buoyancy, and thus sedimentation the dominant mortality cause, just like in April 2014. Sedimentation accounted for 77% of the mortality. The eggs with low specific gravity managed to stay buoyant but died from oxygen deficiency. The cause of mortality in May 2015 was therefore comparable with the situation in April 2014 (p>0.05).

Temperature had no impact on egg survival probability in either of the basins and years, as the observed temperature exceeded the threshold value in all of the tests.
Figure 5. Depth profiles for a) Bornholm basin, b) Gdansk basin and c) Gotland basin in 2014 (to the left) and 2015 (to the right), with temperature (°C), oxygen (mg l⁻¹) and salinity (psu) varying with depth along the X-axis. The vertical lines represent mean buoyancy for the egg batches obtained in each basin, and the highlighted vertical field represent the depth range of the egg batches which achieved neutral buoyancy.
Figure 6. Depth profile for Gotland basin in May 2015, with temperature (°C), oxygen (mg l$^{-1}$) and salinity (psu) varying with depth along the X-axis. The vertical lines represent mean buoyancies for the egg batches obtained in each basin, and the highlighted vertical field represent the depth range of the egg batches to achieve neutral buoyancy.

Table 6. Studied egg batches (number) considered dying due to oxygen deficiency or sedimentation, and considered surviving respectively, in the Bornholm, Gdansk and Gotland basins in 2014 and 2015.

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<td>4</td>
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<tr>
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<td>10</td>
<td>26</td>
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<td></td>
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<tr>
<td>Surviving</td>
<td>7</td>
<td>15</td>
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Figure 7. Cumulative causes of death and survival probabilities of pelagic egg batches in the Bornholm, Gdansk and Gotland basins in 2014 and 2015 respectively.
DISCUSSION

Diameter of the pelagic eggs investigated in this study were smaller than those stated by Ojaveer and Kalejs (2005) and Nissling et al. (2002), but they follow the same size pattern, with decreasing egg size from the Gotland basin to the Bornholm basin. The size differences between the eggs in this study and earlier published data may be due to human error sources such as different magnifications at measurements. Egg specific gravity of measured eggs are in accordance with earlier published literature (e.g. Nissling et al. 2002; Petereit et al. 2014), although they are slightly higher regarding Gdansk basin, than those stated by Petereit et al. (2014). However, the differences are small and may be the result of insufficient data collected in this survey (n=4), rather than actual differences. Regardless, data from this study support the theory about at least two management units in the South and Central Baltic Sea; one western spawning population in the eastern Bornholm basin and one eastern spawning population, stretching from the deep areas of the Gdansk basin to the Gotland deep.

Size and specific gravity of teleost pelagic eggs have for a long time been known to vary intra-specifically throughout the distribution area of a species. Earlier research has shown a correlation between lower salinities and lower osmolality in the ovarian fluids, but despite significant osmotic changes according to salinity, transfer experiments have shown that lower osmolality has only a minor effect on the egg specific gravity. During the late 60s and early 70s Solemdal (1971; 1973) investigated potential differences in egg specific gravity, when transferring running flounder females from saline environments off Norway to brackish conditions in the Baltic Sea. The result was a significant increase in egg size, and hence a decrease in egg specific gravity. However, the eggs did not obtain size and specific gravity like the Baltic flounder eggs. Likewise, the eggs obtained from Baltic Sea spawning flounders transferred to higher salinities did not show a decrease in size and specific gravity to match their marine counterparts, indicating that phenotypic plasticity cannot be the factor determining differences in egg specific gravity between areas with different salinities. Similar experiments on cod (Nissling and Westin, 1997) have revealed the same pattern. Differences in egg specific gravity between different subpopulations are thus a result of genetic dissimilarities.

This suggests the brackish water in the Baltic Sea to act as a major evolutionary force, with adaptations to varying salinities occurring through long-time selection processes. One of this adaptations, which has not been fully studied yet, may be the chorion thickness. It is much thinner in the Baltic eggs, than in those of marine origin, reducing egg specific gravity of Baltic eggs. A higher degree of yolk protein hydrolysis to free amino acids causes a higher egg osmolality and a higher water uptake in the post-vitellogenesis phase prior to shedding. The higher water content causes the oocyte to expand at the expense of the chorion. The thickness of the chorion may thus be the result of stretching but it does not necessarily affect egg weight. Rather, the chorion may still comprise the same weight, but relative to the egg size it may still be an important factor determining egg specific gravity, and hence salinity for neutral buoyancy (Thorsen et al., 1996).

In recent investigations it has been shown that the pelagic spawning flounders in the Baltic Sea can be genetically separated between different areas, which further confirms that the differences in egg characteristics between the eggs obtained from females caught in Bornholm and those obtained in Gdansk and Gotland basins reflect a true separation of the stock. Florin and Höglunds (2005) genetic analysis recognized genetic differences between the flounders
inhabiting the eastern parts of the Baltic and those inhabiting areas further southwest. They suggested at least three different spawning stocks of flounder. One spawning population inhabiting the eastern Baltic Sea, ranging from the Gdansk deep in the south to areas surrounding Åland in the Northern Baltic Proper, and stretching to Gulf of Finland in the East. The other spawning population has a more south-westerly distribution range, including flounder spawning in Öresund in the south to areas surrounding the Bornholm basin in the northern parts. Flounder belonging to this spawning population is genetically separated from those spawning in the Skagerrak, Kattegat and the North Sea. Furthermore, several tagging experiments (Otterlind, 1966; 1967; Bagge, 1966 referred to in Höglund et al. 2008; Bagge and Steffensen, 1989), have showed migratory patterns between different areas to be insubstantial, indicating the plausibility of dividing the flounder stock into several different management units. However, landings in Estonian waters in the Gulf of Finland, demonstrates that salt water inflows may affect the migration pattern for pelagic spawning flounder, as spawning stock biomass has been reported to increase in years following inflow events (Drevs, 1999).

Today, pelagic spawning flounders are divided into two populations, according to the ICES subdivisions. One population is found in the Arkona and Bornholm Basins (SD 24 and 25) and the other in the Gdansk and Eastern Gotland basins (SD 26 and 28). There is also one population spawning demersal eggs in the Western Gotland basin (SD 27) and in the northern Baltic Sea (SD 29-32) (Florin, 2008).

Knowledge about stock discrimination is important for achieving sustainable management, as the Baltic flounder has adapted to the different hydrological conditions prevailing in the different spawning areas. It has been proposed that successful reproduction may occur regularly in Bornholm and Arkona basins, but in Gdansk and Gotland basins it is dependent upon inflowing events improving environmental factors in the deeper layers (Nissling et al., 2002), which is of uppermost importance when planning a sustainable fishery. This study clearly demonstrates the importance of Baltic inflows for increased egg survival probabilities, and it confirms the theory stated above.

In Bornholm basin 2014, salinity below the halocline averaged 13.71 ± 1.95, and the depth range for neutral egg buoyancy varied between 59 and 72 meters, except for one outlier at 52 meters, which displayed a notably lower egg specific gravity than the other egg batches. The major Baltic inflow in the winter between 2014 and 2015 caused a salinity increase to 15.46 ± 2.56 in the bottom water, resulting in a lift of the depth range for neutral egg buoyancy to between 53 and 63 meters when excluding the outlier. The uplift of the range of neutral egg buoyancy caused a significant increase in oxygen concentration at the depths where eggs managed to stay buoyant (p<0.01). Oxygen concentration within the depth range for neutral egg buoyancy in 2014, were sufficient to sustain a survival probability of 47%, but the improved salinity conditions of 2015 implied a survival probability of 100%.

In Gdansk basin salinities below the halocline averaged 10.63 ± 1.29 in 2014, and oxygen concentration within the depth range for neutral egg buoyancy was at most depths lower than the critical levels needed for egg survival. Only 4 of the egg batches, displaying the lowest egg specific gravity would have survived the severe conditions prevailing before the inflow event. The shallower depth range for neutral egg buoyancy in 2015, in combination with increased oxygen concentrations allowed survival for all eggs, just like in the Bornhom basin.
Egg survival has always been lowest in Gotland basin (Köster et al., 2005) and that is clearly demonstrated in the results of this study. Even though the inflowing water in the winter of 2014 was the third largest inflow in over 100 years (Mohrholz et al. 2015), conditions in April 2015 was not sufficient to increase egg survival probabilities. All eggs would have died also in 2015, although the dominant mortality cause shifted from sedimentation to oxygen deficiency. This suggests either oxygen conditions so severe before the inflow that the inflowing water was not sufficient to alter them, or the inflowing water had not yet fully reached the deep basin in the eastern Gotland area at the time of investigation.

When comparing the conditions in April with those in May, it seems that the inflowing water had not reached the Gotland basin in May either, and therefore the Eastern Gotland basin did not constitute a suitable spawning habitat for flounder in 2015. As the Baltic Sea has a long turnover rate, it is still possible that the Major Baltic inflow of 2014 may contribute to improved spawning conditions in upcoming years. Hence, to correctly analyse the inflow effect upon spawning conditions in the Eastern Gotland basin it is of importance to continue investigations on egg survival probabilities in the years to come.

Bornholm basin is situated closer to the shallow straits, connecting the Baltic Sea to the North Sea, thus even smaller, baroclinic inflows may improve conditions in the bottom water. Baroclinic inflows are driven by the salinity gradient between the Baltic Sea and the Kattegat, and they usually occur during long calm periods in summer. However, such inflows typically have reduced oxygen concentrations, due to biogeochemical processes consuming most of the oxygen (Mohrholz et al. 2015). Although baroclinic inflows do not generally improve oxygen conditions in the bottom water, the addition of saline water helps the eggs to achieve neutral buoyancies higher up in the water column. Hence the eggs are less likely to be exposed to the detrimental oxygen levels in deeper layers (Köster et al. 2005). Areas located closer to the straits are also supplied with saline water during minor barotropic events, and as they usually occur in the winter season they provide oxygen to the deeper layers, which is why the bottom waters in the Bornholm basin seldom gets oxygen depleted, as is the case in the basins situated in the centremost parts of the Baltic, i.e. the Gdansk and Gotland basins (Mohrholz et al. 2015).

Biological fluctuations have been known to occur due to varying hydrological conditions for a long time. In the 1930s salinities in the central Baltic began to rise, and 1951 the biggest inflow ever recorded caused salinities unprecedented since the beginning of recordings in 1902. To be noted is that salinity in the central part of the Eastern Gotland basin reached its’ maximum a few years after the big inflow in 1951. The frequent supply of saline water and oxygen during this time period maintained suitable spawning habitats for pelagic spawning fishes in general, e.g. cod landings were reported to be exceptionally high. However, the years following the inflow event in 1951 consisted of a period of weak intrusions, and already in 1957 anoxic conditions were reported in the Gotland deep (Segerstråle, 1969). When oxygen is present in the bottom waters, phosphorus is fixed in the sediments as an iron-III-hydroxyphosphate complex, but the change in the redox potential when conditions turn from oxic to anoxic allows hydrogen sulfide to reduce this complex, and accordingly phosphate and iron (II) is released in the bottom water (Mohrholz et al., 2015). The stagnation period therefore resulted in an accumulation of phosphates in the deeper layers, and by the time of the next inflow to reach the basin in 1962, the vertical mixing caused an uplift of the nutrient enriched bottom waters, and the summer in 1962 primary productivity exceeded all earlier
observations (Segerstråle, 1969). High primary productivity result in high decomposition which consumes most of the oxygen in the water. Hence, great inflows may only result in shorter periods of suitable spawning habitats (Ojaveer & Kalejs, 2005).

During the 70s, major Baltic inflows occurred regularly and in the southern parts of the Gotland basin both salinity and oxygen conditions generally supported development of flounder eggs. During some years of favourable conditions also the central parts of the basin contributed with suitable spawning habitats, and highest landings occurred during this period (Ustups et al., 2013). In the beginning of the 1980s, the longest stagnation period ever recorded resulted in a freshening of the Gotland basin (Matthäus and Franck, 1992), and consequently the depth range of the suitable reproductive layer declined as it shifted to deeper parts of the water column. The reproductive volume continued to decrease until 1993, when a major Baltic inflow again brought saline water into the central parts of the Eastern Gotland basin, and reoxygenated the bottom waters. The inflowing water had the power to lift the reproductive volume only slightly, and already a few years after the inflow event neither the central nor the southern parts of the basin comprised a suitable spawning ground for pelagic spawning flounder. The inflow of 2003 was only able to improve conditions in the southern part of the basin, and ever since the last inflow, spawning grounds have continued to deteriorate. In 1988 to 1990 as well as in 2001 the reproductive volume was absent, however even in the absence of suitable spawning habitat flounder ichthyoplankton was found in the basin, suggesting that hydrological data do not fully render the complete understanding of oxygen and salinity conditions. Thus, it is likely that the reproductive volume is underestimated. An alternative theory would be that the larvae have drifted from the demersal spawning population, or that the threshold values for egg survival are somewhat incorrect (Ustups et al., 2013).

Considering the present consensus on climatic driven ecosystem changes in the Baltic Sea, it seems that the reduced water inflows observed since the 1980s will not change in the coming decades. Climate modelling indicate higher temperatures, increased precipitation and possible changes in wind direction and speed. Higher precipitation result in lower salinity in the Baltic Sea, as the river runoff increases, and even though higher temperatures will lead to higher evaporation, it will never exceed the precipitation rates. In the past, increased river runoff has elevated water levels in the Baltic, hence inflow frequencies have decreased, and it is likely that the same pattern will continue in the 21st century (MacKenzie 2007). In addition to the threats from decreased inflow frequencies and higher river runoff, elevated temperatures may have severe impacts on the flounder reproduction as well. Oxygen concentrations likely will decrease along with the accelerating oxygen consumption due to higher nutrient cycling in the bottom waters (Meier et al., 2011). Higher winter temperatures will further affect oxygen concentrations in the eastern Baltic as warmer water temperatures cause lower solubility of oxygen in the inflowing water (Hinrichsen et al., 2002).

The results in this study demonstrate the importance of saline water inflows for reproduction of flounder with pelagic eggs, and it urges the need for increased knowledge about the present and future hydrological conditions in different areas of the Baltic Sea. To achieve a sustainable management of the flounder stock as a whole, it is equally important to understand the population structure and migration patterns as the dynamics of reproduction in a changing environment.
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SAMMANFATTNING

Skrubbskäddan (Platichthys flesus) är en marin fiskart som anpassat sig väl till de bräckta förhållanden i Östersjön, och den återfinns i områden med lägre salthalt längre norrut än andra plattfiskar. Att leva i Östersjön, det största bräckvattenområdet i världen har tvingat arter att anpassa sig till de rumsliga och tidsmässiga variationerna i miljöförhållanden som återfinns i vattenansamlingen. Det har därför identifierats åtskilliga skillnader mellan de skrubbskäddor som lever i Östersjön och deras marina motsvarigheter.

I Östersjön kan skrubbskäddan indelas i två sympatriska populationer, en kustlekande som producerar demersala ägg, och en utsjölekande med pelagiska ägg. Pelagiska ägg är för sin överlevnad beroende av att kunna hålla sig flytande på ett djup med gynnsamma syreförhållanden. Reproduktionsframgången för den pelagiskt lekande skrubbskäddan är därför starkt kopplad till de rådande hydrologiska förhållanden i lekområdet. Många författare menar att den låga salthalten i Östersjön har fungerat som en stor evolutionär kraft, med selektion för större ägg med högre vatteninnehåll, som har en lägre specifik vikt och som därför hålls flytande i vatten med lägre salthalt. Olika hydrologiska förhållanden har lett till en genetisk differentiering av populationer som leker i Gotlands- och Gdanskbassängen, från de som leker i Bornholm- och Arkonabassängen, och det har också påvisats att äggens flytförmåga skiljer sig mellan de olika områdena. Det är därför viktigt att förstå de specifika hydrologiska förhållanden som råder i olika områden av Östersjön.


Syrehalten i det inflödande vattnet är säsongsberoende och vanligen är det endast de tillflöden som sker under vintertid som har tillräckligt hög syrekonsentration för att syresätta vattnet i Östersjöns djupbassänger. Syresättningen är också beroende av storleken på inflödet, då mindre inflöden hinner spådas ut innan de når de djupare områdena. Sedan 70-talet har antalet inflöden minskat markant, och sedan 1993 har endast 3 inflöden varit av en sådan magnitud att de nått djuppartierna längs den östra sidan av Gotland. Under de senaste decennierna har alltså Östersjön präglats av en utsöning, ett fenomen som sannolikt påverkat den pelagiskt lekande skrubbskäddans fortpflanzningsförmåga. Frequent förekommande saltvatteninflöden under 70-talet gynnade skrubbskäddans fortpflanzningsförmåga och syrekonsentrationerna i den södra delen av den östra Gotlandsbassängen var generellt tillräckligt höga för en framgångsrik utveckling av pelagiska ägg. Idag däremot har de långa stagnationsperioderna lett till anaeroba förhållanden i stora delar av Gotlandsbassängen, och områden som tidigare
varit framgångsrika lekhabitat har nu för låg salinitet och för låga syrenivåer för att äggen ska kunna överleva.

I december 2014 skedde ett stort saltvattensinflöde, och huvudsyftet med denna uppsats har varit att undersöka om inflödet haft en positiv inverkan på den pelagiskt lekande skrubbskäddans reproduktionsframgång i Bornholms- Gdansk- och Gotlandsbassängen.

Genom att studera förmågan hos olika honors ägg att hålla sig flytande inom reproduktionsvolymen, den delen av vattenmassan där förhållandena överskrider kriterierna för framgångsrik reproduktion (10.6 psu, ≥2 °C and 1.5 ml O₂∙1⁻¹), under våren 2015 och jämföra med de förhållanden som rådde under våren 2014, har det varit möjligt att demonstrera betydelsen av saltvatteninflöden för en ökad äggöverlevnad i de olika lekområdena.

Uppsatser behandlar mätningar på ägg från fisk som fångats i april 2014 samt i april 2015 i Bornholm, Gdansk och Gotlandsbassängerna. Trålning utfördes på ett djup som säkerställde att skrubbskäddorna tillhörde den utsjökande populationen (ca 50 till 90 meters djup). Totalt har ägg från 45 pelagiskt lekande honor använts, varav 15 fångades i Bornholmsbassängen, 4 i Gdanskjupet och 26 i Gotlandsbassängen.

Ägg och mjölke togs från lekande individer, och befruktning utfördes artificiellt i 7°C vatten, med en salthalt på 20 psi, varpå de inkuberades fram till experiments utförande. Den specifika vikten hos ca 30 ägg per hona bestämdes i densitetsgradIENTskolumner, där positionen av ägg jämfördes med positionen av 9-10 densitetsflöten med känd specifik vikt, 24 timmar efter befruktning. Medelvärden för den specifika vikten för ägg som erhållits i respektive bassäng jämfördes med en envägs-ANOVA för att undersöka förekomst av eventuella subpopulationer i de olika områdena.

Den specifika vikten av samtliga äggportioner antydde att de ägg som erhållits från fisk i Gdansk- och Gotlandsbassängen tillhörde samma population, medan ägg från honor som fångats i Bornholmsbassängen tillhörde en annan population. Ägg från Gdansk- och Gotlandsbassängen behandlades därför som samma population och analyserades gemensamt för att undersöka sannolikheten för överlevnad i Gdansk och Gotlandsbassängen.

Djup, vattendensitet, salinitet, temperatur och syrekonzentration mättes med CTD vid varje provtagningsstation, och en station per bassäng användes för jämförelse av sannolikheten för äggöverlevnad mellan 2014 och 2015. Genom att jämföra den specifika vikten hos ägg från honor i respektive område med vattendensiteten som uppmätts 2014 och 2015 i respektive bassäng, kunde djupet där äggen utvecklas bestämmas. Sannolikheten för äggöverlevnad bedömdes i enlighet med de tröskelvärden som föreslagits av Hinrichsen et al. (personal communication), där äggen antas överleva vid >1,5 ml O₂∙1⁻¹ och vid temperaturer >2°C.


Med tanke på den rådande konsensusen om pågående klimatdrivna ekosystemförändringar i Östersjön, verkar det troligt att trenden med fortsatt reducerade vatteninflöden sedan 80-talet kommer fortgå. Klimatmodelleringen förutspår högre temperaturer, ökad nederbörd och möjliga förändringar i vindriktning. En högre nederbörd skulle i och med den ökade avrinnningen från vattendrag innebära en lägre salinitet i Östersjön. Tidigare har även påvisats att ökad avrinning från floder och vattendrag har lett till högre vattennivåer i Östersjön, och därmed har frekvensen av saltvatteninflöden från Nordsjön minskat. En utsättning av Östersjön kan komma att få mycket negativa konsekvenser för den pelagiskt lekande skrubbskäddan, då deras ägg kan få svårigheter att hålla sig flytande vid djup med tillräckliga syrenivåer för äggöverlevnad. Ökade temperaturer kan också bidra till ytterligare försämrade förutsättningar för lekframgång, då syrekoncentrationer kommer minska i takt med accelererande syrekonsommation vid en högre näringsomsättning i bottenvattnet.

Resultaten i den här studien påvisar betydelsen av saltvatteninflöden för en ökad överlevnad för pelagiska skrubbskäddëgg, och den betonar behovet av en ökad förståelse kring de nuvarande och framtidiga hydrologin och ryttmässiga områden av Östersjön. För att åstadkomma ett hållbart fiske är det av yttersta vikt att en ökad kunskap om populationsstrukturer och migrationsmönster, såväl som en ökad förståelse av reproduktionsdynamiken i Östersjöns ständigt föränderliga miljö.