Development of Baltic cod eggs
at different levels of temperature and oxygen content

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Abstract

The influence of ambient temperature (2-7°C) and oxygen level (1.0-8.3 ml·l⁻¹) on the development of Baltic cod eggs was investigated in laboratory experiments. The incubation period, i.e. the time from fertilization to 50% hatching, decreased from 27.5 days at 2°C to 13.0 days at 7°C. Reduced oxygen levels did not significantly affect the time of hatching. Throughout the incubation period highest mortality rates were found during gastrulation and immediately prior to hatching at all tested oxygen levels. Egg survival decreased from around 30% at an oxygen level of 8 ml·l⁻¹ to less than 10% at 2 ml·l⁻¹ oxygen content. At oxygen concentrations below 2 ml O_2·l⁻¹ the development ceased at a very early stage.

Field observations revealed that in the past years Baltic cod eggs were most abundant below the halocline, depth with unfavourable oxygen condition. Besides the effect on egg survival, low environmental oxygen may also affect the initial viability of larvae and consequently their ability to approach the feeding areas close to the sea surface. Thus, the effective reproduction volume of water for cod in the central Baltic may have been smaller than expected and it is suggested that oxygen depletion was the limiting factor determining the reproductive success of cod in this area during the last decade.

Keywords: cod, egg development, mortality, oxygen.

Introduction

Numerous studies with early life-history stages of marine fish species indicate that abiotic factors such as temperature, salinity and oxygen content may have significant effects on their survival. Examples, including cod, can be found in the review by Rosenthal & Alderdice (1976). The influence of temperature on the embryonic development of cod has been intensively studied. A review on this topic is given by Page & Frank (1989) including various cod stocks of the North Atlantic. Westernhagen (1970) and Nissling & Westin (1991a) studied the effect of salinity on the survival of cod eggs from the Baltic. Effects of oxygen concentration on hatching success was examined by Alderdice & Forrester (1971) for Pacific cod. They reported that the eggs may tolerate dissolved oxygen levels down to a minimum of about 2 or 3 ml·l⁻¹ as long as temperatures are between 3-5°C.

In several studies, egg survival has been related to the environmental conditions in the central Baltic (Grauman 1973, 1974, Bulgakova & Grauman 1990, Plikshs *et al.* 1993) or year class strength of cod (Berner *et al.* 1989, Kosior & Netzel 1989, Lablaika *et al.* 1989). These results as well as those from investigations on the

vertical distribution of cod eggs in the Bornholm Basin (Müller & Pommeranz 1984, Wieland 1988, Wieland & Zuzarte 1991) suggest that poor oxygen conditions may substantially affect the recruitment of Baltic cod.

The gradual reduction of salinity to the east and north in the Baltic Sea has caused cod to reach the edge of its distributional range. In comparison to other areas, spawned eggs are of large size in the central Baltic (Ehrenbaum & Strodtmann 1904, Heinen 1912, Nissling & Westin 1991b). The eggs achieve neutral buoyancy at low salinities between 12.3 and 16.9 psu (Nissling & Westin 1991b) and normal egg development has been observed at salinities down to 11 psu (Westin & Nissling 1991). However, a dramatic reduction in sperm activity has been noted at salinities below 12 psu by the same authors.

Acceptable salinity levels for the successful reproduction of cod in the central Baltic exist only within and below the halocline in the deeper basins. In this depth range oxygen deficiency due to water stagnation is a common phenomenon (Krauss & Brügge 1991). The ambient salinity and oxygen conditions depend on inflow of high-saline water from the North Sea (Matthäus & Franck 1992) and consequently the conditions fluctuate and may at times not meet the requirements for successful cod egg development. Nehring & Matthäus (1991) reported a general decrease in salinity and oxygen content of central Baltic waters throughout the last decade. Correspondingly, the depth range providing adequate salinity and oxygen conditions for a successful reproduction of cod has been markedly reduced during this period. However, it is difficult to assess this particular depth range more precisely, since there are few experimental results to quantify the influence of low oxygen levels on development and survival of cod eggs. A first experimental approach was made by Ohldag *et al.* (1991), who incubated cod eggs from the central Baltic at four different oxygen levels at 5°C. Viable hatching was observed at an oxygen level of 4.9 ml$\cdot$l^{-1} and above, while all eggs died before hatching at 2.7 ml $O_2\cdot$l^{-1}. Furthermore, the overall incubation time appeared to be reduced by about three to four days compared to North Sea and Western Baltic cod eggs at normoxic conditions (8 ml $O_2\cdot$l^{-1}) and a premature emergence of the embryos at 4.9 ml $O_2\cdot$l^{-1} was reported. That initial study has been continued and expanded, covering a broader range of temperatures and oxygen levels. The present contribution provides new results from these experiments on the development of Baltic cod eggs and reviews corresponding experimental results from other cod populations for comparison. Additional reference is made to field observations to discuss the relative importance of hydrographic factors for the success of cod reproduction in the central Baltic.

Material and methods

Spawning cod were caught with a pelagic trawl employed from RV *Alkor* and RV *Poseidon* in the central Bornholm Basin in 1991 and 1992. The incubation experiments were started on board and were later continued at the Institut für Meereskunde in Kiel.

Egg batches from nine different females were obtained by stripping and fertilized with sperm from one or several males. After the first cleavage (4 -8 h after fertiliza-

Table 1: Experimental conditions. Temperature and oxygen content given as arithmetic mean ± standard deviation. Each numbered experiment corresponds to one egg batch obtained from a single female. Experimental groups enclosed in brackets were terminated prior to hatching, due to an insufficient initial number of eggs: experiment 1, 4.5 ml oxygen·l^{-1} was terminated in stage III, 2.6 ml oxygen·l^{-1} in stage IB; experiment 8 & 9 in stage III.

Exp.	Date	Name of ship	No. of parallels	Temp., °C	Oxygen concentration, ml·l^{-1}					
1	Apr. '91	Alkor	1	2.0±0.2	7.7±0.4	(4.5±0.4)	–	(2.6±0.3)	–	1.3±0.2
2	July '91	Alkor	1	6.0±0.2	7.4±0.1	4.7±0.4	3.6±0.1	2.7±0.2	2.3±0.2	1.1±0.4
			1	7.0±0.2	7.3±0.2	4.7±0.1	3.6±0.2	2.6±0.3	2.0±0.3	1.0±0.3
3	July '91	Alkor	1	6.0±0.2	7.4±0.1	4.7±0.4	3.6±0.1	2.7±0.2	2.3±0.2	1.1±0.4
			1	7.0±0.2	7.3±0.2	4.7±0.1	3.6±0.2	2.6±0.3	2.0±0.3	1.0±0.3
4	May '92	Alkor	2	5.7±0.4	8.0±0.2	6.4±0.3	5.1±0.4	3.6±0.4	2.0±0.5	–
5	May '92	Alkor	2	5.7±0.4	8.0±0.2	6.4±0.3	5.1±0.4	3.6±0.4	2.0±0.5	–
6	July '92	Poseidon	1	3.0±0.2	air saturation level					
			1	4.0±0.2	air saturation level					
			2	5.0±0.1	8.3±0.1	6.5±0.3	5.1±0.3	3.6±0.4	2.1±0.2	–
7	July '92	Poseidon	1	3.0±0.2	air saturation level					
			1	4.0±0.2	air saturation level					
			1	5.0±0.1	air saturation level					
8	July '92	Poseidon	1	4.0±0.2	(air saturation level)					
9	July '92	Poseidon	1	5.0±0.1	(air saturation level)					

tion, depending on the experimental temperature), the eggs were transferred into the incubation system, in which the salinity was adjusted to achieve neutral buoyancy (13.0-13.5 psu). The incubator was operated at selected temperatures and oxygen levels (Table 1). During incubation the eggs were kept in darkness except for the handling periods necessary to operate the incubation system.

The different oxygen concentrations required for the experiments were obtained by mixing filtered sea water of low and high oxygen content. Water with high oxygen content was stored in a tank (60 l), where it was continuously aerated to keep the oxygen concentration close to air saturation. To reduce the oxygen content, nitrogen was bubbled through water in a second storage tank (60 l). The water was mixed with a peristaltic pump and distributed into the incubation bottles (3.0 l). The water-flow (0.25-0.75 l·h^{-1}) through the incubation bottles allowed the developing eggs to float in the water column building up a 2-3 cm layer some cm below the top of the bottles. In experiments 1, 2 & 3 (Table 1) the system was operated manually. About every 10 hours the two storage containers were replaced. Before new containers were connected to the system, the water was either de-oxygenated (0.2-0.5 ml oxygen·l^{-1}) with nitrogen, or aerated close to air saturation with atmospheric air. The oxygen level of the water delivered to the peristaltic pump was read by oxygen electrodes and recorded on a flatbed recorder. Oxygen levels at the outflow of the incubation bottles (n = 12) were repeatedly checked (Winkler method) and flow rates (0.2-0.4 l·h^{-1}) were adjusted to keep the oxygen concentration at the required level. The outflowing water was discharged.
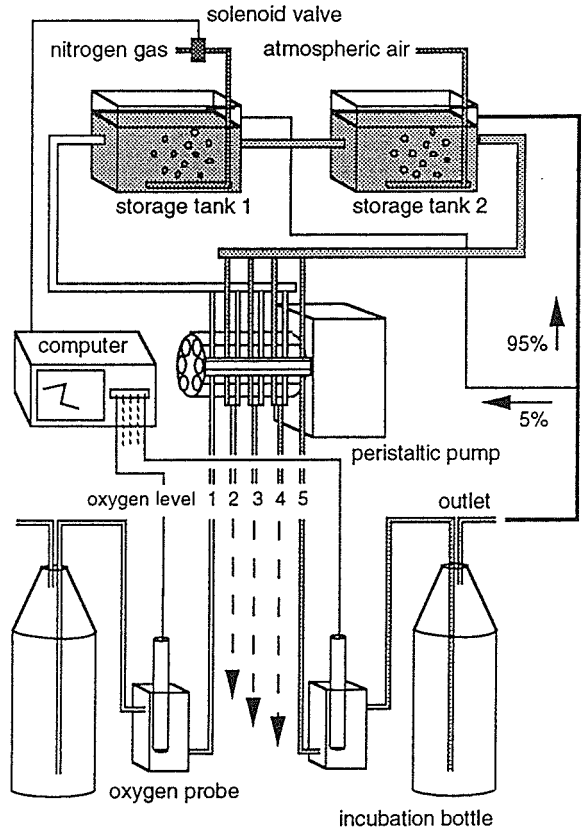
Figure 1. Schematic drawing of the incubation system.

In experiments 4, 5 & 6 the system was computer controlled (Figure 1). The lowest oxygen level was maintained by controlling the nitrogen input with a solenoid valve. The oxygen content of the water in the storage tanks as well as the oxygen concentration after mixing were continuously recorded. From time to time the oxygen concentrations of the water which had passed through the incubation bottles were measured and flow rates were adjusted (0.25-0.75 $l \cdot h^{-1}$) to maintain the selected oxygen levels. The water was recirculated allowing a higher number of incubation bottles (n = 20) to be used. 95% of the recirculated volume was fed into the storage tank for high-oxygen water, where it was aerated with atmospheric air to achieve an equilibrium of dissolved gases. The remaining 5% of the recirculated water was fed into the storage tank for low-oxygen water. To balance the water levels in the storage tanks, they were connected with a tube through which water could flow passively in either direction. The water in both storage tanks was completely exchanged on alternate days.

During ship-board operation on RV *Poseidon* (Table 1) experimental temperature was maintained by submerging storage containers and incubation bottles in a temperature controlled tank. Because of space restrictions, the volume of the water storage units and the number of incubation bottles had to be reduced to 10 l and

10 pieces, respectively. On board RV *Alkor* and after ships had returned to Kiel, the entire system was placed in a temperature-controlled laboratory ($\pm 0.3°C$). The room temperature was set to the lowest experimental temperature. Higher incubation temperatures were established by placing the incubation bottles in a water filled tank, in which the water was heated to the desired temperature. Before the water was fed into these incubation bottles it had passed through a heat-exchanger made of tygon or stainless steel tubing.

Every day subsamples of 10-20 eggs were collected from all incubation bottles and the developmental stage was determined according to the criteria given by Thompson & Riley (1981) and Westernhagen (1970). These eggs were discarded from the continuing experiment. When approaching the end of a developmental stage samples were taken at least every 8 hours. Hatched larvae were removed every 12 hours. Dead eggs accumulating at the bottom of the incubation bottles were removed every other day.

To determine the possible impact of the oxygen level on developmental times, the results obtained for each egg stage at different experimental temperatures were adjusted to 5°C using the following equation:

$$t_{adj,s} = t_s(5) / t_s(T) \cdot t_{obs,s}$$

$t_{adj,s}$	incubation time adjusted to 5°C temperature;
$t_s(5), t_s(T)$	incubation time at 5°C and experimental temperature, respectively, as obtained from incubation time–temperature relationship at normoxic conditions;
$t_{obs,s}$	incubation time observed;
s	egg stage.

Observations based on less than 10 eggs or hatched larvae were excluded from the results on developmental time.

In experiments 5 & 6, dead eggs and any accidentally removed vital eggs were preserved in 4% buffered formalin and counted later. In order to estimate mortality at different oxygen levels, the initial numbers of eggs allocated in the incubation bottles were calculated retrospectively by adding the numbers of hatched larvae, dead eggs and collected developing eggs. As developing eggs were removed more frequently than dead eggs, the mortality rates had to be estimated by an iterative process assuming a constant mortality over the corresponding interval. The calculations were based on the equation given by Ohldag *et al.* (1991):

$$N_i = N_{i+1} \cdot \exp(z_i \cdot dt_{i,i+1}) + \sum_j N_j \cdot \exp(z_i \cdot dt_{i,j})$$

N_i	number of developing eggs at the start of interval i;
N_{i+1}	number of developing eggs at the end of interval i;
N_j	number of developing eggs removed at time j within interval i;
$dt_{i,i+1}$	time difference between subsequent removals of dead eggs;
$dt_{i,j}$	time difference between removal of developing eggs and the start of interval i;
z_i	instantaneous mortality coefficient for interval i.

An arithmetic mean was calculated from all mortality rates obtained for successive periods within a developmental stage, weighted by the length of the individual periods covered.

Results

Developmental time

The present study identified five developmental stages (IA, IB, II, III, and IV according to Westernhagen 1970). The larvae always hatched prior to stage V. On this stage neither the tail had grown past the head nor had the pigment bands developed as typical for the first larval stage.

The time from fertilization to the end of successive developmental stages strongly depended on the incubation temperature. At the lowest temperature tested (2°C, Table 1), the end of stages IA, IB, II, and III was observed after 4.8, 7.3, 13.1, and 22.1 days, respectively. The end of stage IV, defined as the time when 50% of the embryos had emerged, was observed after 27.4 days. In the two experiments conducted at 7°C (Table 1), the end of stages IA, IB, II and III were observed after 2.0, 3.6, 5.8, and 10.1 days, respectively. At this temperature the end of stage IV was reached after 13.4 days. Thus, at 2°C test temperature the developmental period was almost doubled compared to that determined in the experiments at 7°C. The relationship between temperature (x) and incubation time from fertilization to the end of different developmental stages (y) can be described by exponential equations:

stage IA $y = \ \ 8.38 \cdot \exp(-0.21 \cdot x)$, $r^2 = 0.93$, $n = 15$
stage IB $y = 12.22 \cdot \exp(-0.18 \cdot x)$, $r^2 = 0.89$, $n = 15$
stage II $y = 18.05 \cdot \exp(-0.16 \cdot x)$, $r^2 = 0.98$, $n = 15$
stage III $y = 31.27 \cdot \exp(-0.16 \cdot x)$, $r^2 = 0.98$, $n = 15$
stage IV $y = 37.42 \cdot \exp(-0.16 \cdot x)$, $r^2 = 0.91$, $n = 13$.

The fitted lines are shown in Figure 2. They are based on all data obtained under normoxic conditions (7.3-8.3 ml $O_2 \cdot l^{-1}$ or air saturation level, Table 1).

When adjusting all values of developmental times obtained at different temperatures to a standard of 5°C according to the above given equations, these data do not indicate any influence of reduced oxygen levels on the incubation period (Figure 3). The incubation times for all stages were close to the average calculated over all oxygen levels (dotted lines in Figure 3), but there was some variation between experiments. The coefficients of variation amounted to 7.7, 8.6, 4.2, 4.4 and 9.0% for stage IA, IB, II, III, and IV, respectively. Even in stages with low variation (stages II and III) no trend related to oxygen content was obvious (Figure 3) and in no case statistically significant regression equations could be established.

Mortality

At the lowest oxygen levels tested (1.0-1.3 ml $\cdot l^{-1}$) all eggs died in stage IB (experiment 3) or shortly after they had reached stage II (experiments 1 & 2), irrespective of the experimental temperature (Table 2). At higher oxygen concentrations between 2.0 and 2.3 ml $\cdot l^{-1}$ some eggs survived until stage III in two groups, at 7°C,

Time from fertilization to
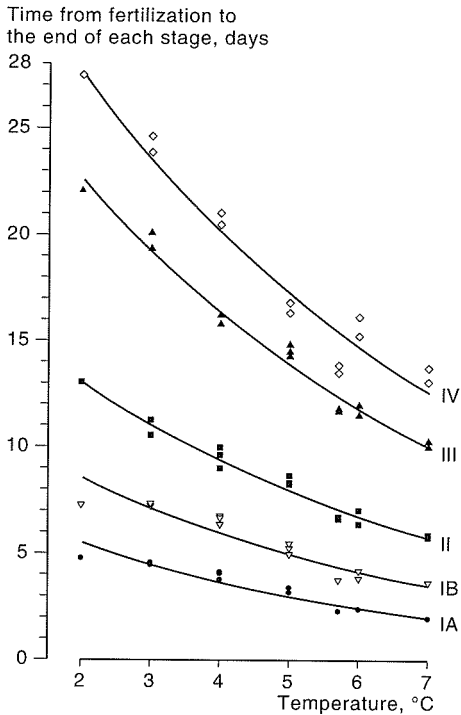the end of each stage, days

Figure 2. Incubation time from fertilization to the the end of successive egg stages at different temperatures. Regression lines are fitted to 13 (stage IV) and 15 (stage IA-III) data points according to the number of experimental groups incubated at oxygen contents ≥ 7.3 ml·l^{-1} or air saturation level (Table 1) and with at least 10 individuals alive at the corresponding time.

Time from fertilization to
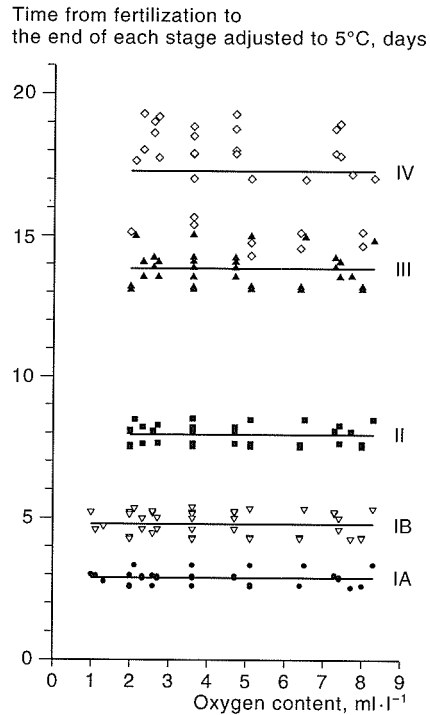the end of each stage adjusted to 5°C, days

Figure 3. Incubation times from fertilization to the end of successive egg stages at different oxygen levels. Incubation times are adjusted to 5°C temperature according to regressions in Figure 2. The number of data points ranges from a minimum of 34 (stage IV) to a maximum of 43 (stage IA), according to the number of experimental groups with at least 10 individuals alive at the corresponding time. Lines indicate mean incubation times for the different egg stages, averaged over all tested oxygen levels.

Table 2: Stages of development achieved at different oxygen levels;

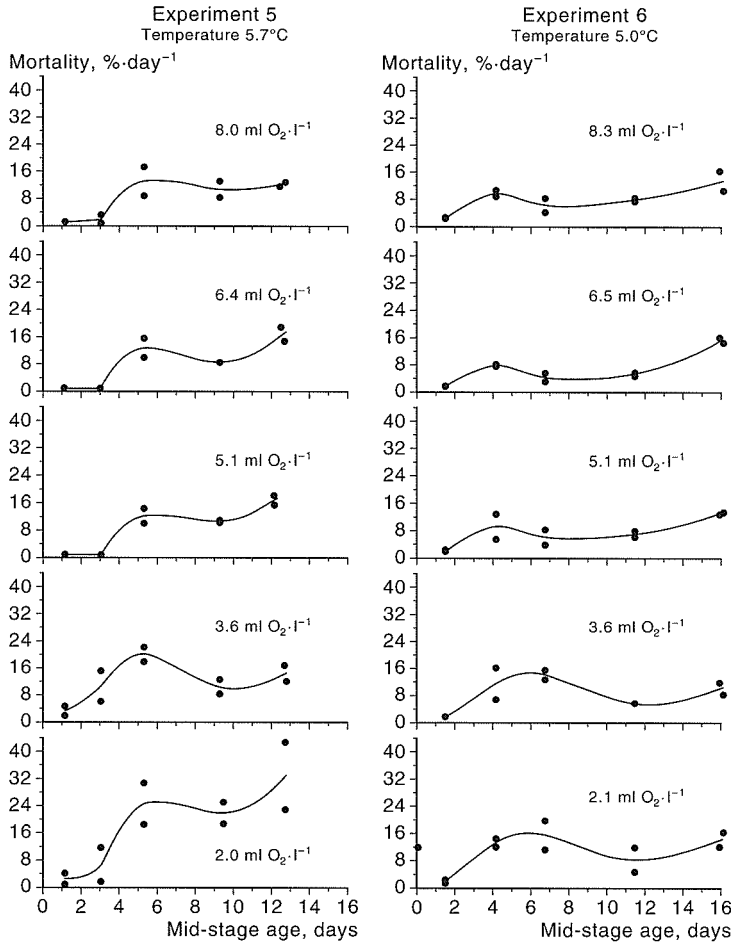| Exp. | Temp., °C | Oxygen concentration, ml·l^{-1} | | |
		1.0-1.3	2.0-2.3	≥ 2.6
1	2.0	II	no obs.	Hatching
2	6.0	II	IV	Hatching
	7.0	II	III	Hatching
3	6.0	IB	IV	Hatching
	7.0	IB	III	Hatching
4	5.7	no obs.	IV	Hatching
5	5.7	no obs.	Hatching	Hatching
6	5.0	no obs.	Hatching	Hatching

Figure 4: Daily mortality for successive egg stages at different levels of oxygen content. Solid lines indicate the change in mortality based on arithmetic means for the two parallels of each experiment.

and until stage IV in three groups at about 6°C. Development until hatching was achieved in two groups at this oxygen level and in all groups at higher levels. Thus, an oxygen content of about 2 ml·l^{-1} appears to be the critical level for developing cod eggs.

Mortality rates were recorded in experiments 5 & 6 only. Two phases of increased mortality were observed during embryonic development: first, during gastrulation (stage IB) and before closure of the blastoporus (stage II), and second, prior to hatching in stage IV (Figure 4).

At the start of development, in stage IA, mortality never exceeded 5% per day, even at the lowest oxygen levels tested (2.0-2.1 ml·l^{-1}). For stage IB the values ranged between 1 and 13% in experiments with oxygen levels above 5 ml·l^{-1},

while it was slightly higher (2-16% $\cdot$ d^{-1}) at lower oxygen levels (< 5 ml $\cdot$ l^{-1}). The mortality in the following stages was somewhat increased at low oxygen levels: in stage II the rates ranged from 3 to 17% $\cdot$ d^{-1} at high oxygen concentrations and increased to 11-31% $\cdot$ d^{-1} at oxygen levels below 5 ml $\cdot$ l^{-1}.

The generally reduced mortality values for stage III appear still dependent on oxygen content amounting to 5-13% $\cdot$ d^{-1} at high oxygen levels and 6-25% $\cdot$ d^{-1} at the levels below 5 ml $\cdot$ l^{-1}.

For stage IV, the two experiments provided very different results: extremely high daily mortality rates (24-43% $\cdot$ d^{-1}) were found in experiment 5 at the lowest oxygen concentration of 2 ml $\cdot$ l^{-1}, whereas in experiment 6 the daily mortality rates ranged between 8 and 16%, irrespective of the oxygen content.

The overall survival of cod embryos from fertilization to 50% hatching is given in Figure 5 for the different oxygen levels employed in the experiments 5 & 6. The percentage survival at mean hatching time ranged between 22 and 37% at oxygen concentrations above 5 ml $\cdot$ l^{-1}, while at 3.6 ml $O_2 \cdot$ l^{-1} 12 to 27% and at 2 ml $O_2 \cdot$ l^{-1} 3-18% of the eggs survived until hatching. Even though survival rates for low and high oxygen levels were partly overlapping, a downward trend in survival occurred at oxygen concentrations below 5 ml $O_2 \cdot$ l^{-1}.
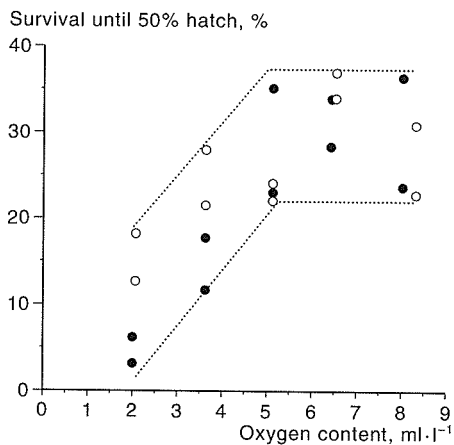

Figure 5: Percentage egg survival until 50% hatch at different oxygen levels. Dotted lines indicate the range of egg survival in the two experiments.

Discussion

In the present study cod larvae always hatched during developmental stage IV, which is in agreement with the experimental studies of Westernhagen (1970) and Ohldag et al. (1991) and field studies of Müller & Pommeranz (1984) and Wieland (1988). The morphological criteria described for egg stage V of North Sea cod by Thompson & Riley (1981) were not met in this study, but the emergence of the embryos before the tail had grown past the head may be a result of the large size of Baltic cod eggs.

Information on cod egg development in relation to temperature were published by Westernhagen (1970) for the Western Baltic, by Nissling & Westin (1991a) for
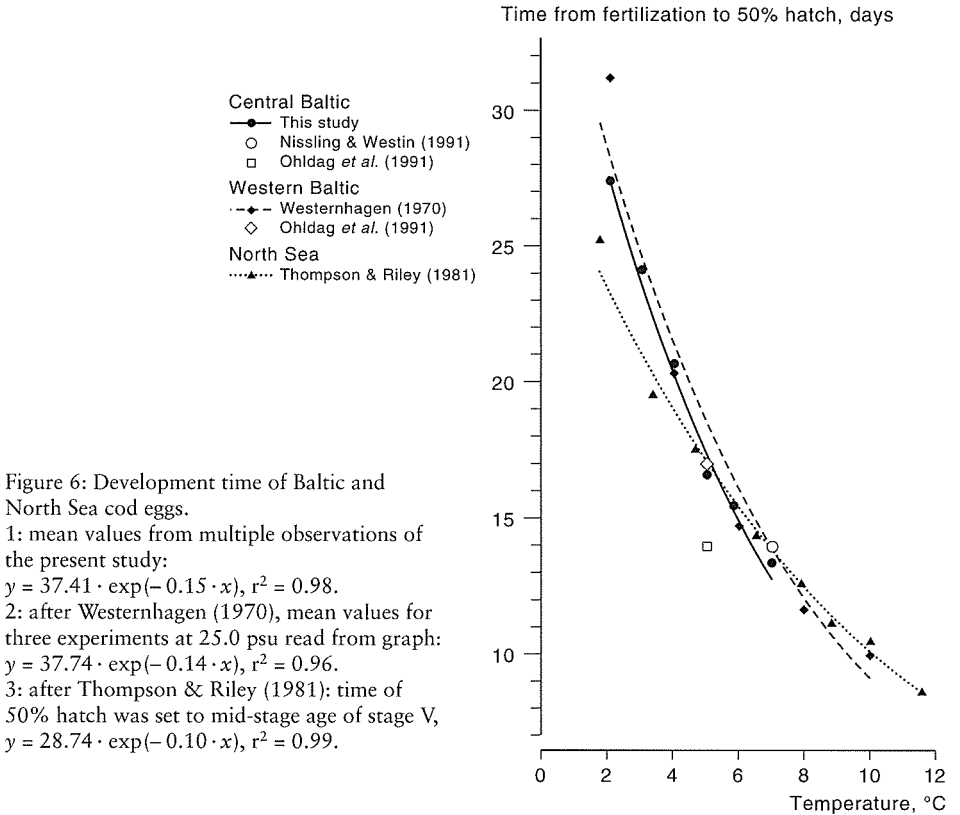
Time from fertilization to 50% hatch, days

Central Baltic
—●— This study
○   Nissling & Westin (1991)
□   Ohldag *et al.* (1991)
Western Baltic
·–◆–· Westernhagen (1970)
◇   Ohldag *et al.* (1991)
North Sea
····▲···· Thompson & Riley (1981)

Figure 6: Development time of Baltic and
North Sea cod eggs.
1: mean values from multiple observations of
the present study:
$y = 37.41 \cdot \exp(-0.15 \cdot x)$, $r^2 = 0.98$.
2: after Westernhagen (1970), mean values for
three experiments at 25.0 psu read from graph:
$y = 37.74 \cdot \exp(-0.14 \cdot x)$, $r^2 = 0.96$.
3: after Thompson & Riley (1981): time of
50% hatch was set to mid-stage age of stage V,
$y = 28.74 \cdot \exp(-0.10 \cdot x)$, $r^2 = 0.99$.

Temperature, °C

the central Baltic, and by Ohldag *et al.* (1991) for both areas. These results are sum-
marized in Figure 6, which also includes comparative data for North Sea cod from
Thompson & Riley (1981). The findings for Baltic cod are generally in good agree-
ment, except for one experiment with cod eggs from the Bornholm Basin (central
Baltic). The incubation time of 14 days at 5°C temperature reported by Ohldag *et
al.* (1991) does not agree with the results of Nissling & Westin (1991a) and is also
not supported by the results of the present study. Compared to the Baltic cod stocks
North Sea cod embryos appear to emerge earlier at temperatures below 5°C but re-
quire similar time for complete development at higher temperatures.

It has been reported for other fish species that adverse oxygen conditions may
cause a retardation of development (Hamdorf 1961, Siefert & Spoor 1974) or lead
to premature hatching due to the early release of hatching enzymes (DiMichele &
Taylor 1980). Ohldag *et al.* (1991), using in a single experiment with Baltic cod
eggs, observed a premature emergence of embryos at the lowest oxygen level at
which successful development was obtained ($4.9 \text{ ml} \cdot l^{-1}$). The present study does not
provide any significant indication for a premature hatching of cod eggs at reduced
oxygen levels although the hatching dates showed some relatively high variation.
Thus, from an individual experiment the impression of a retardation or an early

emergence may easily be obtained, even if there is no systematic effect. On the other hand, the high variance could also mask any possible underlying trend if it is not a very pronounced one.

Mortality rates were estimated from the number of dead eggs collected from the incubation bottles. It was assumed that dead eggs quickly accumulated at the bottom. No serious bias is expected from this assumption as all floating eggs, taken for the determination of developmental speed, were vital.

Periods of elevated egg mortality in cod, as seen in the present study for stages IB-II and IV, have previously been reported by several authors investigating the influence of environmental factors like temperature (Bonnet 1939, Iversen & Danielsen 1984), salinity (Nissling & Westin 1991a), combinations of temperature and salinity (Westernhagen 1970, Laurence & Rogers 1976), and organic pollutants (Kühnhold 1974, Dethleffsen 1977) on egg development. The period from gastrulation to the closure of the blastoporus and the time shortly before hatching appear to be especially critical. Davenport & Lönning (1980) and Serigstad (1987) found that the oxygen uptake of cod eggs slightly increases during development with a steep increase at the time of hatching. Thus, there is no indication that the observed fluctuations in mortality are related to a corresponding change in oxygen demand during development. It is evident, on the other hand, that failures during early ontogenesis (cellular multiplication and subsequent differentiation) may inhibit further development and may lead to an increased mortality at a later stage. High mortality just prior to hatching has been observed at all oxygen levels tested and it appears to be a general phenomenon which is not necessarily related to low environmental oxygen content.

The overall egg survival until hatching averaged around 30% in the present study at normoxic conditions. This agrees with the survival rates reported by Ohldag *et al.* (1991) and Nissling & Westin (1991a) at similar temperature and salinity levels for Baltic cod eggs. As further comparison, Figure 7 summarizes laboratory observations on egg survival for various cod populations at temperature and salinity levels which are common in their specific habitats. In experiments with Atlantic cod (Laurence & Rogers 1976), Norwegian coastal cod (Iversen & Danielsen 1984) and

Figure 7: Experimental results on egg survival in various cod populations. Atlantic cod (Laurence & Rogers 1976), Norwegian coastal cod (Iversen & Danielsen 1984), Western Baltic cod (Westernhagen 1970), Baltic cod (Nissling & Westin 1991a, Ohldag *et al.* 1991, this study). Range of egg survival of Atlantic and Western Baltic cod refer to means over all temperatures at selected salinity levels. Results by Ohldag *et al.* (1991) and from the present study represent normoxic conditions (≥ 8 ml $O_2 \cdot l^{-1}$).
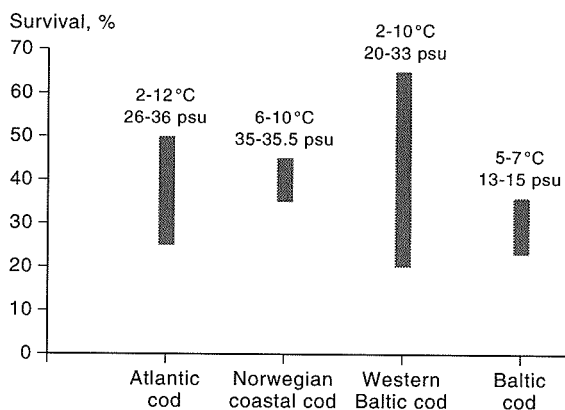
Western Baltic cod (Westernhagen 1970), egg survival was on average higher compared to Baltic cod eggs, but the range of values overlap. Nissling (1993) reported that the survival of central Baltic cod eggs in short-term experiments (48 h, 7°C) was significantly higher at 15 psu than at 11 psu salinity when the eggs were exposed to oxygen deficiency (0.7-2.0 ml·l^{-1}). No difference between the two salinities was found at 100% oxygen saturation. This emphasizes the importance of low ambient salinity levels in addition to the reduced oxygen concentrations in the central Baltic. It can be concluded that the conditions for cod reproduction are generally more favourable in the Bornholm Basin than in the eastern spawning areas, i.e. the Gdańsk Deep and the Gotland Basin, as these latter areas are less frequently influenced by North Sea water influxes.

With regard to the minimum requirements of cod eggs for salinity (11 psu, Westin & Nissling 1991) and oxygen content (2 ml·l^{-1}, present study), the hydrographic conditions in the central Baltic during the last decade (Nehring & Matthäus 1991) allowed a successful egg development only in the Bornholm Basin. No reproduction has been possible in the other important spawning grounds, i.e. the Gdańsk Deep and the Gotland Basin, since the early 1980s. But the vertical distribution of cod eggs in the Bornholm Basin during 1986 to 1992 shows that even in this area the maximum egg concentration was mostly encountered at ambient oxygen levels below 4 ml·l^{-1} (Wieland 1988, Wieland & Zuzarte 1991, Wieland, in prep.). It is of note that in 1989 about 60% of the egg population was floating in a depth range with an oxygen content of less than 2 ml·l^{-1} (Figure 8). Since 1990 weak or moderate inflows of saline and oxygenated bottom water slightly improved the environmental conditions in the Bornholm Basin. The eggs occurred in a more extended depth range and in 1992 they were most abundant at oxygen levels between 3.5 and 3.1 ml·l^{-1} (Figure 8). This is still below the favourable level but it is apparent that even small changes in the oxygen conditions can result in a substantial increase of the depth range where eggs may survive.

The vertical distribution of the eggs suggests that in recent years Baltic cod larvae have emerged into adverse environmental conditions. Field observations suggest that older cod larvae are distributed close to the sea surface (Wieland & Zuzarte 1991) implying an upward movement after hatching. Waller (unpubl.) observed yolk sack larvae to swim upwards to the surface at an average speed of 4 mm·s^{-1} regardless of the ambient salinity. When the larvae were resting, the sinking speed (2.0-0.6 mm·s^{-1}) was inversely related to the salinity (11.0-15.5 psu). It is unlikely that cod larvae can maintain migratory behaviour at reduced environmental oxygen levels. Hence, larvae may not survive for longer times, because low ambient oxygen levels do not allow them to approach the feeding areas actively. Further, Nissling (in press) using short-term experiments (48 h) found that yolk sack larvae exposed to oxygen levels below 2.1 ml·l^{-1} were mostly inactive or moribund, and at 1.1 ml·l^{-1} almost 50% of the larvae did not survive the experiment. This emphasizes that besides the hatching success the viability and the behaviour of larvae is highly depending on environmental oxygen. The the present study shows a steep increase in egg mortality at oxygen levels below 5 ml·l^{-1} approaching 100% below 2 ml O_2·l^{-1}. Hence, an oxygen concentration of at least 2 ml·l^{-1} seems to be required by the early live
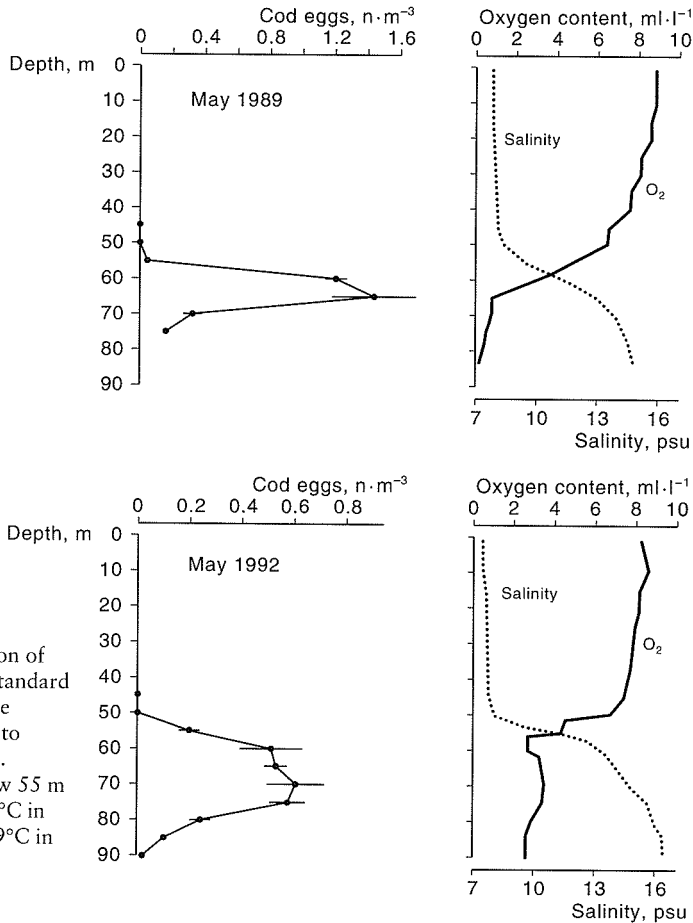
Figure 8: Vertical distribution of cod eggs (mean value and standard error from 5 parallels) in the Bornholm Basin in relation to salinity and oxygen content. Ambient temperature (below 55 m depth) ranged from 4.9-7.0°C in May 1989 and from 5.7-6.9°C in May 1992.

stages of cod. Future experimental work should include studies on the initial viability of larvae hatched from eggs which have developed at reduced oxygen content and should focus on the survival and the behaviour of the early larval stages.

Long-term oceanographic observations (1952-1991) for the Bornholm Basin, the Gdańsk Deep and the Gotland Basin, were used by Plikshs *et al.* (1993) to calculate the cod reproduction volume as the water mass with salinity and oxygen content above 11 psu and 2 $ml \cdot l^{-1}$, respectively. The results revealed a strong positive correlation between reproduction volume and egg survival rates. Egg survival was high in aeration periods when abundant year classes were formed and low in stagnation years when poor year classes occurred. Based on a comprehensive correlation between year class strength and salinity, oxygen and temperature conditions established by various authors, Bagge (1993) pointed out that other factors besides hydrographic ones are also involved in the recruitment process of Baltic cod.

The present results do yet not allow any precise definition of the prerequisites for a successful development of the eggs and early larval stages. However, as no

abundant year class has been formed without a preceding inflow of saline and oxygenated water (Kosior & Netzel 1989), it is considered that oxygen depletion has been the most important factor limiting the reproductive success of Baltic cod during the last stagnation period. In addition to the direct effect on egg survival, reduced oxygen supply during egg development may also affect the initial viability of larvae and their ability to migrate upwards and to learn to hunt for food. Thus, the effective reproduction volume for cod in the Baltic cannot yet be defined adequately and may have been much smaller than assumed to date. The effects of other processes related to the recruitment of Baltic cod, e.g. predation on the early life stages of cod by herring and sprat (Köster & Schnack 1994) and parental influences on egg quality (Kjörsvik *et al.* 1984), will become more evident when the oxygen conditions become more favourable.

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