Within-season variation in growth of larval plaice (*Pleuronectes platessa* L.)

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Plaice larvae were sampled during immigration into one of their nursery grounds, the Dutch Waddensea, from February to May 1987. Previous growth was estimated using increment widths of their sagittal otoliths. The time of increment formation was back-calculated and otolith growth rates for the first 40 increments are related to the time and to the estimated seawater temperature during deposition. Otolith growth rates differ greatly during the season, and are related to the water temperature. It seems, though, that growth accelerates in mid-February, several weeks before the temperature increases. Although no firm conclusions can be drawn, the discrepancy in time between the increase in growth and the increase in temperature could support the “match-mismatch” hypothesis, in which the growth and survival of fish larvae is related to the timing of the spring plankton bloom.

Introduction

Plaice (*Pleuronectes platessa* L.) is an important flatfish in the North Sea. Spawning takes place in three main areas, the English Channel, the Southern Bight and the German Bight, beginning in December in the Channel, and shifting through the Southern Bight to the German Bight during February–March (Simpson, 1959; Harding et al., 1978). Residual currents normally transport the eggs and larvae in a northeasterly direction (Harding et al., 1978; Talbot, 1977, 1978). After metamorphosis the juveniles settle in coastal areas, preferably tidal areas, of which the Waddensea is the most important one (Zijlstra, 1972; Rauck and Zijlstra, 1978).

From studies on larval and juvenile mortality (Rauck and Zijlstra, 1978; van der Veer, 1985, 1986) it was concluded that year-class strength is to a large extent determined during the pelagic stages. Total egg mortality has been estimated at ca. 50 to 85%, and seems to be positively correlated with temperature (Zijlstra and Witte, 1985). Not much is known, however, about factors causing mortality, although herring has been shown to predate on plaice eggs (Daan et al., 1985; Pommeranz, 1981). Larval mortality is estimated at ca. 60 to 99% (Gulland, 1965; Harding et al., 1978), but hardly anything is known about the causal factors.

Growth is in general recognized to be a key factor in larval fish ecology (Houde, 1986), and it influences the duration of predation, the timing of immigration into the nursery areas and possibly the settlement success. The discovery of daily growth increments in larval otoliths (Pannella, 1971), which has later been shown to be daily in many species (Campana and Neilson, 1985; Jones, 1986) provides a tool for determining age and growth of field-caught specimens. Given daily deposition of increments, and a relationship between otolith and larval size, the width of the increments can be used to estimate previous growth of the larvae. (Brothers and McFarland, 1981; Lough et al., 1982; Neilson and Geen, 1982; Wilson and Larkin, 1982; Methot, 1981; Campana, 1984; Volk et al., 1984; Govoni et al., 1985; Neilson et al., 1985; Penney and Evans, 1985; Thomas, 1986; Barkman and Bengtson, 1987).

Although numerous experiments have been performed on the growth of plaice larvae in the laboratory (Riley, 1966; Ryland 1964, 1966; Ryland et al., 1975; Shelbourne, 1974; Shelbourne et al., 1973) there are no estimates of growth in the sea.

This study was undertaken to gain more insight into growth processes taking place during the larval stages. Throughout the period of immigration in the Marsdiep, one of the main inlets of the Dutch Waddensea, meta-
Figure 1. The spawning-grounds of plaice as illustrated by the distribution of stage 1 eggs (from Harding et al., 1978). A, B, and C: locations from where temperatures were used. Arrow: location of sampling.

morphosing plaice was sampled daily. Growth rates were estimated by means of light microscopical analysis of growth increments in the sagittal otoliths, and related to the temperature during increment formation.

Methods

Immigrating larvae were sampled from 8 February to 17 May 1987 in the Marsdiep (Fig. 1). Most larvae were sampled with a net moored at a jetty about 15 m offshore (opening 1 m² mesh size 1 mm) which was emptied ca. every 24 h. Some additional catches were made at the Marsdiep or near the entrance of the tidal channels of the Balgzand area. Because of climatological circumstances (storm, ice-floes) samples could not be taken every day. In periods when larvae were abundant a random sample of 10 larvae per day was drawn for otolith analysis, otherwise all larvae caught were taken. This resulted in a total of 400 larvae used for this study. Standard length and the height of the myotomal musculature at the height of the anus were measured with a precision of 0.05 mm using a stereo microscope and an ocular micrometer, and the larvae were divided into 5 stages according to Ryland (1966). Sagittal otoliths were removed, air-dried, and mounted in clear nail polish. Small otoliths were mounted sulcus side down, larger otoliths were mounted sulcus side up. After preliminary light microscopical inspection, otoliths in which increments were not clearly visible were ground and polished with respectively 800 grain sandpaper and 1200 grain polishing powder.

Otoliths were photographed on high-contrast black and white film using transmitted light at magnifications varying from 250 to 2000× (Fig. 2). The negatives were framed and projected with a slide projector. Otolith increments were counted and the position of every tenth increment relative to the midpoint of the otolith was measured, if the otolith was clear enough. For each otolith 3 counts were made. If the lowest and highest count differed by more than 10% of the average the otolith was rejected. In a number of cases no counts could be made at all because of faintness of increments or overgrinding of the otolith. In this way a total of ca. 300 otolith readings was obtained. The transect of reading was chosen where the increments were most clearly visible, and when accessory primordia were present they were not included in the transect of reading or in the otolith diameter.

To obtain a size-weight relationship larvae were caught at sea and preserved in a 4% formaldehyde solution. The larvae were staged and measured, and
dried for ca. 40 h at 70°C, after which they were weighed with a precision of 0.01 mg.

Seawater temperatures were obtained from the Royal Dutch Meteorological Institute from three locations in the southern and central North Sea (A, B, and C in Fig. 1).

Data analysis

Dates of first increment formation were calculated by subtracting the number of increments from the day of capture.

Daily growth rates of the otoliths for 10-day periods (periodic specific growth rates: PSGR) were calculated as:

\[ \text{PSGR} = \frac{(\ln R_1 - \ln R_0)}{10} \]

in which \( R_0 \) is the otolith radius at the beginning of the period, and \( R_1 \) the radius at the end of the period and 10 is the number of increments between the radius \( R_0 \) and \( R_1 \).

Because the otoliths are not always circular, and because the midpoint may be located asymmetrically all distances were standardized to a mean otolith radius by
calculating a standardized measurement:

\[ M_s = M_d \times (R_s / R_t) \]

\( M_d \) is the distance as measured, \( R_t \) is the radius of the reading transect and \( R_s \) is the standard radius of the otolith, which was calculated as \((\text{minimum diameter} + \text{the maximum diameter})/4\). Some bias may be introduced here when the shape of the otolith alters during its growth. The period from December 1986 to May 1987 was divided into 10-day periods, and average increment widths were calculated for increments formed during these periods. January 1–10 was taken as period no. 1, so periods in 1986 have negative numbers. Average increment widths were calculated separately for ring 1–10, 11–20, 21–30 and 31–40. Averages calculated from less than 15 individuals have been omitted in further analysis.

Relationships between length, height, and weight of larvae and otolith diameter were established using normal (predictive) linear regressions. Correlations between growth rates and temperature were calculated using Spearman's rank correlation coefficient. Although the temperatures from three locations show the same trend, temperature differences may be as much as three degrees, especially during periods of rapid change. As it is not known where the larvae have been during their previous life, and which temperatures they have undergone, the mean of the three values has been used.

A Gompertz growth curve of the type

\[ W_t = W_0 \times e^{(k \times (1 - e^{-\alpha \times t}))} \]

was fitted to the back-calculated average otolith size at each tenth increment. No weighing was applied for decreasing numbers of measurements or increasing standard deviation.

Results

Number of immigrating larvae

Immigration of larvae started about 20 February, after which it rapidly rose to a peak in the first week of March. Numbers then decreased until about 20 April (yearday 110) after which a small second peak was observed (Fig. 3).

Relation otolith diameter–dry weight

A good linear relationship exists between the mean otolith diameter (OD) and the product of length and squared height \((L \times H^2)\) of the larvae (Fig. 4):

\[ L \times H^2 = -59.64 + 1.8055 \times \text{OD} \quad (r = 0.94 \ N = 111) \]

\( L \times H^2 \) is correlated with larval dry weight (DW) (Fig. 5):

\[ \text{DW} = 18.82 + 1.3947 \times L \times H^2 \quad (r = 0.97 \ N = 156) \]
This leads to a linear relationship between otolith diameter and larval dry weight of:

\[ DW = -64.36 + 2.5181 \times OD \]

Otolith diameter can thus serve as an estimate of larval dry weight.

The first increment is, on average, seen at a radius of ca. 20 \( \mu m \). The otolith radius of a newly-hatched plaice larvae has a radius of ca. 10 \( \mu m \), so the first increment must have been formed some time after hatching, presumably at the start of first feeding. The fact that increments are not observed in an earlier stage may be due to the resolution of light microscopy, although different optical properties of the first increments cannot be excluded. The theoretical limit of the microscope used is (under ideal circumstances) between 0.22 and 0.28 \( \mu m \), depending on the objective used. The smallest increments observed were just below 0.4 \( \mu m \), and as increment widths below 0.7 \( \mu m \) were only observed in the increments 1-10, it was assumed that after formation of the first light microscopical visible increments all increments were observed and that they had been deposited at a rate of one increment per day. When increment counts had been taken as the real age of the larvae the ages would be biased, but in back-calculating to the first day of (visible) increment formation this bias will not exist. In this paper, however, no assumptions have been made about the real age of the larvae.

In Figure 6 the average increment widths and standard deviations of increment 1-10, 11-20, etc. are plotted. Increment width starts at ca. 0.9 \( \mu m \) and increases up to the fiftieth increment, after which the widths decrease. It must be noted that data on the increments 70 to 90 are less reliable because of the small numbers of larvae in these age groups.

Otolith growth is plotted in Figure 7, together with the fitted curve and standard deviations. The fitted growth curve is:

\[ W_t = 12.85 \times \exp(2.2132 \times (1 - e^{-0.03495 \times t})) \]

For each 10-day period between 10 December and 20 April, the average width of increment 1-10, 11-20, 21-30 and 31-40 formed during that period is plotted, which gives an impression of the absolute growth of the otoliths for the first 40 increments (Fig. 8). Values and standard deviations are given in Table 1. Periodic specific growth rates are plotted in a similar way in Figure 9. Both graphs (Figs. 8, 9) give roughly the same information. Growth is declining during period 2 (ca. 20 December).
Table 1. Average increment widths, standard deviations and numbers of increments 1–10, 11–20, 21–30 and 31–40 for each period in which the first of each ten increments (= 1, 11, 21, 31) was formed.

<table>
<thead>
<tr>
<th>Period of formation</th>
<th>Incr. no. 1–10</th>
<th>11–20</th>
<th>21–30</th>
<th>31–40</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dec 12, Dec 21 – 2</td>
<td>1.02 0.21 15</td>
<td>– – –</td>
<td>– – –</td>
<td>– – –</td>
</tr>
<tr>
<td>Dec 22, Dec 31 – 1</td>
<td>1.07 0.25 24</td>
<td>1.11 0.25 15</td>
<td>– – –</td>
<td>– – –</td>
</tr>
<tr>
<td>Jan 1, Jan 10 – 1</td>
<td>1.10 0.28 41</td>
<td>1.36 0.35 23</td>
<td>1.21 0.23 15</td>
<td>– – –</td>
</tr>
<tr>
<td>Jan 11, Jan 20 – 2</td>
<td>1.01 0.27 34</td>
<td>1.29 0.34 41</td>
<td>1.50 0.27 22</td>
<td>1.36 0.37 15</td>
</tr>
<tr>
<td>Jan 21, Jan 30 – 3</td>
<td>0.85 0.19 42</td>
<td>1.23 0.30 33</td>
<td>1.43 0.34 41</td>
<td>1.42 0.37 22</td>
</tr>
<tr>
<td>Jan 31, Feb 9 – 4</td>
<td>0.80 0.18 23</td>
<td>1.09 0.32 42</td>
<td>1.36 0.31 32</td>
<td>1.43 0.32 39</td>
</tr>
<tr>
<td>Feb 10, Feb 19 – 5</td>
<td>0.76 0.19 30</td>
<td>1.01 0.32 23</td>
<td>1.19 0.37 40</td>
<td>1.40 0.32 27</td>
</tr>
<tr>
<td>Feb 20, Mar 1 – 6</td>
<td>0.83 0.17 24</td>
<td>0.89 0.19 29</td>
<td>1.07 0.29 22</td>
<td>1.19 0.31 35</td>
</tr>
<tr>
<td>Mar 2, Mar 11 – 7</td>
<td>0.73 0.18 26</td>
<td>1.05 0.23 24</td>
<td>0.98 0.25 29</td>
<td>1.18 0.31 21</td>
</tr>
<tr>
<td>Mar 12, Mar 21 – 8</td>
<td>0.78 0.22 15</td>
<td>0.94 0.21 26</td>
<td>1.23 0.24 21</td>
<td>1.07 0.28 27</td>
</tr>
<tr>
<td>Mar 22, Mar 31 – 9</td>
<td>– – –</td>
<td>1.08 0.39 15</td>
<td>1.17 0.33 24</td>
<td>1.44 0.26 19</td>
</tr>
<tr>
<td>Apr 1, Apr 10 – 10</td>
<td>– – –</td>
<td>– – –</td>
<td>1.37 0.36 15</td>
<td>1.47 0.43 22</td>
</tr>
<tr>
<td>Apr 10, Apr 19 – 11</td>
<td>– – –</td>
<td>– – –</td>
<td>– – –</td>
<td>1.66 0.50 13</td>
</tr>
</tbody>
</table>

Conclusions and discussion

Growth

Figure 7 shows that the otolith growth has a sigmoid form, which is expected, as larvae normally start to grow exponentially, but growth is slowed down during metamorphosis. Laboratory-reared plaice larvae almost stopped feeding during metamorphosis (Riley, 1966) and immigrating plaice larvae are usually found with empty guts (Creutzberg et al., 1978; pers. observation).

A Gompertz growth curve was applied because it is a flexible growth curve with an inflexion point, which has been used in a number of studies, and seems to
Figure 11. Relation between periodic specific growth rates and the temperature on the fifth day of the period for increments 1-10 (A), 11-20 (B), 21-30 (C), and 31-40 (D).
describe larval growth rather well (Zweifel and Lasker, 1976).

If the growth curve found is extrapolated to the point of hatching, e.g. an otolith diameter of 20 µm, the estimated average time before first increment formation is ca. 20 d. Results from larvae caught offshore (unpublished) show that first increment formation starts during stage 2 (after absorption of the yolk sac), which is (according to Ryland, 1966) at an age of ca. 20 days. Otolith deposition would thus take place at a rate of 0.5 µm per day, which is about the minimal deposition found during this study. The Gompertz curve thus seems to describe the otolith growth adequately.

Differences in growth rates

From Figures 8 and 9 it is clear that different growth rates occur within the season, which are related to different periods. In general, growth rates in the beginning of the season are high, except for the first period. Growth rates then decline until late February, after which they increase.

Analysis of variance shows that differences in growth are significant for increment 1–10, 11–20 and 31–40, but not for increment 21–30, although it shows the same general trend. The analysis of variance, however, only shows that at least some differences between some periods are significant, but does not tell us whether the general shape is to be relied on. This was checked by drawing five random subjects of 50% and 25% of all data, after which the same graphs were plotted. With a sample size of 50%, five out of five draws showed the same pattern, and with a sample size of 25% the same pattern was observed in two out of five draws, and it was concluded that the sample size used had been sufficiently large for describing the observed pattern.

Significant correlations are found between growth rates and temperature for growth of increments 1–10, 11–20, and 31–40 (Table 1). It must be noted that the temperature used here is only an estimate of the real temperatures which the larvae have undergone, but because of the large number of larvae used and the similarity between the three temperature curves this will probably not have affected these correlations very much.

From Figure 8, it appears that larvae start to grow faster in period 5 (10–19 February), while the temperature starts to increase between 1 and 20 March, depending on the latitude, which is ca. 20–40 d later. Highly significant positive correlations are found between growth and growth in the preceding period, a phenomenon which has also been described by Barkman and Bengtson (1987). Either growth rates do not change abruptly, which can be explained by the fact that temperatures do not change rapidly, or otolith growth is responding only slowly to the actual growth, as has formerly been observed in the otoliths of Dicentrarchus labrax (Gutierrez and Morales-Nin, 1986).

Temperature and food availability are probably the most important factors influencing larval growth. A positive influence of temperature on growth is to be expected within a certain range (Brett, 1979; Laurence, 1975). A negative effect of temperatures above 8°C has been reported for yolk sac larvae (Ryland and Nichols, 1967). It seems that growth no longer increases with temperatures above 8°C (Fig. 11 A-D) but only a few observations are available for these temperatures. Within-year variations of larval otolith growth have been described before (Methot, 1981; Townsend and Graham, 1981; Jones, 1984), and a direct relation between recent temperature and otolith growth has been demonstrated by Thomas (1986).

The diet of plaice larvae has been studied relatively well and consists mainly of Oikopleura dioica, a planktonic tunicate (Ryland, 1964; Shelbourne, 1953; White, 1968). Shelbourne (1957) reported the larvae to be in a better condition in patches containing higher concentrations of Oikopleura. Food availability may have contributed to the observed growth acceleration, as phytoplankton development, and thus zooplankton development is more related to light conditions and stability of the water column than to temperature (Cushing, 1972; Townsend and Cammen, 1988).

If Figures 3 and 8 are compared, it seems that fast growth of larvae is associated with a high immigration rate. The largest widths of the most recent increments used in this study (increment 31–40) are observed during late January–early February (period 3–5) and late March–early April (period 9–10) which is a short time before the two peaks in immigration (period 6–7 and period 12–13). In the otoliths of immigrating larvae, an average of 58 increments was observed, which did not change much during the seasons. This means that the increments 30–40 were formed ca. 21–30 d before immi-

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**Table 2. Spearman’s rank correlations between periodic specific growth rates (PSGR) and the temperature on the fifth day of the period.** $P_{(0.05,250)} = 0.125.$

<table>
<thead>
<tr>
<th>Temp</th>
<th>PSGR 1–10</th>
<th>PSGR 11–20</th>
<th>PSGR 21–30</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>PSGR 1–10 ............0.491</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>287</td>
</tr>
<tr>
<td>PSGR 11–20 ............0.288</td>
<td>0.526</td>
<td>–</td>
<td>–</td>
<td>283</td>
</tr>
<tr>
<td>PSGR 21–30 ............0.025</td>
<td>0.159</td>
<td>0.438</td>
<td>–</td>
<td>271</td>
</tr>
<tr>
<td>PSGR 31–40 ............0.174</td>
<td>–0.066</td>
<td>–0.029</td>
<td>0.408</td>
<td>250</td>
</tr>
</tbody>
</table>
migration, which explains the observed time lapse of 21–30 d between the periods of fast growth and high immigration rates.

Although the second immigration peak is not very conspicuous it has had a considerable effect on numbers of settling juveniles (unpublished data) and so it has been more important than it appears.

Origin of larvae

In former studies on the drift of plaice larvae, it has been suggested that most larvae from the English Channel enter nursery areas in the estuaries of the rivers Thames or Schelde, and larvae from the Southern Bight in the Dutch Waddensea (Houghton and Harding, 1976; Harding and Talbot, 1973; Harding et al., 1978; Talbot, 1977, 1978). The average age of immigrating larvae, including egg development, is about 90–100 d (Harding et al., 1978). This means that the first and largest batch of immigrants, caught late February, was spawned in December. It has been shown (Cushing, 1969) that the time of spawning of plaice is constant, with spawning in the Channel peaking in December and in the Southern Bight in the second half of January. If the average speed of the residual current is estimated at 2.6–5.6 km per day (Lee, 1980) the estimated transportation will be 234 to 560 km, which from Texel southward is well into the Dover Straits or the English Channel. This means that at least in 1978 many larvae entering the Marsdiep were spawned in the English Channel.

It should be noted, however, that all studies relating otolith and somatic growth must be regarded with caution. While somatic growth can be zero, or even negative, otolith growth does not exist and zero otolith growth does not exist and zero otolith growth cannot be detected (Mosegaard and Titus, 1987). An uncoupling between somatic and otolith growth would be apparent in a lowered correlation coefficient between otolith and larval size, as was indeed the case in immigrating larvae. Therefore only the growth rates of the first 40 increments have been used in this study.

As only one location has been sampled, it is possible that there has been a certain effect caused by sampling only slow-growing larvae from the English Channel and only fast-growing larvae from the Southern Bight. Size selective predation may also cause apparent differences in growth, but as little is known about predation on plaice larvae in the open sea, this possibility can only be speculated on.

No firm conclusions can be drawn from this study, and it seems that much more detailed studies are needed. Otolith-based research may provide a useful tool to facilitate such studies.

References


