

# Variation in egg buoyancy of Baltic cod *Gadus morhua* and its implications for egg survival in prevailing conditions in the Baltic Sea

Anders Nissling<sup>1</sup>, Harald Kryvi<sup>2</sup>, Lars Vallin<sup>1</sup>

<sup>1</sup>Department of Systems Ecology, Section Gotland, Stockholm University, S-10691 Stockholm, Sweden

<sup>2</sup>Zoological Laboratory, University of Bergen, Allégaten 41, N-5007 Bergen, Norway

**ABSTRACT:** In the Baltic Sea successful spawning of cod is restricted to the deep basins, and egg buoyancy is regarded as a major factor that allows eggs to avoid the stressful oxygen conditions that often prevail in the deep layers. In this study eggs of 3 to 5 yr old spawners (the basis of the spawning stock of Baltic cod *Gadus morhua* L. nowadays) maintained neutral buoyancy at a salinity of  $14.5 \pm 1.2$  ppt, with great variation among eggs from different females. Egg buoyancy was significantly correlated with yolk osmolality and chorion thickness and weakly correlated with egg size. Measurements of egg buoyancy in successive batches from the same female indicated that egg buoyancy increased with batch number. The significance of neutral buoyancy for cod egg survival in prevailing conditions in the Baltic was evaluated by comparing the ability of eggs to achieve neutral buoyancy in the Baltic cod spawning areas during June of the 6 years 1977–1980, 1982 and 1987. The results suggest that the ability of eggs to maintain neutral buoyancy should be included in attempts to find explanations for fluctuations in recruitment of Baltic cod.

**KEY WORDS:** Cod · Egg · Buoyancy · Size · Osmolality · Chorion · Spawning layer

## INTRODUCTION

In the Baltic Sea, a large estuarine system, cod reaches the border of its distribution, and egg buoyancy is regarded as a limiting factor for successful spawning. The low salinity of the water in the Baltic restricts successful spawning of cod to the deep basins, i.e. the Bornholm, the Gdansk and the Gotland basins, where there is a halocline at 50 to 80 m depth with denser, more saline (10 to 18 ppt) deep water which is only partly mixed with the less saline (6 to 8 ppt) surface water. The deep water is exchanged mainly during periods of saline water inflow from the North Sea. Due to the irregularity of these inflows stagnant water prevails for years, accompanied by the development of unfavourable oxygen conditions. Consequently egg buoyancy is critical for avoiding the low oxygen levels that often prevail in the deep layers.

In a previous investigation (Nissling & Westin 1991) it was shown that neutral egg buoyancy for Baltic cod

is achieved at a salinity of about  $14.4 \pm 1.1$  ppt, with great variance among batches from different females. This implies that egg buoyancy can regularly be maintained only in the Bornholm basin, as the salinity is only occasionally high enough in the Gdansk and Gotland basins.

The mechanisms of achieving buoyancy include reduction of density by accumulation of less dense components. In pelagic eggs, low specific weight relative to seawater is obtained by maintenance of dilute fluids, i.e. a high water content of the yolk and, later during development, of the subdermal spaces of the embryo. The high water content (92%) of the cod egg is acquired during maturation in the ovary by a breakdown of deposited protein-phosphate into free amino acids, causing high osmolality accompanied by inflow of water (Craik & Harvey 1984). In spite of an osmotic gradient in relation to the environment after the eggs are shed, water loss is minimized by the extremely low water permeability of the vitelline membrane sur-

rounding the yolk (Riis-Vestergaard 1984, Mangor-Jensen 1987). However, prior to hatching the permeability of the membrane increases and is followed by an increase in embryonic volume and formation of dilute subdermal spaces by an uptake of water, causing a change in buoyancy (Mangor-Jensen 1987).

Adaptations of pelagic eggs to gain buoyancy in the less saline water of the Baltic include an increase in size (Strodtmann 1918, Mielck & Künne 1935, Kändler 1944, Kändler & Tan 1965, Solemdal 1967) and a decrease in the thickness of chorion (Lønning & Solemdal 1972, Nissling & Westin 1991). For cod this results in neutral egg buoyancy at salinities of 12.3 to 18.2 ppt for Baltic cod in contrast to the level of 29.5 to 33 ppt (Solemdal & Sundby 1981) observed for Atlantic cod. It has been shown that only minor adaptations in buoyancy and size to the ambient environment are possible after shedding but that these characteristics are fixed in the ovary (Strodtmann 1918, Kändler & Tan 1965, Solemdal 1967). As a presumed adaptation, several investigations have revealed a lowered ovarian osmolality in fishes spawning in brackish water (Strodtman 1918, Kandler & Tan 1965, Solemdal 1967). Further, as discussed by Kjesbu et al. (1992), fishes in brackish environments display a higher degree of hydrolysis of deposited yolk protein into free amino acids during the hydration of the egg. These adaptations result in a higher degree of hydration and thereby more buoyant eggs. However, Lønning & Solemdal (1972) concluded from studies on flatfishes (flounder *Platichthys flesus* and plaice *Platessa platessa*) from the North Sea and Baltic Sea that the osmotic effect on egg buoyancy explains only part of the adaptation; in addition, the decrease in chorion thickness accounts for the reduction in specific gravity of pelagic eggs in the Baltic.

The aim of the present investigation was to elucidate the relative importance of egg size, yolk osmolality and thickness of the chorion for variation in egg buoyancy of Baltic cod, and to further focus upon the importance of low specific gravity relative to the surrounding water for egg survival in prevailing conditions in the Baltic.

## MATERIAL AND METHODS

Eggs and semen were obtained by stripping spawning Baltic cod *Gadus morhua* L., caught with gill nets at 50 to 90 m depth off northern Gotland, Sweden (58° N, 19° E) in May and June 1990 to 1993. Fertilization was carried out artificially in water of 17 ppt salinity (which allows live fertilized eggs to float whereas dead and unfertilized eggs sink) prepared from filtered seawater (0.2 µm cartridge filter) and synthetic sea salt

(hw Marinemix) at 7°C. Eggs were rinsed 2 h after fertilization and incubated in 17 ppt salinity at 7°C.

Neutral egg buoyancy was determined at 7°C using a density gradient column (Coombs 1981) where the positions of the eggs were compared with the positions of 8 density floats of known specific gravity. The linearity of the floats was high (correlation coefficient >0.99) on all occasions. Measurements were performed on 54 egg batches from 54 different females, with 10 to 15 eggs in each determination.

Yolk osmolality was measured on samples of unfertilized eggs, that were dried by sponging off ovarian fluid with paper tissues, crushed and centrifuged. Analyses were performed on 22 egg batches by freezing point depression in an osmometer, and compared to a standard of 300 mOsm kg<sup>-1</sup>.

Egg size (10 to 15 eggs from each batch) was measured under a stereomicroscope at 40× magnification using a micrometer scale.

Thickness of the chorion was determined on 19 batches of eggs in the blastula stage. The eggs were fixed in OsO<sub>4</sub>, dehydrated and embedded in historesin. The samples were sliced (1 µm), stained with toluidine and measured at 1000× magnification under a light microscope (see Kjesbu et al. 1992). For each determination 3 eggs were used and a total of 130 to 210 measurements was performed on each batch. The number of lamellae that formed the chorion was determined on 6 egg batches by transmission electron microscopy. The eggs were dehydrated, embedded in Epon, and sliced (50 nm sections). The number of lamellae that appeared as alternating dark and light zones (see Kjesbu et al. 1992) was counted on 3 eggs from each batch, with 6 measurements on each egg.

Egg sinking rate was measured in water of 4 different salinities (5, 7, 9 and 11 ppt) at 7°C. Nine egg batches with neutral egg buoyancy ranging from 12.6 to 16.2 ppt salinity were selected from 9 different females. The time taken for 4 to 7 one-day-old normally developed eggs to sink 1 m in tubes with water from the different salinities was measured. Graphs were constructed by combining determinations of sinking rates at 5, 7, 9 and 11 ppt salinity, respectively, with determinations of the salinity at which neutral buoyancy was obtained, i.e. sinking rate zero (linearity more than 0.99). Sinking rates in the range of 11 to 15 ppt salinity were then calculated from the equations given by the graphs.

The 'spawning layer' (see Grauman 1973 for expression), i.e. the layer with a salinity of 11 ppt or higher and an oxygen level of more than 1 ml O<sub>2</sub> l<sup>-1</sup> (see Berner & Schemainda 1957, Grauman 1973, Lebedek 1978, Westin & Nissling 1991), was determined from hydrographical data from the main spawning areas in the Baltic Sea: the Bornholm basin (55° 15' N, 15°

59' E), the Gdansk basin (54° 52' N, 19° 14' E) and the Gotland basin (57° 20' N, 20° 03' E), on 6 occasions (June 1977–1980, June 1982 and June 1987).

## RESULTS

Measurements of egg buoyancy in 1991 to 1993 (34 females) revealed neutral egg buoyancies in the range of 12.3 to 18.3 ppt salinity. In Fig. 1 neutral egg buoyancy in 54 egg batches from different females of Baltic cod (pooled data from the present investigation and from that of Nissling & Westin 1991) is shown. Neutral egg buoyancy was, on average, obtained at  $14.5 \pm 1.2$  ppt salinity and there was a considerable variation among batches.

Egg size and neutral egg buoyancy for successive batches [approximately 3 d between batches at 7°C (see Kjesbu 1989)] from 10 different females is shown in Fig. 2. Neutral egg buoyancy increased (decrease in specific gravity) with batch number in 8 of the females, while it was maintained at approximately the same level in 2 of the females. Egg size measurements indicated an increase in egg size with successive batches in 7 of the females, and a decrease in egg size in 1 female. Thus, in the majority of females, egg buoyancy and egg size increased with batch number. The relationships between neutral buoyancy and egg size (1.49 to 1.78; mean  $1.66 \pm 0.07$  mm), yolk osmolality

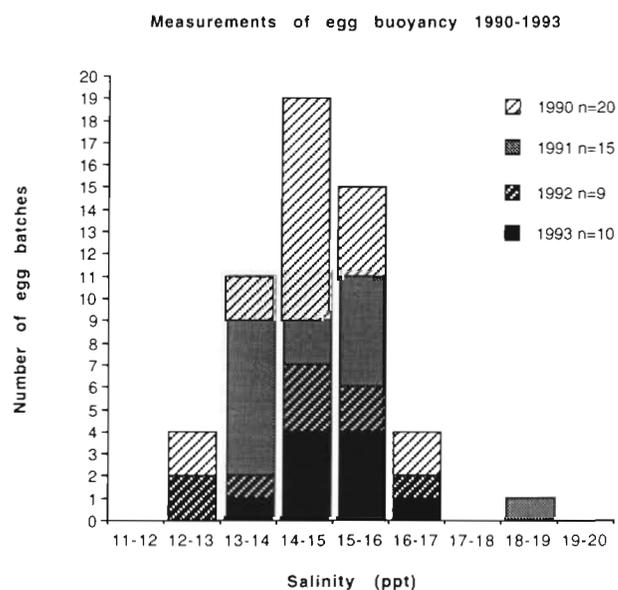


Fig. 1. *Gadus morhua*. Neutral egg buoyancy as determined from measurements of 54 egg batches from different females (female size 43.5 to 62 cm) of Baltic cod in 1990 to 1993. Pooled data from the present investigation and that of Nissling & Westin (1991)

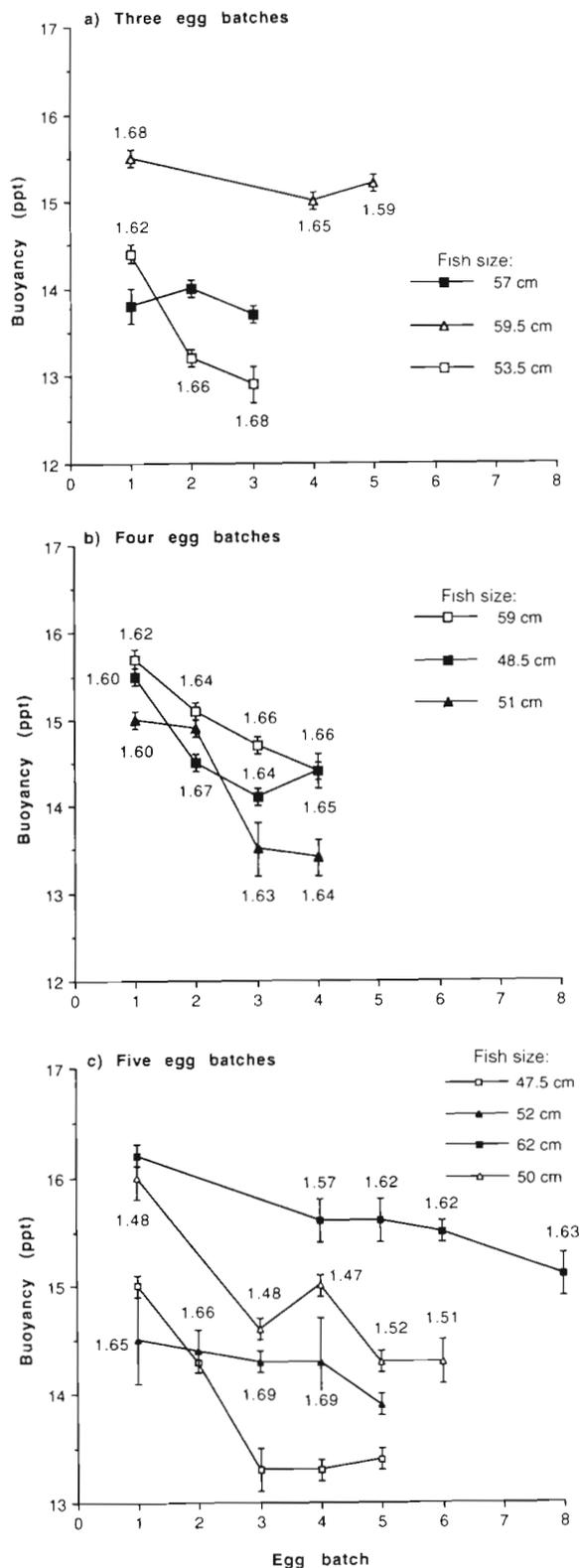
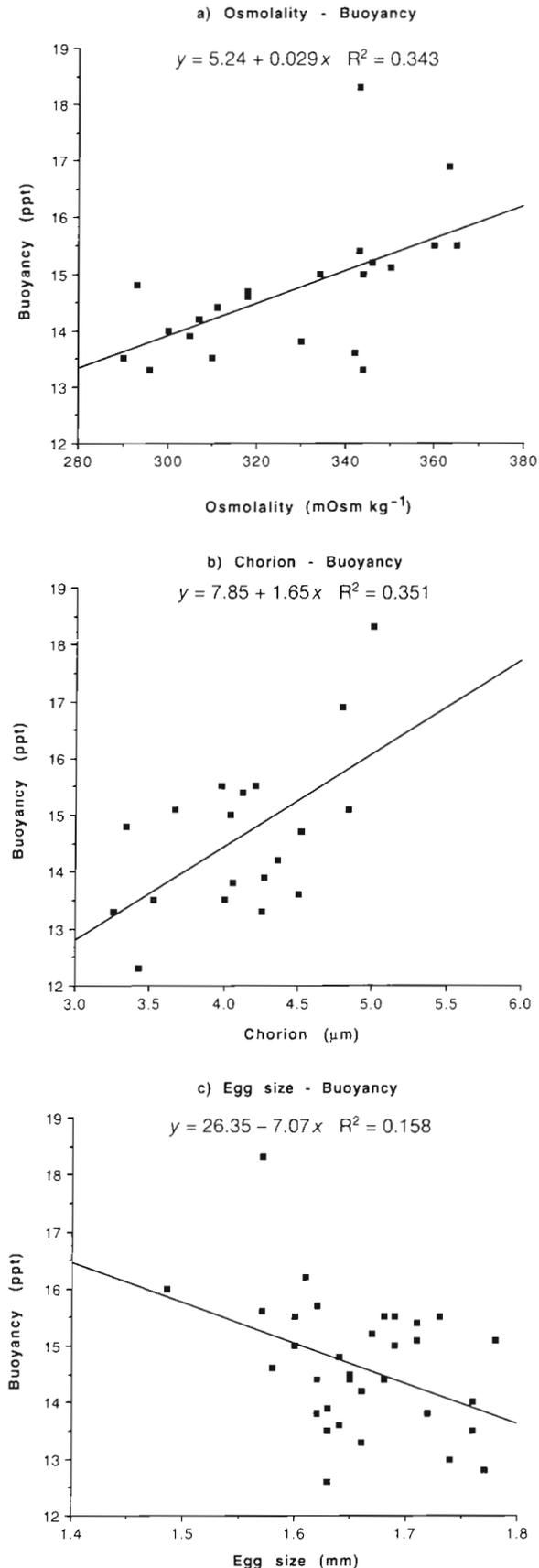


Fig. 2. *Gadus morhua*. Neutral egg buoyancy (ppt salinity) and egg size (mm) in successive egg batches from different females of Baltic cod. (a) 3 following batches. (b) 4 following batches. (c) 5 following batches. (N.B. the number of batches released during spawning period unknown)



(290 to 365; mean  $328 \pm 24$  mOsm  $\text{kg}^{-1}$ ) and thickness of the chorion (3.3 to 5.0; mean  $4.11 \pm 0.50$   $\mu\text{m}$ ) are shown in Fig. 3. Egg buoyancy was correlated to both yolk osmolality (Fig. 3a) and chorion thickness (Fig. 3b) ( $p < 0.01$ ,  $t = 3.387$ ,  $\text{df} = 22$  and  $p < 0.01$ ,  $t = 3.011$ ,  $\text{df} = 17$ , respectively,  $t$ -test correlation). The relationship between egg buoyancy and egg size (Fig. 3c) revealed a weak but significant correlation ( $0.05 > p > 0.01$ ,  $t = 2.447$ ,  $\text{df} = 32$ ). However, if the value for 1 small egg (egg size = 1.49 mm) is excluded, the relationship is barely significant ( $p \approx 0.05$ ). Accordingly, the relationship between egg size and egg buoyancy is of less significance than the relationships between yolk osmolality and egg buoyancy and between chorion thickness and egg buoyancy.

Studies of chorion morphology in eggs from 6 egg batches revealed that the chorion was formed by 4 or 5 lamellae (Fig. 4).

Sinking rates of eggs from 3 different egg batches from different females are shown in Fig. 5. Sinking rate decreased with increasing salinity until neutral egg buoyancy was achieved. The relationship between neutral egg buoyancy and sinking rate is obvious, with a strong negative correlation ( $p < 0.001$ ,  $t = 11.198$ ,  $\text{df} = 7$ ,  $t$ -test correlation) at 11 ppt salinity.

Table 1 shows the salinity and thickness of the estimated spawning layer, based on available data for the main spawning areas in 1977 to 1980, 1982 and 1987 respectively. It also shows which eggs would have been able to maintain neutral buoyancy, or the time that it would take eggs to sink through the 'spawning layer', for each of the 9 egg batches used in the sinking rate measurements (neutral buoyancy at 12.6 to 16.2 ppt salinity). In 1977, high salinities and oxygen levels prevailed in the deep water beneath the halocline in all spawning areas. In the following years the conditions deteriorated, resulting in a decrease in the 'spawning layer' in the Gdansk and Gotland basins during 1978 to 1980. Further, in 1982 and 1987 only the Bornholm basin had a spawning layer with sufficient salinity and oxygen levels. Accordingly, in 1977, all 9 egg batches in the Bornholm basin and 3 of the egg batches in both the Gdansk and the Gotland basins would have been able to maintain neutral buoyancy in the spawning layer. During 1978 to 1980, conditions that would allow almost all of the egg batches to achieve neutral buoyancy persisted in the Bornholm basin, whereas such conditions were limited in the Gdansk and Gotland basins. In 1982 and 1987, only

Fig. 3. *Gadus morhua*. Relationship between neutral egg buoyancy and different egg characteristics of Baltic cod. (a) yolk osmolality ( $n = 22$ ); (b) chorion thickness ( $n = 19$ ); (c) egg size ( $n = 34$ )

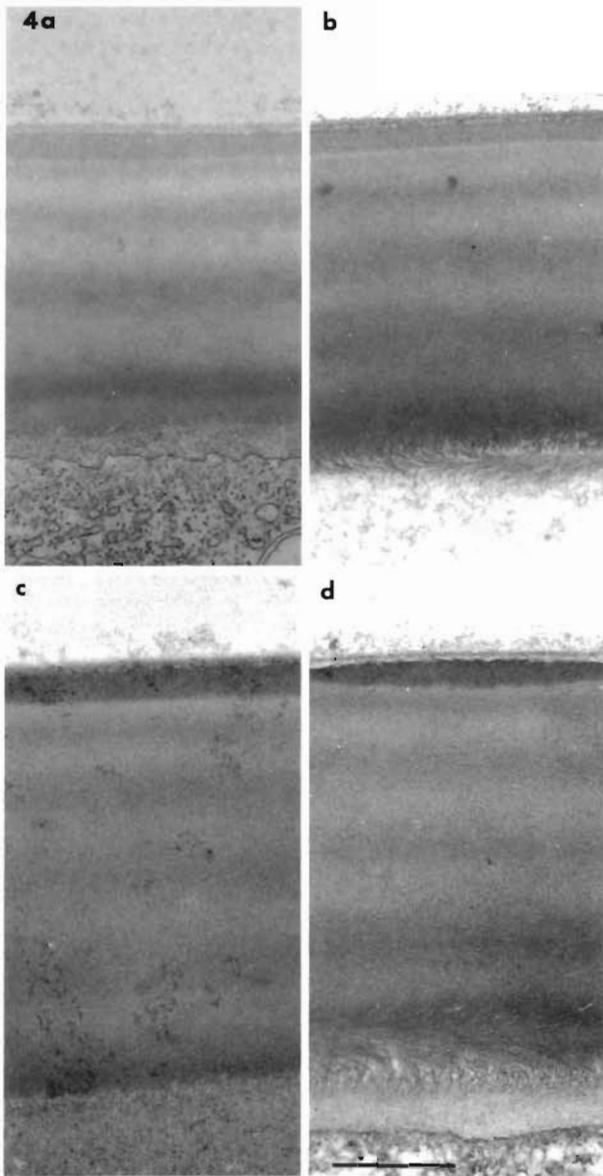


Fig. 4. *Gadus morhua*. Transmission electron micrographs of the chorion of Baltic cod eggs. (a) 3 prominent and 1 relatively thin dark layer. (b to d) are 5-layered chorions; (b) 4 prominent and 1 thin layer; (c & d) 5 prominent dark layers. Magnification 16000 $\times$ ; Scale bar = 1  $\mu\text{m}$  and applies to (a to d)

3 and 5 of the egg groups, respectively, would have maintained neutral buoyancy in the Bornholm basin, and none of the egg batches would have done so in the Gdansk or the Gotland basins.

## DISCUSSION

As pointed out by Craik & Harvey (1987), in teleostean eggs, water and lipid are the only signifi-

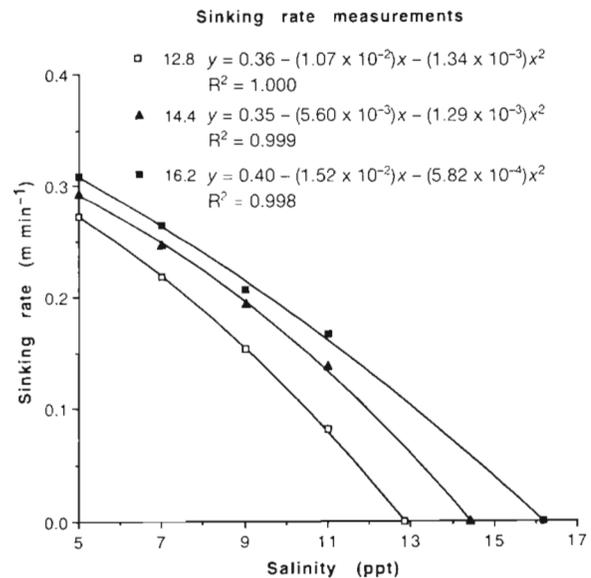


Fig. 5. *Gadus morhua*. Sinking rate of 3 groups of Baltic cod eggs (neutral buoyancy at 12.8, 14.4 and 16.2 ppt salinity respectively) at different salinities

cant components with a density less than seawater. Consequently, a hydrostatic lift is achieved by compensating the weight of protein in yolk and chorion with these less dense components. However, in a marine environment, pelagic eggs owe their buoyancy almost exclusively (90%) to the high water content, whereas lipid accounts for only about 10% (Craik & Harvey 1987), i.e. the water content and quantity of protein deposited in the yolk and the chorion determine egg buoyancy.

The present investigation demonstrates the difference between Baltic and Atlantic cod eggs (Table 2). Eggs of Baltic cod are larger, have thinner shells formed by fewer lamellae, have a somewhat lower yolk osmolality and are more buoyant.

The mechanism of the reduction in specific gravity, which results in large thin-shelled eggs, has been considered by several authors to be an adaptation of pelagic eggs to the low-density brackish water. The lower ovarian osmolality of Baltic cod (Strodtmann 1918, Kändler & Tan 1965, Westin & Nissling 1991) and the higher degree of yolk protein hydrolysis (see Kjesbu et al. 1992) imply a higher degree of hydration of the oocyte before the eggs are shed. Consequently this results in larger eggs with a higher water content (see Solemdal 1973), causing a stretch of the oocyte and thereby a thin chorion (Kjesbu et al. 1992). The significance of this mechanism was shown by Solemdal (1967, 1973) in investigations on flounder from the Baltic and the North seas. Transfer of Norwegian spawning and pre-spawning flounder from high salinity

Table 1 *Gadus morhua*. Thickness and salinity range of the estimated spawning layer, determined as the layer with more than 11 ppt salinity and  $1 \text{ ml O}_2 \text{ l}^{-1}$ , in the main spawning areas of Baltic cod: the Bornholm basin (Bhb), the Gdansk basin (Gdb) and the Gotland basin (Glb), in 1977 through 1980, 1982 and 1987. Also shown is the ability of eggs from 9 egg batches from the sinking-rate experiments to maintain neutral buoyancy (B) or the time that it would take for eggs to sink through the spawning layer

Egg batch (buoyancy)	Year: Spawning area:	1977			1978		1979		
		Bhb	Gdb	Glb	Bhb	Glb	Bhb	Gdb	Glb
	Depth range (m):	56–90	77.5–98.5	85–235	70–86.5	100–165	60.5–86	93.5–101	98–117
	Salinity range (ppt):	11–17.2	11–13.1	11–13.2	11–15.6	11–12.4	11–15.7	11–12.3	11–11.6
	Spawning layer (m):	34	21	150	20.5	65	25	7.5	19
1 (12.6)		B	B	B	B	30 h	B	3 h	6 h
2 (12.8)		B	B	B	B	–	B	–	–
3 (13.0)		B	B	B	B	–	B	–	–
4 (14.0)		B	6 h	37 h	B	–	B	–	–
5 (14.4)		B	–	–	B	–	B	–	–
6 (14.8)		B	–	–	B	–	B	–	–
7 (15.0)		B	–	–	B	–	B	–	–
8 (15.2)		B	–	–	B	–	B	–	–
9 (16.2)		B	–	–	4 h	–	6 h	–	–
Egg batch (buoyancy)	Year: Spawning area:	1980		1982		1987			
		Bhb	Glb	Bhb	Glb	Bhb	Gdb	Glb	
	Depth range (m):	54–85	96.5–98.5	57.5–74	–	62.5–76	–	–	
	Salinity range (ppt):	11–17.5	11–11.1	11–13.6	–	11–14.6	–	–	
	Spawning layer (m):	31	2	16.5	–	13.5	–	–	
1 (12.6)		B	<0.5 h	B	–	B	–	–	
2 (12.8)		B	–	B	–	B	–	–	
3 (13.0)		B	–	B	–	B	–	–	
4 (14.0)		B	–	6 h	–	B	–	–	
5 (14.4)		B	–	–	–	B	–	–	
6 (14.8)		B	–	–	–	3 h	–	–	
7 (15.0)		B	–	–	–	–	–	–	
8 (15.2)		B	–	–	–	–	–	–	
9 (16.2)		B	–	–	–	–	–	–	

to low salinity had a significant effect upon egg characteristics (egg size and buoyancy) as well as on ovarian osmolality, but did not totally account for the difference in egg buoyancy between flounders from the

Table 2. *Gadus morhua*. Differences in egg characteristics between Baltic cod (present investigation) and Atlantic cod

	Baltic cod	Atlantic cod
Egg size (mm)	1.49–1.78	1.19–1.62 <sup>a</sup> 1.13–1.50 <sup>b</sup>
Chorion thickness (µm)	3.3–5.0	5.5–7.7 <sup>b</sup> 6–9 <sup>c</sup>
Number of lamellae	4–5	7–8 <sup>b</sup> 9 <sup>c</sup>
Yolk osmolality (mOsm kg <sup>-1</sup> )	328 ± 24	354 ± 4 <sup>d</sup> 342 ± 5 <sup>e</sup>
Neutral buoyancy (ppt)	12.3–18.3	29.5–33 <sup>d</sup>

<sup>a</sup>Solemdal & Sundby (1981); <sup>b</sup>Kjesbu (1989); <sup>c</sup>Davenport et al. (1981); <sup>d</sup>Kjørsvik et al. (1984); <sup>e</sup>Mangor-Jensen (1987)

Baltic and the North Sea. Further, when flounders from the Baltic Sea were transferred to a marine environment the egg characteristics were, in principle, still maintained after 2 yr. In addition, as concluded by Lønning & Solemdal (1972), a thinner chorion with fewer lamellae [3 in flounder from the Arkona basin (Baltic Sea) compared to 6 in flounder from the North Sea] accounts for the difference in egg buoyancy, and is thus specific for the respective populations. Our investigation revealed a significantly thinner chorion and fewer lamellae in Baltic cod, compared to Atlantic cod. Thus, the larger thin-shelled and more buoyant eggs of Baltic cod is partly caused by a higher degree of hydration of the oocytes, but is also a result of reduced chorion thickness due to fewer lamellae.

We found a high variation in neutral buoyancy among egg batches from different females, with neutral buoyancy obtained at 12.3 to 18.3 ppt salinity. Egg buoyancy was significantly correlated with both chorion thickness and yolk osmolality, but the relationship between egg buoyancy and egg size was weak. This indicates that variation in chorion morphology

and relative water content accounts for most of the variation in egg buoyancy in Baltic cod eggs. Kjesbu et al. (1992) found chorion thickness to vary both between egg batches from different females and between different egg batches from the same female, but within each egg batch (i.e. other parameters constant) the specific gravity of eggs was inversely correlated to egg size in Norwegian coastal cod.

Our results suggest that low yolk osmolality together with a thin chorion is advantageous for Baltic cod eggs to achieve high buoyancy. However, there are probably limits for both lower yolk osmolality (to what extent lower internal concentrations can be tolerated) and decreased chorion thickness (which make the egg sensitive to mechanical forces).

Kjesbu et al. (1992) showed that female age and condition affected egg buoyancy in Norwegian coastal cod. Age and condition caused differences in egg buoyancy among females, but moreover, the pattern of changes in egg buoyancy differed with successive batches from the same female; there was almost stable egg buoyancy in recruit spawners, whereas egg buoyancy decreased with batch in repeat spawners. This may have implications for the Baltic cod, in which both the age structure of the spawning stock and the condition of the spawners vary due to changes in the year class strength (see Baranova 1989, Bagge et al. 1992). Due to poor year classes for several years along with intense fishing efforts and high fishing mortality (Bagge & Thurow 1993) the basis of the Baltic spawning stock is today (early 1990s) formed mostly on young spawners, 3 to 5 yr old (see Anon. 1993). Thus, 3 to 5 yr old spawners (length ca 40 to 65 cm, i.e. like the females in the present investigation), with a neutral egg buoyancy of about  $14.5 \pm 1.2$  ppt salinity, contribute the majority of spawned eggs at present (1993). Although the number of batches released during the spawning period is unknown, our investigation indicates an increase in egg buoyancy with batch number, implying that eggs spawned late during the spawning period may survive better in prevailing conditions in the Baltic. However, egg quality and larval viability have been shown to decrease with batch number (see Kjesbu 1989, Kjesbu et al. 1991, Solemdal et al. 1991) and this is likely to influence egg and larval survival.

Grauman (1973) stated that the thickness of the spawning layer determines the survival of cod eggs. A non-buoyant egg has poor opportunities of surviving in prevailing conditions in the Baltic, since the time it takes for an egg to sink to deeper waters where there is an oxygen deficit is too short to allow embryonic development. The ability of eggs to maintain neutral buoyancy and thereby survive varies both between years and spawning areas, as shown in Table 1. The last major inflow of saline water from the North Sea

occurred in 1976–1977 (Fonselius 1988) and it resulted in favourable conditions in the spawning areas of Baltic cod. In 1977, immediately after the inflow, nearly all egg batches in the Bornholm basin and some egg batches in the Gdansk and Gotland basins would have been able to maintain neutral buoyancy. Consequently, a strong year class was formed. However, in the following years, stagnant deep water caused a decrease in salinity and water oxygen content, and conditions for successful spawning deteriorated. In 1978 and 1979 most of the egg batches in the Bornholm basin and possibly also some highly buoyant batches in the Gdansk and Gotland basins would have been able to maintain neutral egg buoyancy. Thereafter, successful spawning seems to have been restricted to the Bornholm basin, where there were good conditions in 1980 (salinity range 11 to 17.5 ppt) followed by unfavourable conditions in which only a few egg batches would have maintained neutral buoyancy. According to estimations of year class strength for Baltic cod (see Anon. 1993) strong year classes were formed in 1977, 1979 and 1980. In 1978 a year class of medium strength was formed, whereas weak year classes occurred in both 1982 and 1987. It is obvious that egg survival depends on inflows of saline water from the North Sea, and that the Bornholm basin is important, as the short distance to the North Sea provides the most favourable conditions.

The inflows of saline water from the North Sea are highly irregular and the mechanisms are not fully understood (see Franck et al. 1987, Kalejs & Ojaveer 1989, Börngen et al. 1990). Further, the effect of anthropogenic factors, primarily increased nutritional loads during the latest decades, has caused eutrophication followed by increased oxygen consumption in the Baltic deep basins (see Hansson & Rudstam 1990). As a consequence, conditions for successful spawning of the cod in the Baltic have deteriorated, i.e. nowadays periods of favourable oxygen conditions are shorter.

Even though environmental conditions (salinity and oxygen content) have a profound impact on the reproduction success of Baltic cod, the year class strength is also dependent on the size of the spawning stock and the availability of zooplankton. The recruitment of Baltic cod in relation to both abiotic and biotic factors has been considered by several authors (Grauman 1973, Berner et al. 1988, Plikshs et al. 1993) and found to be related to the conditions in the spawning areas or the 'reproductive volume' (Plikshs et al. 1993). Our study suggests that, in addition to salinity and oxygen requirements for successful egg development, the salinity range and the ability of eggs to maintain neutral buoyancy should be considered in attempts to find the causes of fluctuations in recruitment of Baltic cod.

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