

Size-specific vertical distribution of Baltic cod (*Gadus morhua* L.) eggs in the Bornholm Basin in 1993 and 1994

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The vertical distribution of Baltic cod eggs in relation to seawater density in the Bornholm Basin is described. Mean egg diameters, measured on preserved material, were found to be inversely proportional to ambient water density. The mean depths of the centre of egg mass, z , were 66 m and 59 m in 1993 and 1994, respectively, the shallower location in 1994 being related to the larger modal egg diameter in that year. The analysis of egg abundance in two developmental groups showed that older eggs were consistently more abundant in the 10-m depth layer immediately below the layer of z occurrence.

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Introduction

The Baltic Sea is an estuarine system in which salinity strongly influences survival and distribution of its main commercial fish, cod (*Gadus morhua* L.). The minimum salinity required for successful fertilization and initial egg development under laboratory conditions in Baltic cod is 11 (Westin and Nissling, 1991). Based on recent experimental evidence it was established that a concentration of $2 \text{ ml O}_2 \text{ l}^{-1}$ is a cutoff point for developmental cessation of cod eggs (Wieland *et al.*, 1994). Waller *et al.* (1993) found a downward trend in egg survival starting at a concentration of 5 ml l^{-1} ; the lethal oxygen concentration was assumed to be 1.6 ml l^{-1} . Inflows of more saline and well-oxygenated water from the North Sea allow for periodic regeneration of the water in the Baltic. More saline (10–18) and denser water is retained only in the deep basins within and below the halocline, starting at 50 to 80 m depth (Wojewódzki, 1991). These deep basins, such as the Bornholm Basin, are the main spawning grounds of Baltic cod. Unfortunately, oxygen content in the stagnating bottom water of deep basins frequently falls below the critical level of 2 ml l^{-1} which results in a stressful environment for cod egg development. It is therefore crucial that eggs retain buoyancy that secures avoidance of the unfavourable oxygen conditions.

The evidence from laboratory observations indicates that the buoyancy of cod eggs depends on yolk osmolality, chorion thickness and egg batch number (Nissling *et al.*, 1994). At constant salinity the specific gravity of cod eggs decreases up to 8 d post-fertilization and increases until hatching (Nissling and Vallin, 1996). In the field, slow sinking of older eggs into the oxygen-depleted bottom layer may negatively affect egg development as well as the initial viability of hatched larvae. In the Bornholm Basin, cod eggs are most abundant below the halocline in water of density (σ) greater than 1008 and salinity greater than 11 (Wieland, 1988; Wieland and Zuzarte, 1991; this study). Oxygen conditions in this water layer fluctuate in time and the near-bottom stratum occasionally becomes oxygen-depleted (Matthäus and Franck, 1992).

The purpose of this study was to describe in greater detail a relationship between the size of Baltic cod eggs and seawater density, based on field data. In addition, the stage-dependent distribution of eggs was analysed to investigate whether a decreasing buoyancy of later-stage eggs affects their vertical distribution.

Materials and Methods

Sampling consisted of Multinet (0.25 m² mouth opening, 5 net set-up, 300 μm mesh size) horizontal tows at

Table 1. Parameters of the simple linear regression model, egg diameter = $\alpha + \beta$ (sea water density) + ε . All regression coefficients were statistically significant at p-level <5%. Listed p-value refers to the F-statistic; d.f. – degrees of freedom; R^2 – coefficient of determination.

Date	Intercept α	Slope β	R^2	F-statistic	d.f.	p-value
1–2 August, 1993	16.168	– 0.014	0.798	51.21	13	<0.0001
2–3 August, 1993	12.430	– 0.011	0.860	73.92	12	<0.0001
5–6 August, 1993	13.971	– 0.012	0.579	15.12	11	0.0025
23–24 August, 1994	9.313	– 0.008	0.587	24.19	17	0.0001
23–24 August, 1994 density >1008 kg · m ^{–3}	16.322	– 0.015	0.844	64.78	12	<0.0001
7 September, 1994	18.671	– 0.017	0.700	18.65	8	0.0026
1993 combined	13.357	– 0.012	0.650	74.12	40	<0.0001
1994 combined	8.935	– 0.007	0.306	11.92	27	0.0018
1994 combined density >1008 kg · m ^{–3}	18.294	– 0.017	0.657	42.17	22	<0.0001
1993 and 1994 combined	11.222	– 0.010	0.499	68.72	69	<0.0001
1993 and 1994 combined density >1008 kg · m ^{–3}	15.058	– 0.013	0.642	114.70	64	<0.0001

10-m intervals from 0–80 m, along the following transects in the Bornholm Basin:

in August 1993:

55°15.5'N, 15°24.0'E–55°19.0'N, 15°20.4'E;

55°17.7'N, 15°59.8'E–55°21.7'N, 16°00.4'E;

55°12.2'N, 15°51.1'E–55°13.7'N, 15°57.5'E;

in August 1994:

55°14.0'N, 15°59.1'E–55°17.8'N, 15°53.5'E;

in September 1994:

55°14.1'N, 16°07.6'E–55°20.0'N, 15°57.7'E.

From 400 to 700 m³ of water was filtered per net. The hydrological parameters of depth, temperature, salinity and calculated density, were concurrently collected with a CTD probe mounted on the sampling gear. The seawater density values used for plotting the vertical density profiles were calculated from multiple readings recorded every 6 sec in the area of sample collection. For each individual net, average values of water temperature, salinity and density were assigned, based on concurrent parameter readings recorded every 2 sec. Oxygen concentration was measured by the method of Winkler at the ends of each transect, for 10-m depth intervals. Two vertical profiles were later combined into one “averaged” plot to represent the oxygen level for the entire sampled area.

Samples were initially preserved in a 4% buffered formaldehyde–seawater solution and later transferred into Steedman's (1976) fixative. All cod eggs were counted and dead eggs were recorded. Egg developmental stages were identified according to a 6-stage classification by Thompson and Riley (1981) which is based on classifications by Apstein (1911) and Westernhagen (1970). Egg diameters were measured with an optical image analysis system. Mean egg diameters were only

calculated for subsamples that consisted of a minimum of approximately 100 eggs (range: 96–311 eggs), with an average of 210 eggs being measured per sample. Mean egg diameters in 1993 and 1994 were estimated from 42 and 29 independent samples, respectively. Simple linear regressions by the least squares method (model: egg diameter = $\alpha + \beta$ (seawater density) + ε ; α and β – regression coefficients, ε – random error) were fitted to the data from individual surveys and to the pooled data sets to describe a relationship between egg diameter (dependent variable) and seawater density (independent variable). Sigma STP (σ , kg m^{–3}) was used as a measure of density to account for the variations of pressure, salinity and temperature in the sampled layer.

A visual inspection of the plotted data revealed that the data points for σ less than 1008, representing eggs found in the 40–50 m depth layer in 1994, did not follow the linear trend exhibited by the remaining data. The linear regression equations were therefore re-calculated without these points, and reported separately in Table 1 for comparative purposes.

Egg abundance was characterized by the depth of centre of mass, z , because this parameter has been customarily used by other authors to describe the location of the highest concentration of eggs in the water column. The depth of centre of mass is calculated as follows: $z = \Sigma (r_i z_i)$ where r_i is a relative abundance of eggs in stratum i ; z_i is a depth of stratum i .

Eggs were divided into two age groups, i.e. younger eggs (stages IA–II) and older eggs (stages III–IV), and the abundance values of these two groups in 10-m depth layers were calculated, based on the raw data expressed as number of eggs per 1000 m^{–3}. The depth layer of z occurrence was treated as a reference point for making comparisons between the layers.

Results

Sample sizes of approximately 100 eggs used for mean egg diameter estimates seemed to be adequate in this study. The values of coefficient of variation, CV, were less than 0.01%, and individual egg diameter measurements were normally distributed. The minimum and maximum observed egg diameters were 1.356 and 1.970 mm.

The simple linear regression model was fitted to data from individual surveys (upper part of Table 1) and to the pooled data sets (lower part of Table 1). All models and their regression coefficients α and β were statistically significant at $p < 0.05$. The regression results for data points for $\sigma > 1008$ are also reported in Table 1 to show an improved fit of the model. An improved fit of the model was observed after exclusion of data points for $\sigma < 1008$ (R^2 , range: 0.58–0.86) in comparison with the all data points regression (R^2 , range: 0.31–0.86); see Discussion. The oxygen conditions were favourable for egg development in the entire sampled area in August 1993 (Fig. 1). However, oxygen concentrations below the critical level of 2 ml l^{-1} were observed below a depth of 73.3 and 73.6 m in August 1994 and September 1994, respectively. No linear relation was found between the level of oxygen in water and egg diameter.

The mean depth of the centre of mass, z , in 1993 was located 7 m lower than in 1994, and the mean difference between the seawater density at the depth of z in 1993 and 1994 was 1.49 (Table 2). A mode of the frequency distribution rather than the mean of all measured egg diameters was assumed to be a representative egg diameter associated with a particular z value. Smaller modal size of eggs in 1993 was correlated with a downward shift of the depth of the centre of mass in comparison with the z location in 1994; smaller eggs reached their neutral buoyancy point in denser and, therefore, deeper water.

The 40–50 m depth layer is of particular interest because it is in the closest location to the instability zone between two different water masses. A number of eggs collected in that layer disclose some information about a possible egg transport near the boundary zone. In August 1994, the presence of a considerable number of eggs in the 40–50 m depth layer, averaging 259 eggs per 1000 m^{-3} , was observed. The corresponding samples from the 40–50 m depth stratum in August 1993 and September 1994 were scarce and the calculated mean abundance equalled to 26 and 72 eggs per 1000 m^{-3} , respectively.

Stage-specific egg abundance values in the 10-m depth layers were compared, the 10-m depth layer of z occurrence serving as a reference point (bold numbers in Table 3). For all five surveys, older eggs were consistently more abundant in the 10-m depth layer below the layer of z occurrence; the mean increase in abundance of older stages was 4.8%.

Discussion

The physical starting point for an egg in the water column is set at first by the spawning depth. Unless dynamic transport processes take place, egg density and egg size determine its further movement through water in accordance with the Archimedes' principle. In flounder, the initial egg density, determined in the ovary, is strongly affected by ambient salinity (density) of water in which the spawning individuals live, less dense eggs being produced by fish living in less saline waters, and vice versa (Sølemdal, 1967, 1973). The same mechanism was found to exist in cod from Newfoundland waters, but no information on egg size was given (Anderson and de Young, 1994). Baltic cod produce larger and less dense eggs with thinner chorionic membranes than Atlantic cod (Nissling *et al.*, 1994); egg specific gravity decreases from gastrulation and increases prior to hatching (Nissling and Vallin, 1996). Measurements of egg parameters such as specific gravity, osmolality or chorion thickness were not available from the preserved material used in this study. Nevertheless, a strong linear relation was detected between fixed egg size and ambient water density for densities greater than 1008. In practical terms, it means that in the Bornholm Basin below the halocline cod eggs of different diameters were distributed according to a density gradient, with smaller eggs suspended in denser water closer to the bottom. A similar finding of a more general nature was reported for the first time by Grauman (1964) for cod eggs collected in the Bornholm Basin in April 1963.

The linear relationship described in the present study did not apply to the halocline zone where a steady state was disturbed by dynamic boundary processes. Inclusions of warm advected water were found in the sampled areas at 42.5–70 m, 42.5–70 m, and 42–65 m in August 1993, August 1994 and September 1994, respectively (Wojewódzki and Grelowski, 1995). The spreading and sinking of warmer and more saline water could possibly result in an upward movement of the top water layer, with suspended cod eggs. Larger than usual amounts of cod eggs collected in the 40–50 m depth stratum would provide evidence of advection, and such data are presented below. In August 1994, samples of over 100 eggs each were caught during five independent collections in the 40–50 m depth layer. Stage-specific egg distribution from the pooled samples comprised 79.5% of stages IA–II and 20.5% of stages III–IV, which is very close to the values reported for the depth layer of z occurrence (see Table 3). When inspecting Figure 2, plot B, there is an obvious cluster of five samples collected in August 1994 in the 40–50 m depth layer (approx. σ 1007). The location of the cluster suggests that eggs could have been transported straight upward from the lower density stratum of about 1010 kg m^{-3} , possibly by a pocket of warm advected water. The presence of a considerable

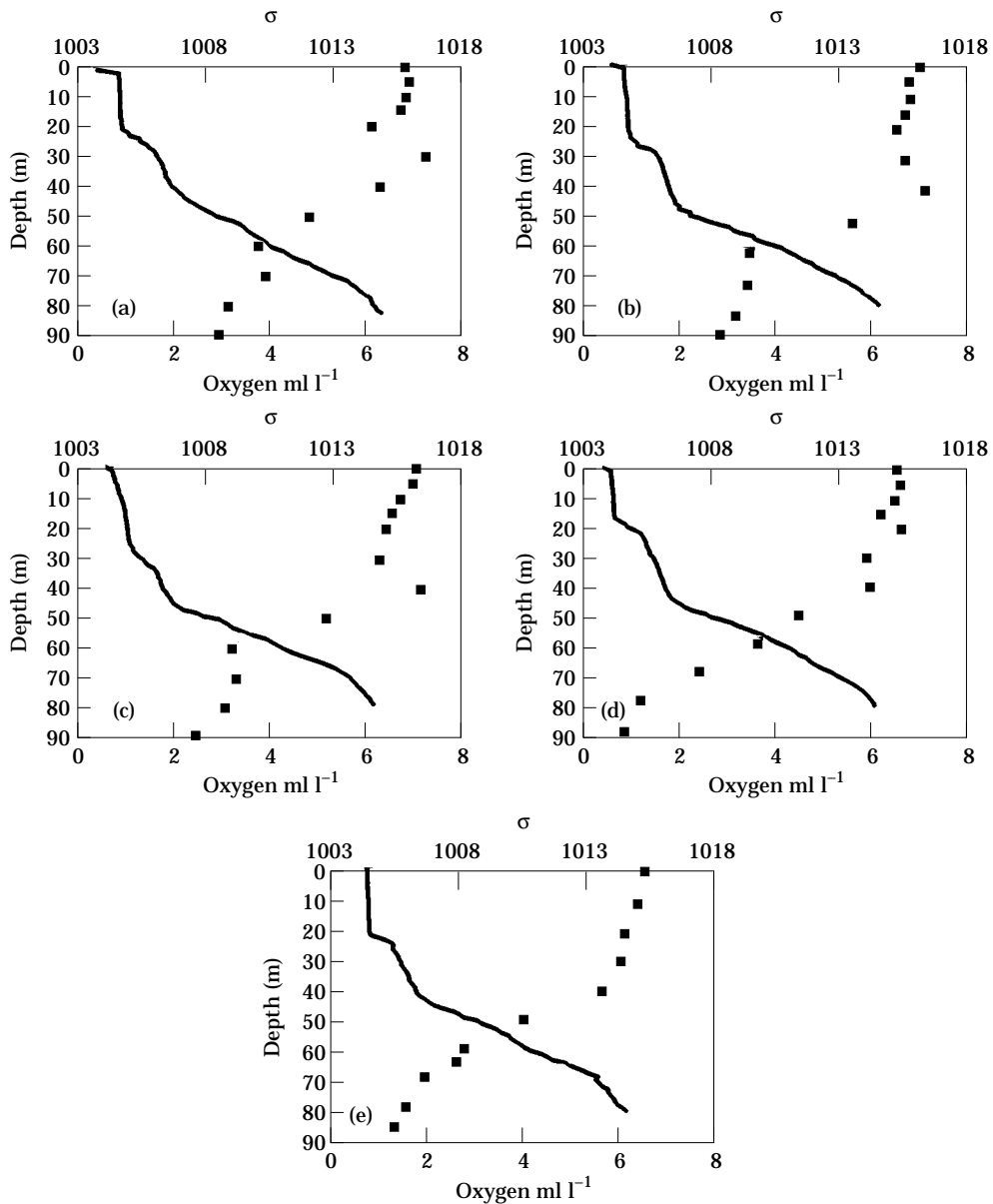


Figure 1. Vertical profiles of seawater density (line) and oxygen concentration (squares) at sampling sites. (a) 1–2 August 1993; (b) 2–3 August 1993; (c) 5–6 August 1993; (d) 23–24 August 1994; (e) 7 September 1994. Reported density is sigma STP; oxygen content measured by the Winkler's method.

amount of eggs in the 40–50 m depth layer in August 1994 (mean: 259 eggs 1000 m^{-3}), could also be explained by active spawning taking place there; such an assumption however, is not in agreement with present knowledge about Baltic cod reproduction (Hardy, 1978). It is hypothesized that a vertical displacement of eggs by the advected water was observed in August 1994 but not in 1993 and September 1994. The time that elapses between the vertical displacement of eggs and sample collection is probably a critical factor in detect-

ing this phenomenon. Mesoscale changes of ambient water density and turbulent water transport experienced by the eggs during advection processes are counter-balanced by sinking of eggs out of the instability zone, back to the point of their neutral buoyancy, and in this way, a steady hydrostatic state is achieved again. The vertical displacement of eggs will go unnoticed if sampling is performed during an advanced sinking stage. The indirect evidence in support of this hypothetical situation comes from the egg abundance data. On

Table 2. Depth of the centre of egg mass, z , and the corresponding hydrological parameters and egg diameters. Reported mean density is sigma STP; modal and mean egg diameters are, respectively, a mode of frequency distribution and a mean of all measured diameters.

Date	z (m)	Mean density at z (kg m^{-3})	Mean temp. at z ($^{\circ}\text{C}$)	Mean salinity at z (ppt)	Mean oxygen content at z (ml l^{-1})	Modal egg diameter (mm)	Mean egg diameter (mm)
1–2 August, 1993	64	1011.62	5.15	14.32	3.86	1.590	1.593
2–3 August, 1993	67	1012.01	5.04	14.79	3.41	1.580	1.599
5–6 August, 1993	67	1012.65	4.75	15.58	3.23	1.594	1.604
23–24 August, 1994	59	1010.66	6.36	13.31	3.92	1.598	1.601
7 September, 1994	59	1010.55	7.48	13.23	3.18	1.624	1.632

Table 3. Stage-specific distribution of cod eggs in 10-m depth layers and in the entire sampled water column. All identified eggs were divided into two groups, younger (stages IA–II) and older (stages III–IV) eggs; percentages of eggs in the groups were calculated for the 10-m depth strata and for the entire sampled volume, using the egg abundance data expressed as eggs 1000 m^{-3} . In bold are numbers for the depth layer of z occurrence.

Date	Total number of identified eggs	Stage	Percent of eggs in depth layers by stage				Percent of total eggs by stage
			40–50 m	50–60 m	60–70 m	70–80 m	
1–2 August, 1993	3805	IA–II	*	79.4	83.1	81.9	82.2
		III–IV		20.6	16.9	18.1	17.8
2–3 August, 1993	3540	IA–II	*	92.6	84.4	76.8	83.0
		III–IV		7.4	15.6	23.2	17.0
5–6 August, 1993	3189	IA–II	*	84.5	83.0	78.9	82.2
		III–IV		15.5	17.0	21.1	17.8
23–24 August, 1993	3323	IA–II	79.5	78.8	76.0	72.0	77.5
		III–IV	20.5	21.2	24.0	28.0	22.5
7 September, 1994	2168	IA–II	*	75.6	67.5	*	72.4
		III–IV		24.4	32.5		27.6

*Small sample size (range: 17–72).

23 August 1994, the proximity of the instability zone and centre of egg mass created good conditions for upward movement of considerable numbers of eggs into the 40–50 m depth layer. Two weeks later, on 7 September, the number of eggs present in that water layer dropped by about 3.6 times (259 vs. 72 eggs 1000 m^{-3}), presumably due to sinking of eggs.

Probably not all sampled eggs were neutrally buoyant at the moment of collection. Anderson and de Young (1994) characterized five distinct types of egg descent trajectories, based on laboratory observations of cod eggs placed in a density gradient column. Eggs collected in the field may represent any of the described trajectories. Eggs collected while still “in motion” will introduce a certain amount of unexplained variability into a linear regression model of egg diameter and seawater density because the steady hydrostatic state principle is violated. The values of the correlation coefficient, R^2 , calculated from simple linear regression of egg diameter and seawater density could be used to assess the instability of the water mass in which eggs develop.

The size of egg is one of the critical factors influencing its vertical location in the water. Nissling *et al.* (1994) reported that under laboratory conditions egg size increased with batch number in the majority of females. This information, however, referred to five consecutive egg batches, not to all batches released during the spawning season. In an investigation on Norwegian coastal cod, progressively smaller eggs were produced throughout the entire spawning season and smaller females shed smaller eggs (Kjesbu, 1989). In general, the mean cod egg diameters reported in this study are comparable with values presented elsewhere. Ehrenbaum (1905–1909) reported that cod eggs collected in August in the Bornholm Basin were, on average, 1.641 mm in diameter (range: 1.38–1.82 mm) while eggs collected by Grauman (1965) in the Bornholm Basin in August 1964 were, on average, 1.60 mm in diameter. In our study the largest eggs were observed at the end of the spawning season in 1994 which is unexpected and difficult to interpret. Wieland (1988) hypothesized that not only an extremely low oxygen

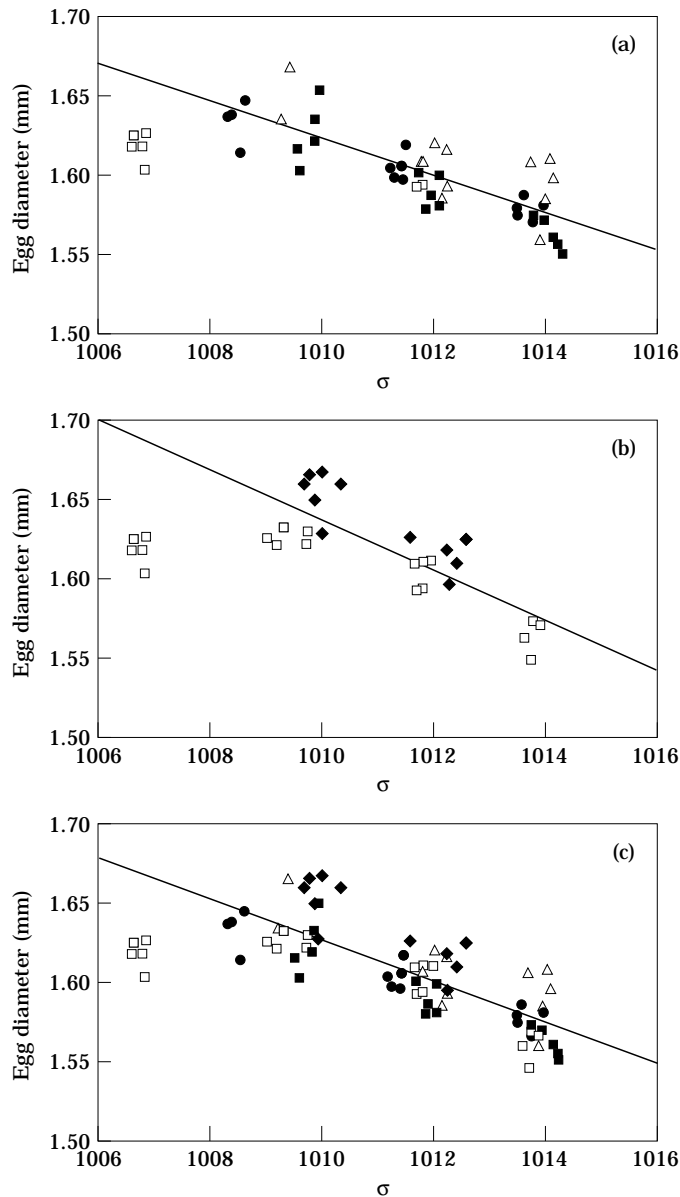


Figure 2. Mean egg diameter plotted against density of ambient sea water. (a) data from 1993; (b) data from 1994; (c) combined results from the period 1993–1994. Filled squares – 1–2 August 1993; filled circles – 2–3 August 1993; triangles – 5–6 August 1993; empty squares – 23–24 August 1994; filled diamonds – 7 September 1994. Lines represent fitted simple linear regression models for seawater densities $>1008 \text{ kg m}^{-3}$.

level, but also its intermediate content in sea water, may be a limiting factor in egg survival. This was later proved by experimental data published by [Wieland *et al.* \(1994\)](#). If oxygen levels in the deeper water layer were insufficient for a development of the last, and therefore, the smallest eggs of the spawning season, then the eggs surviving in the water column would be larger than expected. In addition a combined influence of low

oxygen content and high water temperature in September 1994 could have had more than an additive effect on differential egg survival. [Iversen and Danielssen \(1984\)](#) established under laboratory conditions that cod egg mortality increased rapidly above 10°C and reached 100% at 14°C ; at 12°C 80% of the eggs died during the two first days of incubation. In the same study it was reported that the increase in mortality for temperatures

above 12°C was lower in eggs exposed to the temperatures later in development. No linear relation was found between the content of oxygen in water and egg diameter in this study, but the authors felt that the averaged values of oxygen content used in the analysis were not reliable (see Materials and Methods for details). Different precision used in measuring egg diameters and oxygen concentrations may have prevented the possibility of showing a correlation between the two variables.

Another question addressed in the present study was whether a decreasing buoyancy of older stages affects their vertical distribution in the water column. To answer that question the abundance values of older (IA–II) and younger (III–IV) eggs were compared for 10-m depth layers, using the depth layer of z occurrence as a reference point. On average, there were 4.8% more older eggs in a 10-m depth layer below the z layer than in the z layer itself. Is such a difference meaningful? One would expect to find a higher abundance of older stages in the water below the centre of egg mass because cod egg density increases prior to hatching, which results in a downward flux of older sinking stages. The sinking distance depends on the density gradient along which the egg travels, the steeper the density gradient the shorter the sinking distance.

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