Nutritional situation for larval Atlantic herring (*Clupea harengus* L.) in two nursery areas in the western Baltic Sea

Matthias Paulsen¹,²*, Cornelius Hammer¹, Arne M. Malzahn³,⁴, Patrick Polte¹, Christian von Dorrien¹, and Catriona Clemmesen²

¹Thünen-Institute, Institute of Baltic Sea Fisheries, Alter Hafen Süd 2, 18069 Rostock, Germany
²Helmholtz Centre for Ocean Research (GEOMAR), Düsternbrooker Weg 20, 24105 Kiel, Germany
³Department of Marine Science and Fisheries, College of Agricultural and Marine Sciences, Sultan Qaboos University, PO Box 34, PC: 123 Al-Khod, Sultanate of Oman
⁴Alfred Wegener-Institute for Polar and Marine Research, Biologische Anstalt Helgoland, Postbox 180, 27483 Helgoland, Germany

*Corresponding author: tel: +49 431 6004567; fax: +49 431 6004553; e-mail: mpaulsen@geomar.de
‡Present address: Institute of Baltic Sea Fisheries, Alter Hafen Süd 2, 18069 Rostock.


Received 31 October 2012; accepted 11 September 2013; advance access publication 8 October 2013.

The Greifswalder Bodden (GWB) is considered to be the most important spawning and nursery area for the western Baltic spring-spawning herring. However, the biotic and abiotic reasons for this are still unclear. Consequently, we investigated larval growth conditions in the GWB and in the Kiel Canal (KC), another nursery and spawning area of Baltic herring. We investigated prey quantity and quality [copepod abundance and essential fatty acid (EFA) concentration] as well as biochemically derived growth rates and fatty acid content of larval herring in spring 2011. A significant correlation between larval growth and larval EFA concentration could be observed in the GWB. The highest growth rates and EFA concentrations in the larval herring coincided with high food quality. Compensating effects of food quality on food quantity and vice versa could be observed in both the GWB and the KC. While larval growth rates in the KC were high early in the season, highest growth rates in the GWB were achieved late in the season. In conclusion, neither area was superior to the other, indicating similar growth conditions for larval herring within the region.

**Keywords:** DHA, EPA, essential fatty acids, food quality, growth, prey density.

**Introduction**

Early life stages are crucial for the determination of year-class strengths. A hundred years ago, Hjort (1914) already hypothesised that large numbers of suitable prey items during the stage of first feeding are responsible for good recruitment in marine fish stocks. This has been the basis of recruitment research ever since, and his hypothesis was continually refined and supported by modelling, experimental, and field-workers alike (Rosenthal and Hempel, 1970; Cushing, 1974; Sinclair and Tremblay, 1984; Anderson, 1988; Sinclair, 1988; Cury and Roy, 1989; Cushing, 1990; Buckley and Durbin, 2006). However, it is still not possible to reliably predict recruitment simply based on biotic and abiotic parameters. Hence, other uninvestigated or only rarely investigated factors seem to play an important role as well.

Although the strong effects of food quality on larval rearing are well known from aquaculture as well as experimental work, this issue is mostly neglected in field studies. In particular, the effect of essential fatty acid (EFA) supply on the performance of marine fish larvae is well documented in experiments. Total amounts of docosahexaenoic acid (DHA) and eicosapentaenoic acid (EPA) as well as their ratio, along with arachidonic acid affect development, growth, and survival of marine larval fish (Mouretra et al., 1991; Bell et al., 1995; Furuita et al., 1998; Copeman et al., 2002; Van Anholt et al., 2005).
constant, while the RNA content varies with the nutritional condition is based on the assumption that the DNA content of a cell is 1994; Caldarone ical method to determine the condition of fish larvae (Clemmesen, 1972). 

Eurytemora affinis RNA content of food source (Schnack, 1972). 

suitable for Baltic herring. The question remains if both areas are logical features in common; for example, high nutrient load, no differences between GWB and the KC, they have important hydro- GWB, the KC is an artificial inland waterway. Despite the obvious as the Kiel Canal (KC). In contrast to the natural habitat of the many other quantitatively less important spawning grounds, such tentative differences are between this major spawning ground and the 

The principle of using RNA/DNA ratios as an indicator of con- current study was performed, but the RNA content was measured in fish larvae simultaneously from the GWB and KC. 

DHA, in the diet of laboratory-reared cod larvae was reflected in an increase in larval growth using this method (St John et al., 2001). 

Based on our observations that larval growth is affected by food quality in experimental work and that the GWB potentially provides more recruits than other spawning areas of the western Baltic spring-spawning herring, we defined the following two hypotheses: (i) food quality as determined by concentrations of EFAs significantly affects larval growth in situ, and (ii) the GWB provides better nutritional conditions for larval growth than the KC. To test this, we analysed and compared food quantity and quality in terms of DHA and EPA and investigated larval growth, based on larval RNA/DNA ratios, as well as DHA and EPA concentration of larval herring simultaneously from the GWB and KC.

Material and methods

Sampling

Herring larvae (Clupea harengus L.) were sampled along with meso- zooplankton and abiotic parameters to compare the growth conditions of larval herring in different spawning sites. One sampling site was located in the KC at a station 15 km inland from the open Baltic Sea (ICES Subdivision 22; Figure 1a), whereas the other sampling site was located in the GWB (ICES Subdivision 24; Figure 1b). All samples were collected between April and June 2011 during the seasonal occurrence of larval herring.

Herring larvae were sampled with a bongo net (60 cm diameter, 335 and 500 µm mesh size, respectively) that was heaved in an oblique haul. All larvae were frozen on board within 30 min of the haul. Before further analysis, larval standard length was measured to the lower 0.1 mm and freeze-dried for 24 h using a freeze drier (CHRIST ALPHA 1–4 LSC). Thereafter, the larvae were weighed to the nearest 0.1 µg (SARTORIUS microbalance SC2). The prey field was sampled with a WP2-net (200 µm mesh size) that was 

Figure 1. Sampling sites for larval herring and copepods in the western Baltic Sea during spring season. (a) KC; (b) GWB.
hauled once vertically from 3 m above the bottom to the surface in the KC, and from 1 m above the ground in the GWB.

**Mesozooplankton abundance**

The mesozooplankton samples, conserved with 4% formaldehyde, were separated in a plankton divider (Kott, 1953) up to the point where at least 100 individuals of the most abundant copepod species were available in the section that was counted. All copepods were determined to the species level where possible, although for *Acartia* species, some remained classified at the genus level.

**Fatty acids**

Fatty acids (FA) were measured as FA methyl esters by gas chromatography slightly modified after Malzahn et al. (2007a, b). Lipids were extracted with dichloromethane/methanol (vol. 2:1) for a minimum of 72 h at −80°C. After the extraction, larvae were removed and stored in a desiccator to vaporize the adhering dichloromethane. Copepod samples were treated similarly, but with an additional 30 min of ultrasound bath after the 72 h extraction at −80°C.

**RNA/DNA analysis**

For better comparability of the RNA/DNA ratio and the EFA concentration of the larvae, RNA/DNA ratio and FA were measured in the same larval individuals. This was possible by first defatting the herring larvae and then homogenizing the defatted carcass for the RNA/DNA analysis according to Clemmesen (1993) and Belchier et al. (2004). For both analyses, complete larvae were used. Therefore, the ratio determined is a whole larva respond neglecting the fact that different tissue types respond differently to changes in food availability (Olivar et al., 2009). Some modifications were necessary because of the increased elasticity of the larvae due to the missing lipids. The cells of the defatted larvae were homogenized in three steps: (i) freeze-dried larvae were placed in a cell mill for 15 min together with different sized glass beads (diameter 2.0 and 0.17–0.34 mm), (ii) supersonic treatment in Tris–sodium dodecyl sulphate (SDS) buffer (Tris 0.05 mol l⁻¹, NaCl 0.01 mol l⁻¹, ethylenediaminetetra-acetic acid 0.01 mol l⁻¹, SDS 0.01%), and (iii) larvae together with buffer and glass beads were placed in the cell mill for 15 min. Then, the homogenate was centrifuged at 3829 g (6800 rpm) at 0°C for 8 min (Sigma Laboratories Centrifuge 3–18k). A combined fluorometric measurement of RNA and DNA in the homogenate in a microtiter fluorescence reader (Labsystems, Fluoroscan Ascent) followed. Next, RNase was added to the samples to digest the RNA (30 min at 37°C) and the remaining DNA was measured. The difference of the sum of total nucleic acids and the remaining DNA was assigned to be RNA. By using the calibration curve fitted to the standard measurements (23s r RNA Boehringer), the amount of RNA was calculated. The RNA calibration was repeated every measurement day. The DNA concentrations were calculated using the relationship between RNA and DNA described by Le Pecq and Paoletti (1966) with a slope ratio of 2.2 for DNA to RNA.

**Growth calculation**

Larval instantaneous growth rates were calculated according to Buckley et al. (2008). The best-fit multispecies growth model that was chosen for further calculation was:

\[
G_i = 0.0145 \times sRD + 0.0044 \times (sRD \times T) - 0.078,
\]

where \(G_i\) is the instantaneous growth rate, \(sRD\) the standardized RNA/DNA ratio (Caldarone et al., 2006), and \(T\) the temperature at the given date. Results have to be interpreted in the way that a value of 0 would mean no growth at all and a value of 1 would be a doubling of the weight of the larva per day.

**Estimation of larval herring production in both nursery areas**

To gain a rough estimation of the larval herring production of the KC and the GWB to relate the productivity of both systems, available larval abundance data (\(n\) m⁻³) from the whole season were used to calculate the median of larval herring abundance. For the GWB (area: 512 km²), abundance data of 36 stations were available and used to get the best approximation possible. Analyses of larval growth as well as chlorophyll a data from four stations in the GWB have shown limited spatial variability (Paulsen et al., in prep.), indicating comparable conditions within the system. Owing to logistic

![Figure 2](http://icesjms.oxfordjournals.org/)
Silica and chlorophyll a concentrations
Silica as well as chlorophyll a concentrations were analysed according to Grasshoff et al. (1999).

Statistics
Statistical analyses were performed using the statistic software package STATISTICA (version 6). The data were checked for normal distribution and homogeneity of variances using the Shapiro–Wilk and the Levene tests. When variances were heterogeneous, data were transformed by extracting the cube and fourth root, respectively. To check between sampling days, a one-way analysis of variance (ANOVA) was conducted and a Tukey honestly significant difference (HSD) test was used for post hoc comparison. Linear regressions were performed to test for effects of larval EFA on larval growth. To test for differences between the two habitats, the season was split into two time windows, where drastic changes in prey availability and larval growth were observed. Larval growth rates, larval and copepod EFA concentration, as well as copepod abundance within each time window and region were pooled. Thereafter, the different parameters were tested with a t-test between the two regions.

Results
Greifswalder Bodden
The mesozooplankton assemblage of the GWB consisted mainly of copepods. Acartia spp. was the dominant genus until 25 May, contributing 60–80% to the copepodid community. The strong increase in prey abundance on 1 June was driven by increasing Eurytemora abundance. This species contributed 70% of the copepodids on that day. Thereafter, the contribution of Eurytemora decreased strongly and Acartia became dominant again on 15 June (97% of all copepodids).

In the GWB, instantaneous growth rates of larval herring followed the copepodid abundance (Figure 2i). An exception was the time window between 1 and 15 June, when growth remained constantly on a high level despite an approximate halving in prey abundance. Prey DHA concentration increased significantly between 4 and 18 May (ANOVA, Tukey HSD, p < 0.05), which was reflected in the significantly increasing DHA concentration of the larvae (ANOVA, Tukey HSD, p < 0.05, Figure 2ii). Growth rates increased significantly on 1 June (ANOVA, Tukey HSD, p < 0.01) when prey abundance increased sixfold. However, not only growth rates increased, but also average larval standard length (Table 1). This affects larval growth rates, since during adequate growth conditions, larger larvae generally have higher growth rates than smaller ones (Clemmesen, 1994). While copepodid abundance decreased by 50% between 1 and 15 June, DHA concentration of the copepods showed an increasing trend and larval growth remained constant. Variance in growth and DHA concentration of the herring larvae was low when nutritional conditions were bad between 4 and 25 May. Although growth conditions in terms of prey abundance and copepod DHA concentration were similar between 18 May and 15 June, larval growth rates were significantly higher on 15 June. However, temperatures were 7°C higher on 8 June than on 11 May (Figure 8). The EPA concentration of the copepods increased similar to the DHA concentration between 27 April and 18 May. As a result, EPA concentrations increased in the larvae as well (Figure 2iii).

Table 1. Average standard length per date in the GWB.

<table>
<thead>
<tr>
<th>Date</th>
<th>27 April</th>
<th>4 May</th>
<th>11 May</th>
<th>18 May</th>
<th>25 May</th>
<th>1 June</th>
<th>8 June</th>
<th>15 June</th>
</tr>
</thead>
<tbody>
<tr>
<td>Length</td>
<td>9.5 ± 2.0</td>
<td>9.8 ± 1.8</td>
<td>10.8 ± 2.4</td>
<td>12.4 ± 2.5</td>
<td>12.9 ± 3.4</td>
<td>15.3 ± 2.3</td>
<td>14.0 ± 2.8</td>
<td>13.1 ± 1.9</td>
</tr>
</tbody>
</table>

Figure 3. KC. Error bars indicate standard deviations. (i) Instantaneous growth rate ($G_i$) of larval herring and copepodid abundance per cubic meter over time. (ii) DHA concentration of larval herring and copepods over time. (iii) EPA content in larval herring and in copepods over time. Different letters besides the data points denote significant differences.
Kiel Canal

*Eurytemora* dominated the copepodite assemblage during late April and throughout May (90–100% of all copepodites sampled) in the KC. From late May on, *Acartia* dominated (70–80% of all copepods). Similar to the GWB, growth rates of larval herring followed prey abundance in the KC (Figure 3i). However, growth rates remained constant, even when prey abundance increased eightfold on 13 May. This occurred when DHA concentration of the copepods decreased significantly (ANOVA, Tukey HSD, *p* < 0.05) and DHA of the larvae showed an increasing trend (Figure 3ii). Since larvae were larger on 13 May compared with 3 May (Table 2), a faster growth due to the increase in size would be expected. When food quantity abruptly became limited on 31 May, growth rates of the larvae decreased significantly. While DHA concentration in the larvae increased during the whole season (Figure 3ii), EPA remained constant after an initial increase (Figure 3iii).

Comparison of both areas

In the GWB, larval growth was significantly correlated with the DHA and EPA concentration in the larvae (*p* < 0.01, Figures 4 and 5). Highest growth rates were achieved at highest DHA and EPA concentrations in the larvae. When DHA and EPA concentrations in the copepods were highest on 18 May, larvae had the highest DHA and EPA concentrations and grew at the highest rates. In contrast to this, no significant correlation between DHA and larval growth was detected in the KC (Figure 6), though one between larval growth and EPA was found (Figure 7).

Over the whole season, chlorophyll *a* values were higher in the GWB when compared with the KC (Figures 8 and 9). Silica values were very low (<1 μmol l⁻¹) in the GWB until 11 May, when silica values started to recover (Figure 8). In contrast, silica values were above 21 μmol l⁻¹ in the KC throughout the whole season (Figure 9).

As aforementioned, to better compare both habitats, the season was divided into two time windows according to drastic changes in prey availability and larval growth. The first time window reached from 27 April to 25 May, while the second one made up of two or three samplings from 31 May to 15 June, depending on the habitat. In contrast to significantly different prey abundances in both time windows (*p* < 0.05, Table 3), prey DHA concentration was only significantly different in the second time window (*p* < 0.05, GWB > KC, Table 3). In the first time window, larvae grew significantly faster in the KC, whereas growth rates were significantly higher in the GWB in the second time window (Table 4). This was true for all ontogenetic stages. Larval FA data were only available for the first time window. Contrary to larval growth rates, DHA and EPA concentrations were only significantly different in certain ontogenetic stages (Table 4). Yolk-sac larvae (<9 mm) had significantly higher DHA and EPA concentrations in the KC than larvae from the GWB. At first feeding, no differences could be detected, while EPA was significantly higher in pre-flexion larvae (11–14 mm) of the GWB. In post-flexion larvae, EPA as well as DHA were significantly higher in the GWB compared with the KC irrespective of the bad growth conditions in terms of prey abundance and prey EFA concentration during that time window.

The calculation of the rough estimate of total larval production of the different spawning sites revealed a 24-fold higher production of larval herring in the GWB compared with the KC.

Discussion

Though growth of fish larvae is dominantly affected by food availability and temperature, other factors such as salinity, oxygen, and the larval’s interactions with other organisms are known to be influencing factors (Clemmesen, 1994; Johnes, 2002). Furthermore, it is known from experimental work that food quality can also be an important factor (Copeman *et al.*, 2002; Malzahn and Boersma, 2009). The present study shows that high food quality is able to compensate...
for low food quantity and vice versa for larval fish in the field. This can lead to constant growth rates in larval herring even when both parameters develop in opposing directions. Examples for these effects can be found on 15 June in the GWB and on 13 May in the KC. However, the increase in copepod DHA was relatively modest compared with the decrease in prey abundance on 15 June in the GWB, which leads to the assumption that other uninvestigated factors, for instance, essential amino acids, vitamins, sterols (Cahu et al., 2003), or abiotic factors, might have played a role in addition to the increase in DHA. A possible explanation for this compensatory effect is that the demand for essential components is assumed to be constant, depending on the developmental stage of the larva. When food quality decreases, the larva needs to capture more prey to accommodate this demand, which is an energy-consuming process. In addition, the EFA are needed as construction material and precursors to build-up neural tissue along with cell membranes and hormones (Sargent et al., 1999). Therefore, growth is limited when essential component supply is limited.

Although it is possible to compensate for nutritional value and food quantity to a certain extent, this does not necessarily happen. During the early season in the GWB, very low food quantity was coupled with extremely low food quality, and this led to very low growth rates. Variances in larval growth data were very small during this period, apart from the first date when yolk-sac larvae appeared who had not begun to externally feed. Growth of aquatic larval organisms is at least partly genetically determined (Meyer and Manahan, 2010), and slow-growing individuals may have an advantage when growth conditions are poor. Fast-growing individuals starve during bad feeding conditions leading to small variances in larval growth. In contrast, variance of larval growth is high when growth conditions are moderate or good (Houde, 1987; Voss et al., 2006). In this case, relatively slow- and fast-growing individuals occur simultaneously, although the fast-growing individuals may have an ecological advantage.

Growth of larval herring in the GWB increased significantly and remained on a constant high level from 1 June onwards. Here, different aspects might have played a role: first, food quantity increased strongly on 1 June, which enabled the larvae to take up more prey with a constant quality. Second, temperature increased more than 3°C between 25 May and 1 June. This enabled the larvae to take full advantage of the improved nutritional situation. Similarly, a temperature increase of 7°C is a possible reason for higher growth rates despite very similar food quality and quantity conditions between 18 May and 15 June.

We could show in the GWB that larval growth increases with increasing DHA and EPA concentration in the larvae. The highest DHA and EPA concentrations of the copepods were reflected in the
highest DHA and EPA concentrations of the larvae and both these concentrations were likely two important factors that led to the highest larval growth rates. Conversely, only larval EPA showed an effect on larval growth in the KC, while larval DHA did not affect larval growth in our correlation analysis. The reason for the pronounced effects of larval EFAs in the GWB and EPA in the KC is that the development of prey EFA was consistent while prey quantity remained constant over the course of several weeks consequently leading to an accumulation or dilution of EFA in the larvae. In the KC, no correlation between larval DHA and their growth rates existed. Here, high food quality was offset by low food quantity, and vice versa, and this might have been a reason for the very similar DHA values found in the larvae over a 4-week period. Nevertheless, prey DHA probably affected larval growth in the KC, for example, on 13 May, although the strong decrease in larval DHA did not lead to decreasing DHA concentrations in the larvae themselves due to high prey quantities. St John and Lund (1996) showed that it takes 13 days until larval cod FAs were in equilibrium with the prey. However, this is just the complete effect on the FA in the larvae themselves, and not related to larval growth. The larvae are not able to take up EFA selectively, but depend on the composition delivered by the food. FAs in the larvae change successively, starting at the point when food with a different FA composition is taken up. As a result, the larvae are able to grow faster when more essential components are delivered, leading to an up-regulating of their RNA content. Contrary to their FA metabolism, larval growth is actively regulated since they are able to build-up and catabolize RNA actively. Though we suppose that this is an ongoing process, we expect a detectable time delay between the DHA concentration of the prey and larval growth of ~3 - 4 days at the latest, according to experimental data regarding the time delay in herring larvae facing different prey quantities (Clemmesen, 1994). However during short time frames, significant effects in larval DHA are expected only when prey quality changes strongly. Even when the effect of a changing food quality or quantity on larval DHA is not significant yet, the process is nonetheless ongoing. This could explain the constancy of larval growth and EPA during adequate growth conditions in the KC, because contrary developments of EPA in the prey and prey abundance were occurring. Additionally, other parameters not investigated in this study influence larval growth, for instance, essential

**Table 3.** Results from t-tests between prey quantity and quality of GWB and KC.

<table>
<thead>
<tr>
<th>Prey abundance</th>
<th>27 April - 25 May</th>
<th>31 May - 15 June</th>
</tr>
</thead>
<tbody>
<tr>
<td>% DHA</td>
<td>p &lt; 0.05, KC &gt; GWB</td>
<td>p &lt; 0.05, GWB &gt; KC</td>
</tr>
<tr>
<td>% EPA</td>
<td>p &gt; 0.05</td>
<td>p &gt; 0.05</td>
</tr>
</tbody>
</table>

**Table 4.** Results from t-tests of larval herring originating in GWB and KC.

<table>
<thead>
<tr>
<th>Length Class</th>
<th>9 – 11 mm</th>
<th>11 – 14 mm</th>
<th>&gt;14 mm</th>
</tr>
</thead>
<tbody>
<tr>
<td>G1 I</td>
<td>p &lt; 0.001; KC &gt; GWB</td>
<td>p &lt; 0.001; KC &gt; GWB</td>
<td>p &gt; 0.05; KC &gt; GWB</td>
</tr>
<tr>
<td>G1 II</td>
<td>–</td>
<td>–</td>
<td>p &lt; 0.001; GWB &gt; KC</td>
</tr>
<tr>
<td>% DHA</td>
<td>p &lt; 0.05; KC &gt; GWB</td>
<td>p &gt; 0.05</td>
<td>p &gt; 0.05</td>
</tr>
<tr>
<td>% EPA</td>
<td>p &lt; 0.05; KC &gt; GWB</td>
<td>p &gt; 0.05</td>
<td>p &lt; 0.01; GWB &gt; KC</td>
</tr>
</tbody>
</table>

The length classes reflect different ontogenetic stages of the larvae: yolk-sac (<9 mm), first feeding (9 – 11 mm), pre-flexion (11 – 14 mm), and post flexion (>14 mm). The season is divided into two time windows, according to drastic changes in prey availability and larval growth in both habitats. G1 I and DHA and EPA are results from time window 1, reaching from 27 April to 25 May, while G1 II shows results from time window 2, 31 May to 15 June. Larval FA data to test exist only from time window 1, these results are shown.
column, and it was not distinguished between prey quantity and prey availability. Copepods tend to accumulate in patches, e.g. in fine layers close to the thermocline. However, both areas, GWB and KC, are well mixed due to very shallow waters in the GWB (5.6 m in depth on average) or heavy shipping traffic for the KC. Though it is not expected that patchiness does not occur in these areas, it might be reduced due to the strong mixing. Since larval growth data from both areas follow quite well the observed prey field development, we are confident that our method is reliable to describe prey field development in our investigation areas. According to Schnack (1972), prey biomass of 14 mm estuarine western Baltic herring larvae consisted of 90% copepods and adults, and only 10% of nauplii. At least at the first-feeding stage, it is expected that the larvae feed on nauplii and protozoans. However, because most of the analysed larvae were beyond that stage, it is assumed that samples taken with 200 μm mesh size sufficiently describe prey field conditions for estuarine larval herring.

In the KC, prey abundance was significantly higher and larval growth rates were significantly higher compared with the GWB up until 25 May. As the season proceeded, however, in the GWB, the larvae experienced favourable growth conditions with significantly higher prey abundance and DHA concentration of the prey that led to significantly higher growth rates than in the KC. In contrast, the KC growth conditions worsened late in the season due to a strong decline in prey abundance. Interestingly, at least in recent years, this pattern of larval growth conditions seems to be typical for both nursery areas. The time-series of the KC (Catriona Clemmesen, GEOMAR) shows the same trend in prey field succession since 2005 (Donner, 2006; Peschutter, 2008; Paulsen, 2010), indicating that recruits from the KC originate mainly from early in the season. In contrast, data from the GWB time-series (Institute of Baltic Sea Fisheries) revealed that the late season provided the most recruits in recent years (Polte et al., 2014). At this time, growth rates of the larvae were also highest. Since predators selectively prey upon slow growing larvae (Takasuka et al., 2003), larval growth data in the present study support the recruitment data mentioned above. Our results are also consistent with calculations by Houdé (1987) where even relatively small changes in growth rates can lead to strongly increased mortality in larval Atlantic herring.

Since no strong differences in larval growth conditions of both areas could be detected, there have to be other reasons for the potential importance of the GWB as a nursery area (Oeberst et al., 2009b). The rough estimate of total production of both GWB and KC showed that the GWB produced 24 times as many larvae as the KC did. Although our sampling site in the KC is at the edge of the main spawning area and the true production is probably higher than the calculated one, results indicate that a possible reason for the importance of the GWB as a nursery area is simply a size effect. Since the volume of water used for spawning of the GWB is 41 times larger than that of the KC, this is tenable. This would also mean that while the KC may provide more recruits per cubic metre of water available, in absolute numbers, the GWB is superior to the KC. We are well aware that this is a very rough estimate and not a precise calculation, but it does provide one possible reason for the GWB’s importance.

In conclusion, we found support for our first hypothesis that food quality significantly affects larval fish growth in situ. Food quality was able to compensate for quantity effects, and vice versa. However, our second hypothesis that the GWB generally provides better nutritional conditions for larval herring than other nursery areas in this region do was rejected. Therefore, we propose that other factors, like habitat size, might be the reason for the great importance of the GWB as a nursery area for the western Baltic spring-spawning herring.

Acknowledgements
The authors want to thank Bettina Oppermann for measuring CHN of copepod samples. Thank you to the staff of the Institute for Baltic Sea Fisheries for participating in the sampling in the GWB. Thanks also to the research vessel crews of FB “Polarfuchs” and FFK “Clupea” for their help during sampling. We would like to thank Paul Kotterba for creating Figure 1, and Luke Phelps for improving the language of the text. Thank you very much to three unknown reviewers, who helped to improve the manuscript significantly.

The research was partly financed and conducted as part of the Fehmarn Belt Science Provision Project.

References


Handling editor: Claire Paris