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

by

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Abstract

The vertical distribution of the Baltic cod eggs in dependence on sea water density in the field is described, based on the data collected in August 1993, August 1994 and September 1994, in the Bornholm Basin. A simple linear regression model by the method of least squares was fitted to the mean egg diameter (dependent variable) and sea water density measurements from individual surveys and from the pooled data sets (R^2, range: 31-86%). An improved fit of the model was observed after exclusion of data points for densities < 1008 kg/m^3 (R^2, range: 58-86%); density 1008 kg/m^3 approximately corresponds to a depth of halocline zone at 40-50 m. Mean egg diameters were found to be inversely proportional to ambient water density. Mean depth of the center of egg mass, z_{cm}, was 65.71 and 59.04 m in 1993 and 1994, respectively; a shallower location of z_{cm} in 1994 was due to a larger modal egg diameter that year. Stage-dependent distribution of eggs in two arbitrarily chosen water density strata (shallower layer and deeper layer, with a break-point at density 1013 kg/m^3) did not show a consistent pattern. Stage-specific mortality rates (Z) in the depth stratum of the center of egg mass ranged from 0.139 to 0.534 per day. Mean overall egg mortality rates from stage I through stage IV in the water layer 50-80 m were 97.8, 93.1 and 84.6% in August 1993, August 1994 and September 1994, respectively.

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.). A minimum salinity required for successful fertilization and initial egg development under laboratory conditions in Baltic cod is 11 ppt (Westin and Nissling, 1991). Based on the recent experimental evidence it was established that oxygen content is also a critical factor in egg development and a concentration of 2 ml O_2/l was found to be a cut-off point for development cessation (Wieland et al., 1994). Waller et al. (1993) found a downward trend in egg survival starting at concentration 5 ml/l; the lethal oxygen concentration was assumed to be 1.6 ml/l. Inflows of more saline and well oxygenated water from the North Sea allow for periodic regeneration of the Baltic's waters, however, more saline (10-18 ppt) and denser water is retained continuously only in the deep basins within and below the halocline, starting at depth 50 to 80 meters (Wojewódzki, 1991). These deep basins, such as the Bornholm Basin, are the main spawning grounds of Baltic cod. Unfortunately, oxygen content in stagnating bottom water of deep basins frequently falls below the critical level of 2 ml/l which results in a stressful environment for cod egg development. Therefore, it is crucial that eggs retain buoyancy which would secure avoidance of the unfavorable oxygen conditions.

The evidence from laboratory observations indicates that cod egg buoyancy depends on yolk osmolality, chorion thickness and egg batch number (Nissling et al., 1994). Under steady salinity condition buoyancy increases up to day 8 post-fertilization and it decreases until hatching (Nissling and Vallin, 1994). In the field, slow sinking of older eggs into 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 greater than 1008 kg/m^3 and salinity greater than 11 ppt (Wieland, 1988; Wieland and Zuzarte, 1991; this study). Oxygen conditions in this water layer fluctuate in time and the near-bottom stratum ocassionally becomes oxygen-depleted (Matthäus and Franck, 1992).

The purpose of this study was to describe a relationship between the Baltic cod egg size and sea water density in the field. Also, stage-dependent distribution of eggs in two arbitrarily chosen density strata was analyzed in an effort to find out whether decreasing buoyancy of older stages affects their vertical distribution. Comparisons of obtained mortality estimates with values cited elsewhere were performed in an attempt to elucidate the phenomenon of dwindling Baltic cod stock.

Material and Methods

Sampling consisted of Multinet (0.25 m^2 mouth opening, 5 net set up, 300 μm mesh size) horizontal tows at 10-meter intervals from 0-80 m in the Bornholm Basin areas shown in Fig. 1. From 400 to 700 m^3 of water was filtered per net. The hydrological parameters, namely, depth, temperature, salinity and calculated density, were concurrently collected with a CTD probe mounted on the sampling gear. Sea water density values used for plotting of the vertical density profiles were calculated from multiple readings recorded every 6 seconds in the area of sample collection. For each individual net, the average values of water temperature, salinity and density were assigned, based on the concurrent parameter readings recorded every 2 seconds. Oxygen concentration was measured by the method of Winkler at two distal points 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-sea water solution and later transferred into a conserving solution of formulation cited by Steedman (1976). All cod eggs were enumerated in each sample and dead eggs were reported separately. 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 v.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) to ensure good precision of estimates. On average, 210 eggs were measured per sample. Simple linear regressions by the least squares method were fitted to the data from individual surveys and to the pooled data sets in an effort to describe a relationship between egg diameter (dependent variable) and sea water density (independent variable). Sigma STP was used as a measure of density to account for variations of pressure, salinity and temperature in the sampled layer.

Egg abundance was characterized by the depth of center of mass, z_{cm}, calculated as follows: $z_{cm}= \Sigma\ (p_i z_i)$ where p_i is a relative abundance of eggs in stratum i; z_i is a depth of stratum i. Stage-specific egg abundance was expressed as percentage of eggs in two arbitrarily chosen age classes, that is, stages IA through IB (younger stages) and stages II through IV (older stages), based on the mean egg abundance per 1000 m^3 of water, in 10-m depth layers. Additionally, the abundance of younger and older stages was compared for two arbitrarily chosen sea water density strata, density $\geq$1013 kg/m3 and density<1013 kg/m3, in an effort to find out whether decreasing buoyancy of older stages affects their vertical distribution. Chi-square test for a 2x2 contingency table, with Yates continuity correction, was performed to check whether the proportions of older and younger eggs are the same in two chosen density strata. The alternative hypothesis was two-sided and the α-level equal 5%.

Daily production and instantaneous daily mortality rates in successive egg stages were estimated for 10-meter depth strata. Daily production was defined as a number of cod eggs at different developmental stages produced per day below a standard area (Saville, 1964; Saville and Schnack, 1981). Mortality rates were calculated using constant birth method under constant spawning intensity assumption (Smith and Richardson, 1977). Based on the exponential decay of the egg population, the following equation was used:

$Z_{i-j} = (\ln N_i - \ln N_j) / (t_j - t_i)$ where, Z_{i-j} is an instantaneous daily mortality rate during stage i to j; N_i is a daily production of eggs at stage i; N_j is a daily production of eggs at stage j; $(t_j - t_i)$ is a temperature-dependent age between stages i to j, in days (midstage age).

Stage duration was calculated from empirical equations in Wieland et al. (1994) for temperatures assigned to individual nets. The stage duration estimates for temperatures above 7°C were obtained by extrapolation; 11.2°C was the maximum temperature for which stage duration had been extrapolated. Stages IA and IB were combined for estimating instantaneous daily mortality rates; overall egg mortalities in distinct depth strata were calculated for eggs below a 50 m depth. Either individual values for single surveys or averages from data pooled by year are reported.

Results

Sample size of about 100 eggs used for mean egg diameter estimation 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. Mean egg diameters in 1993 and 1994 were estimated from 43 and 28 samples, respectively.

A visual inspection of the plotted data revealed a linear relationship between mean egg diameter and sea water density for densities greater than 1008 kg/m^3; density 1008 kg/m^3 approximately corresponds to a depth of halocline zone at 40-50 m (Fig. 2). Simple linear regression model, egg diameter= $\alpha+\beta$(sea water density)+ε, was fitted to the data from individual surveys (upper part of Table 1) and to the pooled data sets (lower part of Table 1). The regression results for data points for sea water densities >1008 kg/m^3 are also reported in Table 1 to show an improved fit of the model under exclusion rule. All models and their regression coefficients α and β were statistically significant at p-level <0.05. An improved fit of the model was observed after exclusion of data points for densities <1008 kg/m^3 (R^2, range: 58-86%) in comparison with all data points regression (R^2, range: 31-86%), which pointed to the nonlinear character of the egg diameter - sea water density relation for densities less than 1008 kg/m^3.

A mean depth of the center of mass, z_{cm}, in 1993 was located 6.68 m lower than a mean z_{cm} in 1994 (Table 2). A mode of the frequency distribution of all measured egg diameters was assumed to be an "average" egg diameter associated with a particular z_{cm} value. Smaller modal size of eggs in 1993 resulted in a downward shift of the depth of the center of mass in comparison with the z_{cm} location in 1994; smaller eggs reached their neutral buoyancy point in denser and, therefore, deeper water.

Stage-dependent egg abundance was analyzed for two water density layers: a shallower water layer of lower density (<1013 kg/m^3) and a deeper water layer of higher density (≥1013 kg/m^3). A break-point at density 1013 kg/m^3 was chosen arbitrarily, based on the visual inspection of the plotted data (see Fig. 2); the upper limit of this density layer was observed at depths ranging from 66.5 to 70.0 m.

In August 1993, from 45.4 to 51.5% of eggs in the higher water density layer consisted of older stages (II,III, IV) while in the lower water density stratum older eggs made up only 34.2 to

44.8% of all eggs in that layer (Table 3). The results of the chi-square test showed statistically significant differences in number of eggs from younger and older stages in two density strata. In August 1994, there was a very small and statistically non-significant difference in stage-dependent distribution of eggs between the lower and higher water density layers; older stages constituted 56.0 and 54.3% of all eggs in the respective density strata. In September 1994, only 1.7% of all eggs were collected in the deeper layer (compare with 23.9 and 3.5% in August 1993 and August 1994, respectively). Approximately 51.3% of eggs in the shallower stratum in September 1994 were older stages. The stage-specific distribution of eggs in September 1994 did not differ in two water density layers as indicated by the values of the chi-square statistic. Oxygen conditions were favorable for egg development in the entire sampled area in August 1993 (Fig. 3). However, oxygen concentrations below the critical level of 2 ml/l were observed below a depth of 73.3 and 73.6 m in August 1994 and September 1994, respectively.

In figure 4, three main zones of egg distribution, considered in this study, were plotted: 1) a depth range for water density 1008 kg/m^3 which is assumed to be a site of instability, based on hydrological data and linear regression analysis, 2) a depth of the center of egg mass, z_{cm}, 3) a depth of occurrence of sea water at density ≥1013 kg/m^3 which marks the beginning of the arbitrarily chosen higher water density layer. Numbers in boxes represent mean egg abundance per 1000 m^3 in the 40-50 m depth stratum. The 40-50 m depth layer is of particular interest because it is in the closest location to the instability zone; a number of eggs collected in that layer discloses some information about a possible egg transport near the boundary zone. In August 1994, the presence of a considerable amount 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 average abundance equal 26 and 72 eggs/1000 m^3, respectively.

Daily production of successive cod egg stages were calculated for 10-m depth strata. The highest values of daily production, corresponding to the presence of the center of egg mass, were observed in the depth layers 60-70 and 50-60 m in 1993 and 1994, respectively (Fig. 5). A sharp decline of egg production in September 1994 was indicative of the end of spawning season.

Instantaneous daily mortality rates, Z, increased with increasing age of eggs in almost all depth strata (Fig. 6). Stage-specific mortality rates, calculated for the depth stratum of center of egg mass, ranged from 0.139 to 0.534 per day. These values are equivalent to loss rates of about 13.0 and 41.4% per day. Egg mortality rates from stage I through stage IV in the water layer 50-80 m, calculated as arithmetic means from overall rates in three 10-m strata, were 97.91% (SD=0.90%), 91.47 (SD=2.31) and 86.08 (SD=6.60) in August 1993, August 1994 and September 1994, respectively (Table 4).

Discussion

The initial egg density and its size at spawning are two important factors which determine the physical starting point for an egg in the water column. In flounder, the initial egg density is strongly affected by ambient salinity (density) of water in which spawning occurs; less dense eggs are produced by fish inhabiting less saline waters, and vice versa (Solemdal, 1967; 1973). The same mechanism was found to exist in cod from Newfoundland waters (Anderson & de Young, 1994). The Baltic cod produces larger and less dense eggs with thinner chorionic membranes than those of the Atlantic cod (Nissling et al., 1994). Regretably, more sophisticated measurements of egg parameters such as, specific gravity, osmolality or membrane thickness, were not available from the preserved material used in this study. Nevertheless, a strong linear relation was detected between the egg size and ambient water density for densities greater than 1008 kg/m^3, based on the collected data. In practical terms, it means that in the Bornholm Basin below the halocline cod eggs of different diameters were distributed according to the density gradient, with smaller eggs suspended in denser water closer to the bottom. A similar finding of a more general nature was reported by Grauman (1964) for cod eggs collected in the Bornholm Basin in April 1963. The linear relation 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 advective water were found in the sampled areas at depth 42.5-70 m, 42.5-70 m and 42-65 m in August 1993, August 1994 and September 1994, respectively (Wojewódzki & Grelowski, in prep.). The spreading of warm and more saline water could possibly result in an upward movement of less dense top layer, with suspended cod eggs. Larger than usual amounts of cod eggs collected in the 40-50 m depth stratum would evidence such phenomenon.

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 data comprised 48.3% of stages IA and IB, and 51.7% of older stages which falls within the range of the values reported for the other surveys. The stage-specific distribution in the younger (IA-IB) and older (II-IV) stages did not depend on the egg location in the water column, that is, whether eggs came from the 40-50 m depth layer or from the water below it (chi^2-statistic=1.779, p=0.182). When inspecting Fig. 2, plot B, one can easily notice a cluster of five samples collected in August 1994 in the 40-50 m depth layer (approx. density 1007 kg/m^3). The location of the cluster suggests that eggs were shifted straight upward from the lower density stratum of about 1010 kg/m^3, possibly by a pocket of warm advective water. The presence of a considerable 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, however, such assumption is discrepant with the up-to-date knowledge about the Baltic cod reproduction (Hardy, 1978). Therefore, it was concluded that a vertical displacement of eggs by the advective water was observed in August 1994 but not during the other surveys. Time elapsed between the vertical displacement of eggs and sample collection is probably a critical factor in detecting this phenomenon. Mesoscale changes of ambient water density and turbulent water transport experienced by the eggs during advection processes are counterbalanced by sinking of eggs out of the instability zone, back to the point of their neutral buoyancy, and this way, a steady hydrostatic state is achieved again. The vertical displacement of eggs will go unnoticed if sampling is performed during advanced sinking stage. The indirect evidence in support of this hypothetical situation comes from graphical presentation of the egg abundance data (Fig. 4). On 23 August, 1994, the proximity of the instability zone and center of egg mass created good conditions for uplifting of considerable amounts 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), probably due to sinking of eggs. The sequence of events in the instability zone can not be re-created from the hydrological data collected during the surveys; the vertical uplift hypothesis is an oversimplification of a much more complex scenario, probably involving, i.e. gyres, geostrophic flows and density currents.

Nissling et al. (1994) reported that under laboratory conditions egg size increased with batch number in the majority of females, however, this information referred to 5 consequitive egg batches, not to all batches released during the spawning season. In general, progressively smaller eggs are produced throughout the entire spawning season and smaller females shed smaller eggs (Kjesbu, 1989). In this study the largest eggs were observed at the end of the spawning season in 1994 which is rather unexpected and difficult to interpret. Probably, other unquantified factors acting upon the egg population should be considered (i.e. changes in egg density due to metabolic processes or a genetic make-up of the egg) which resulted in a differential egg survival. Wieland (1988) hypothesized that not only extremely low oxygen level but also its intermediate content in sea water may be a limiting factor in egg survival; this postulate was later proved by experimantal data published by Wieland et al. (1994). If oxygen level 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. A combined influence of low oxygen content and high water temperature in September 1994 could have had more than an additive effect on egg survival.

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). According to Grauman (1965), the mean cod egg diameter in the Bornholm Basin in August 1964 was 1.60 mm which is comparable with the values presented in this study.

Not all sampled eggs were neutrally buoyant at the moment of collection. Anderson and de Young (1994) characterized five distinct types of descent trajectories, based on laboratory observations of cod eggs placed in the density gradient column. Overall, two types of descent profiles end with a total decelaration of eggs at a stable level in the column while the other three, with eggs sinking to the bottom in a varying time period. Differing abilities to osmoregulate due to varying egg condition were suggested as an explanation for different descent profiles. 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 sea water density because the steady hydrostatic state principle is violated. The values of correlation coefficient (R^2) calculated from simple linear regression of egg diameter and sea water density could be used to assess the instability of the water mass in which eggs develop.

Calculation of egg mortality rates from a one-time collection in the field yields relatively precise estimates as long as the assumptions of the used method hold. The main assumption of the constant birth model employed in this study is the constant rate of egg production. The negative instantaneous daily mortality rate, Z, obtained in August 1994, is indicative of the violation of this assumption due to a lowered egg production at the end of the spawning season (see Table 4 and Figure 5C). In the authors' opinion, the highest precision in estimating instantaneous daily mortality and overall egg mortality rates was attained for the depth stratum of the z_{cm} occurrence because eggs were most abundant in this particular water layer and the collected samples represented the population the best. The values presented in Table 4 are in a general agreement with the values reported elsewhere. Grauman (1973) determined that the total mortality of Baltic cod eggs (from the beginning of cleavage to hatching) in the Bornholm Basin ranged from 79 to 98.8%. The extrapolated mortality for the entire egg incubation period in the Bornholm Basin in May and June 1986, assessed by the cohort method, was 99.9% (Wieland, 1988). Ohldag et al. (1991) reported total mortality rates of 72, 85 and 98%, measured in the laboratory for oxygen concentrations 8.0, 4.9 and 2.7 ml/l, respectively; larvae hatched at the lowest oxygen level were not viable. In this study, the overall mortality rate from stage I through IV in the depth layer of the z_{cm} occurrence ranged from 92.8 to 98.9%; the overall mortality estimates for the depth strata outside the z_{cm} layer were lower.

Average daily mortality rates measured under laboratory conditions in Baltic cod by Ohldag et al. (1991) were relatively stable during the first three developmental stages (IA, IB and II) ranging from 17 to 18% per day for oxygen concentration of 8 ml/l; for lower oxygen levels, namely, 4.9 and 2.7 ml/l, these rates ranged from 11 to 36% per day. For stages III and IV average daily mortality rates were largely decreased (range: 1.9-3.8%) for the two higher oxygen concentrations while at 2.7 ml O_2/l the egg development ceased at stage III. According to field measurements reported by Grauman (1973), percentage mortality during stage I for Baltic cod eggs in the Bornholm Basin was the highest (83%); for stages II, III and IV, it leveled off to 44, 10 and 1%, respectively. In this study, stage-specific instantaneous daily mortality rates (Z) for the depth stratum of z_{cm} occurrence increased with age of egg and ranged from 0.139 for stage I (equivalent to 13% loss per day) to 0.534 for stage III (41.4%/day). The increased egg mortality with increasing age was previously reported by Wieland (1988), based on the cohort analysis of cod eggs in the Bornholm Basin; the estimated values of mortality coefficient Z for two cohorts were 0.31 and 0.32 which is equivalent to 26.9 and 27.5% loss per day, respectively. Because of the different methods used by Wieland and in this study, a direct comparison of mortality rates is impossible. However, an average Z value was calculated from the values reported in Table 4 for August 1993; the average was weighted by stage duration for the assumed mean temperature 5.75°C. Such obtained mean Z value equal 0.314 (26.9% loss per day) which falls strikingly close to the estimates reported by Wieland for two cohorts of eggs from the Bornholm Basin.

Stage duration time, calculated from empirical equations in Wieland et al. (1994) had to be extrapolated for temperatures higher than 7°C. For the depth range 50-80 m, the average sea water temperature reached values higher than 7°C in 9 out of 46 sampled 10-m depth strata in 1993 (maximal temperature 11.2°C) while in 1994, only in 1 out of 30 layers (maximal temperature 8.0 °C). All temperatures exceeding 7°C were recorded in the 50-60 m depth layer. It can only be speculated what kind of bias was introduced by extrapolation, however, the underestimation of rates is most likely. Iversen and Danielssen (1984) established under laboratory conditions that the cod egg mortality increased rapidly above 10°C and it had 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 had been lower in eggs exposed to the temperatures later in development. In summary, a length of exposure to sea water of low oxygen content and high temperature, and egg developmental stage at such exposure, are the most influential factors in egg survival. Further investigations of cod egg distribution, spatially and temporally synchronized with hydrological measurements, could potentially yield a more detailed picture of the cod recruitment processes in the Bornholm Basin.

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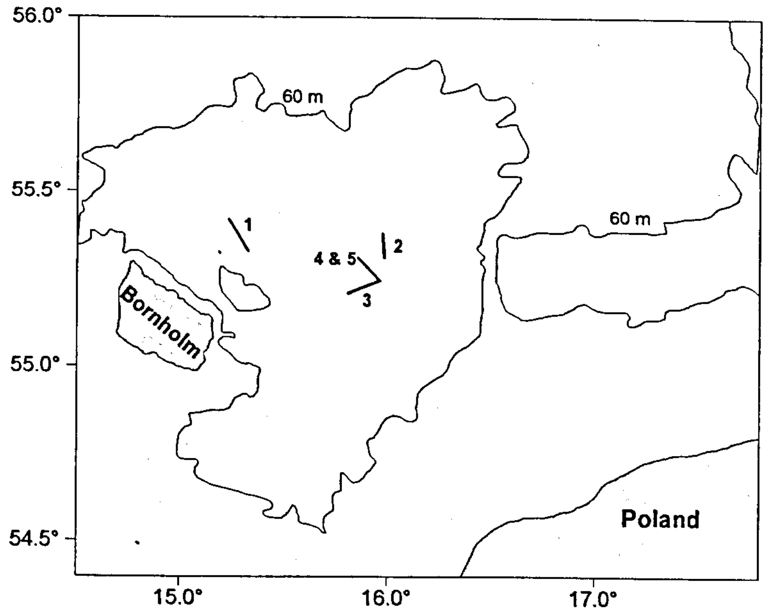

Figure 1. Sampling sites: 1 - August 1-2, 1993, 2 - August 2-3, 1993, 3 - August 5-6, 1993, 4 - August 23-24, 1994, 5 - September 7, 1994.

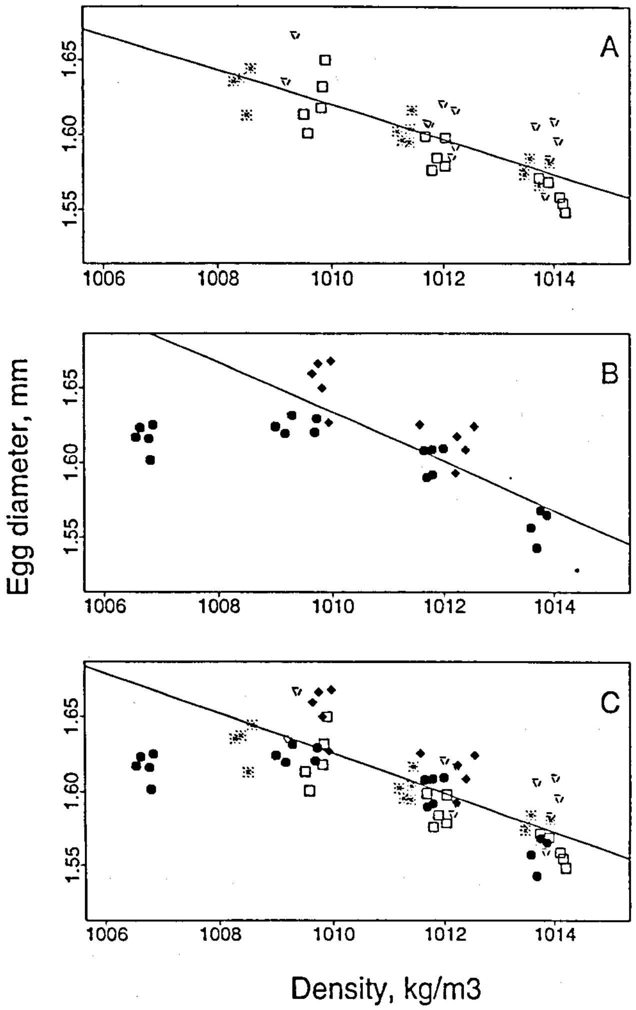

Figure 2. *Gadus morhua* L., mean egg diameter plotted against density of ambient sea water. A - data from 1993, B - data from 1994, C - combined results from the period 1993-1994. Empty squares - survey 1, stars - survey 2, triangles - survey 3, filled circles - survey 4, filled diamonds - survey 5. Lines represent fitted simple linear regression models for sea water densities >1008 kg/m^3.

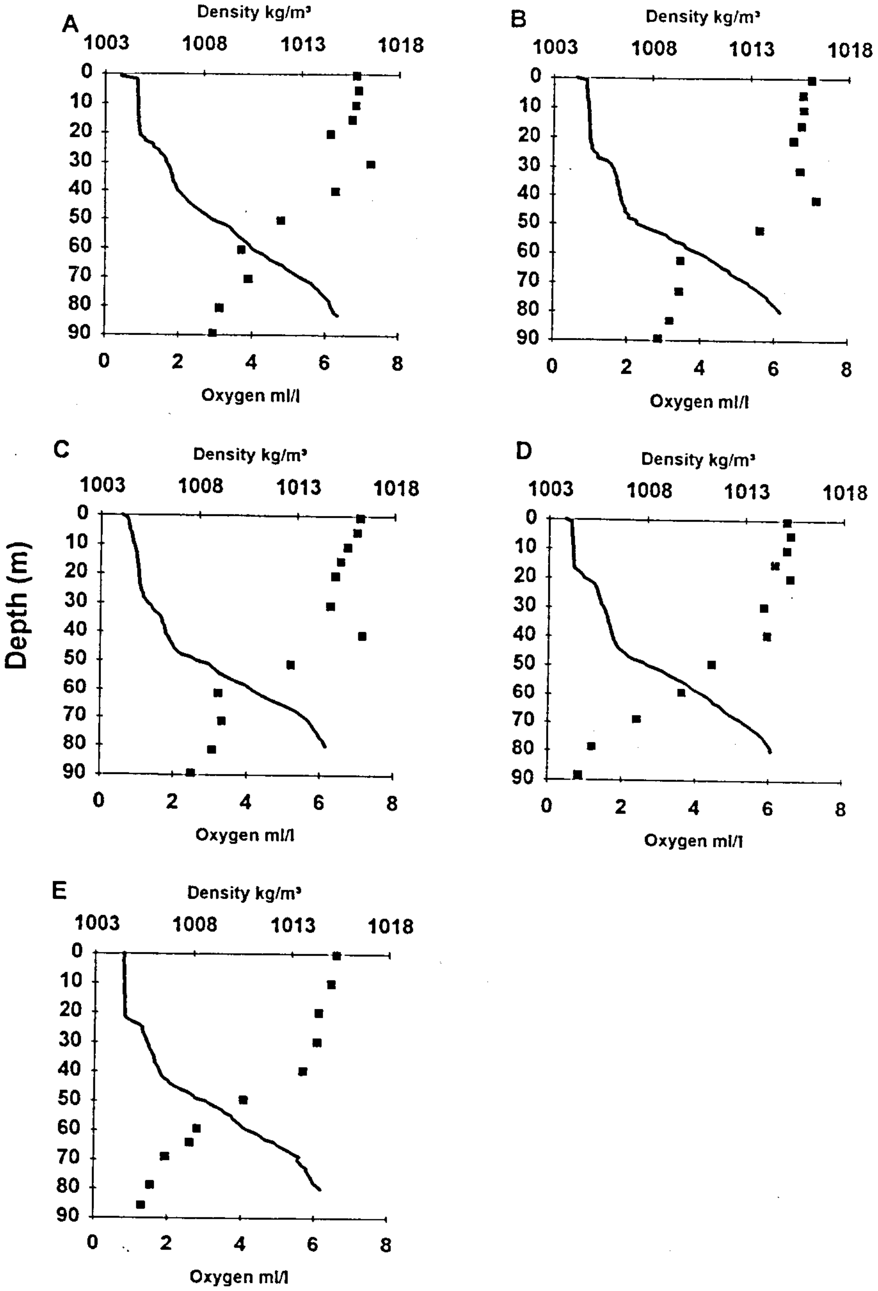

Figure 3. Vertical profiles of sea water density (solid lines) and oxygen concentration (squares) at sampling sites. A - 1-2 August, 1993, B - 2-3 August, 1993, C - 5-6 August, 1993, D- 23-24 August, 1994, E- 7 September, 1994. Reported density is sigma STP; oxygen content measured by the Winkler's method.

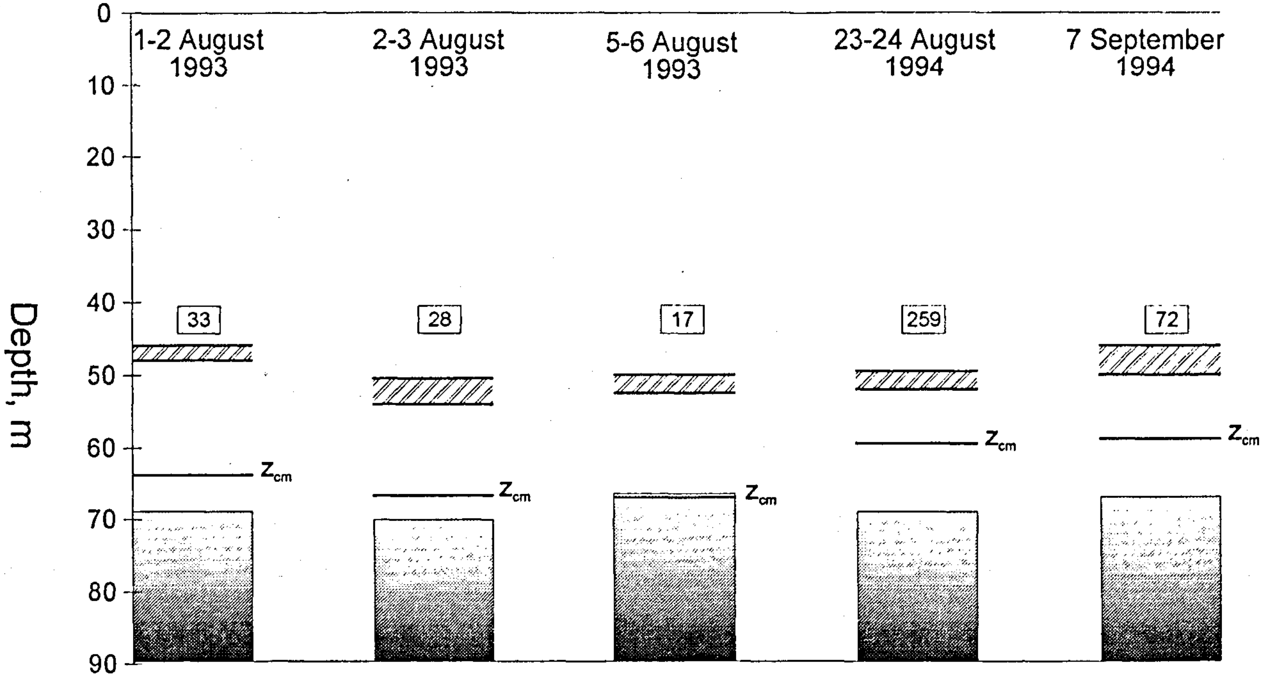

Figure 4. *Gadus morhua* L., schematic presentation of location of the center of egg mass, z_{cm}, in relation to two sea water density layers, 1008 kg/m^3 (hatched area) and ≥1013 kg/m^3 (gradually shaded area). Numbers enclosed in boxes represent total egg abundance per 1000 m^3 of water, in the 40-50 m depth stratum.

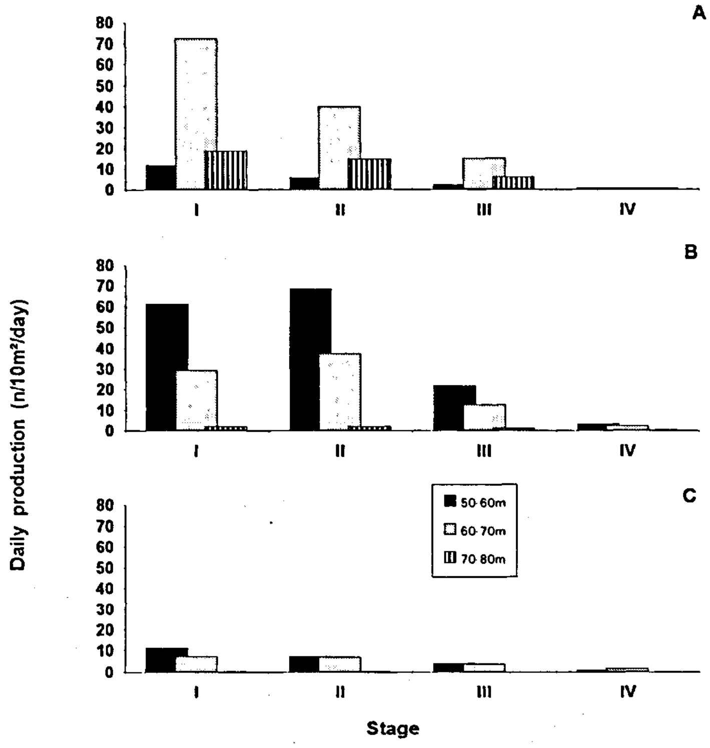

Figure 5. *Gadus morhua* L., daily production of successive egg stages in sampled layers. A - combined data from surveys 1-3, B - survey 4, C - survey 5.

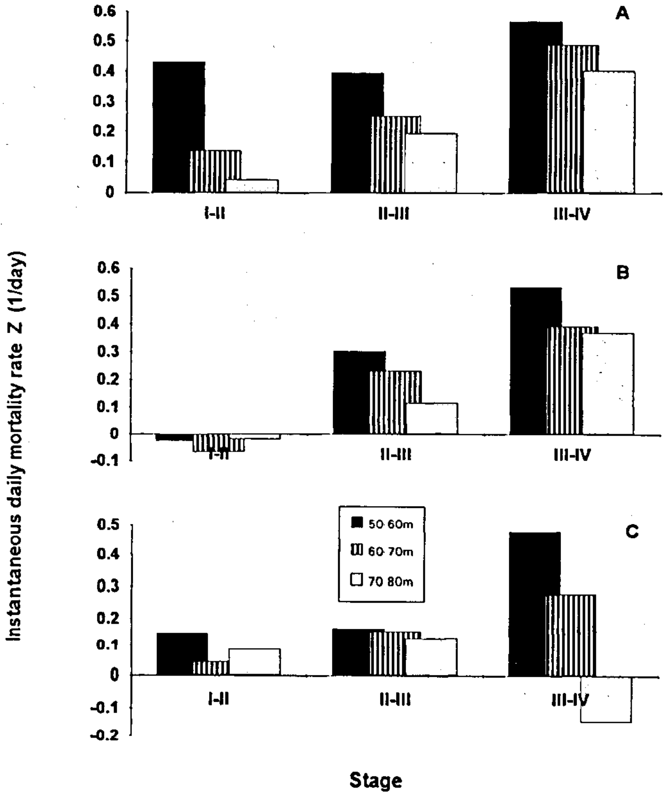

Figure 6. *Gadus morhua* L., instantaneous daily mortality rates of successive egg stages, Z, in sampled layers. A - combined data from surveys 1-3, B - survey 4, C - survey 5.

Table 1. *Gadus morhua* L. 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; df - degrees of freedom; R^2 - coefficient of determination.

Code*	Date	Intercept α	Slope β	R^2 (%)	F-statistic	df	P-value
1	1-2 August, 1993	16.168	-0.014	79.8	51.21	13	<0.0001
2	2-3 August, 1993	12.430	-0.011	86.0	73.92	12	<0.0001
3	5-6 August, 1993	13.971	-0.012	57.9	15.12	11	0.0025
4	23-24 August, 1994	9.313	-0.008	58.7	24.19	17	0.0001
	23-24 August, 1994 density >1008 kg/m^3	16.322	-0.015	84.4	64.78	12	<0.0001
5	7 September, 1994	18.671	-0.017	70.0	18.65	8	0.0026
	1993 combined	13.357	-0.012	65.0	74.12	40	<0.0001
	1994 combined	8.935	-0.007	30.6	11.92	27	0.0018
	1994 combined, density >1008 kg/m^3	18.294	-0.017	65.7	42.17	22	<0.0001
	1993 & 1994 combined	11.222	-0.010	49.9	68.72	69	<0.0001
	1993 & 1994 combined density >1008 kg/m^3	15.058	-0.013	64.2	114.70	64	<0.0001

* Code refers to Fig. 1: location of sample collection

Table 2. *Gadus morhua* L. Depth of the center of egg mass z_{cm}, and the corresponding hydrological parameters and egg diameters. Reported mean density is sigma STP; modal egg diameter is a mode of frequency distribution of all measured diameters; mean egg diameter is an arithmetic mean.

Code*	Date	z_{cm} (m)	Mean density (kg/m^3)	Mean temp. (oC)	Mean salinity (ppt)	Mean oxygen content (ml/l)	Modal egg diameter (mm)	Mean egg diameter (mm)
1	1-2 August, 1993	63.79	1011.62	5.15	14.32	3.86	1.590	1.593
2	2-3 August, 1993	66.72	1012.01	5.04	14.79	3.41	1.580	1.599
3	5-6 August, 1993	66.61	1012.65	4.75	15.58	3.23	1.594	1.604
4	23-24 August, 1994	59.37	1010.66	6.36	13.31	3.92	1.598	1.601
5	7 September, 1994	58.70	1010.55	7.48	13.23	3.18	1.624	1.632

Table 3. *Gadus morhua* L. Stage-dependent egg distribution in two sea water density strata. Percentages were calculated from the egg abundance data, expressed as number of eggs per 1000 m^3 of water. Chi^2-statistic was calculated from the chi^2 test for independence of observations in a 2x2 contingency table, with Yate's continuity correction; number of younger (stages IA+IB) and older (stages II-IV) eggs in two sea water density strata (<1013 and ≥ 1013 kg/m^3) were compared.

Date	Total number of identified eggs	Stage	Percent of total eggs by stage	Percent of eggs in density stratum <1013 kg/m^3 by stage	Percent of eggs in density stratum >1013 kg/m^3 by stage	Chi^2- statistic for 2x2 table	P-value
1-2 August, 1993	3805	IA + IB	59.9	61.2	54.6	26.75	0
		II + III + IV	40.1	38.8	45.4		
2-3 August, 1993	3540	IA + IB	62.3	65.8	53.5	129.40	0
		II + III + IV	37.7	34.2	46.5		
5-6 August, 1993	3189	IA + IB	53.6	55.2	48.5	15.61	0.001
		II + III + IV	46.4	44.8	51.5		
23-24 August, 1994	3323	IA + IB	44.0	44.0	45.7	0.34	0.561
		II + III + IV	56.0	56.0	54.3		
7 September, 1994	2168	IA + IB	49.0	48.8	64.3 *	2.07	0.150
		II + III + IV	51.0	51.3	35.7		

* small sample size; total number of eggs at all stages equals 65

Table 4. *Gadus morhua* L. Instantaneous daily mortality rates and overall mortality rates of eggs from stage IA through IV at different depth strata.

Date	Depth stratum of z_{cm} (m)	Instantaneous daily egg mortality rate for depth stratum of z_{cm} occurrence (1/day)			Overall egg mortality rate from stage I - IV, in depth strata (%)		
		I-II	II-III	III-IV	50-60 m	60-70 m	70-80 m
1-6 August, 1993	60-70	0.139	0.253	0.490	97.27	98.94	97.53
23-24 August, 1994	50-60	-0.027	0.303	0.534	93.76	91.49	89.15
7 September, 1994	50-60	0.148	0.163	0.476	92.78	79. 58	85.90