

# Process oriented model of egg mortality for Central Baltic cod, *Gadus morhua callarias* L.

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## Abstract

A simple, process-oriented mathematical model is developed for the mortality of eggs of cod *Gadus morhua callarias* in the Central Baltic sea. The model is based on a synthesis of existing knowledge of both direct and indirect effects of hydrography on the survival of the eggs. The direct effects are the influence of low levels of oxygen and salinity on survival. The indirect effect is the predation by sprat, with the vertical overlap between sprat and cod eggs being determined by the hydrography. The model reproduces the direct effect of low survival in years without inflows oxygenrich and saline. It also indicates that predation is important for the total mortality than the direct effect of the hydrography. In addition it is shown that effects related to the changing bouyancy of of the eggs due to age of mother fish, batch number and stock structure does not influence the survival significantly.

## 1 Introduction

The Central Baltic cod (*Gadus morhua callaris* L.) was one of the most productive gadoid stocks in the world ocean in the late 1970ies/early 1980ies (REF). Since the late 1980ies stock sizes declined drastically to historically low levels (Bagge *et al.*, 1994; Köster *et al.*, 2003). The main reasons for the decline were overfishing in parallel to recruitment failure. High egg mortality due to unfavorable hydrographic conditions was observed to be the main reason for low reproductive success (Köster *et al.*, 2001). Unlike other cod stocks, the eggs of Central Baltic cod

float in deep water, i.e. in a narrow depth range within and below the permanent halocline of the deep Baltic basins (Wieland and Jarre-Teichmann, 1997). Only in this layer the salinity of the brackish Baltic Sea is sufficient to ensure a normal development of the eggs;  $s > 11$  psu (Westin and Nissling, 1991). However, in this layer, cod eggs might encounter too low oxygen conditions for survival (Wieland *et al.*, 1994). The stable stratification of the water column does not allow an exchange with upper layers, and thus the renewal of the bottom water with respect to salinity and oxygen is only possible through intermittent inflows of oxygen-rich, highly saline

Table 1: Overview of the model

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|                                                                                                                        |
|------------------------------------------------------------------------------------------------------------------------|
| Normal distribution:                                                                                                   |
| $\varphi(x, \mu, \sigma) = \frac{1}{\sigma\sqrt{2\pi}} e^{-(x-\mu)^2/(2\sigma^2)}$                                     |
| Vertical and temporal distribution of cod eggs:                                                                        |
| $p_{egg}(z) = \varphi(s(z), s_{egg}, \sigma_{egg}) \left( \int \varphi(s(z'), s_{egg}, \sigma_{egg}) dz' \right)^{-1}$ |
| $p_{egg}(t) = \varphi(t, t_{spawn}, \sigma_{spawn})$                                                                   |
| Oxygen survival function:                                                                                              |
| $p_{oxygen}(x) = (1 - e^{-ax})^b$ , with $a = 0.71$ l/ml and $b = 11.63$                                               |
| Vertical and temporal distribution of sprat:                                                                           |
| $p_s(z) = 2\varphi(z, z(o_{sprat}), \sigma_{sprat}); 0$ if $z < z(o_{sprat})$                                          |
| $p_s(t) = \varphi(t, t_{sprat}, \sigma_{sprat})$                                                                       |
| $p_s(z, t) = p_{sprat}(z)p_{sprat}(t)$                                                                                 |
| Predation:                                                                                                             |
| $\Delta p_{egg}(t, z) = (1 - e^{-\alpha_p p_s(t, z)}) p_{egg}(t, z)$                                                   |

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water along the bottom. Major water intrusions, so called “major Baltic inflows” are necessary to improve hydrographic conditions and are strongly dependent on the prevailing atmospheric forcing (Matthäus and Franck, 1992; Matthäus and Schinke, 1994). The last two decades were characterized by an unusual low frequency of inflow events, which has been hypothesized to be related to the persisting positive state of the North Atlantic Oscillation (Hänninen *et al.*, 2000). Increasing runoff resulted in sea level variations which may have hindered major inflow events (Matthäus and Schinke, 1994). As a consequence minimum required reproductive conditions for cod existed only in the most western spawning area of the stock, i.e. the Bornholm Basin (MacKenzie *et al.*, 2000).

Another important agent of mortality in Central Baltic cod eggs is predation by the abundant planktivore stocks of herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) (Köster and Schnack, 1994; Köster and Möllmann, 2000). The magnitude of the egg predation appears also to be driven by hydrography, with stagnant periods (periods without

inflows) generally characterized by a high vertical predator-prey overlap and thus high predation rates, and vice versa after inflow events (Köster and Möllmann, 2000). Additionally, the seasonal overlap in occurrence among cod eggs and predators in the deep basins is important for the magnitude of predation mortality. Consequently the shift in spawning of cod in the 1990ies from spring to summer (Wieland *et al.*, 2000) has resulted in reduced predation pressure by sprat, which generally spawn in spring (Köster and Möllmann, 2000). However, due to low cod predation and high reproductive success the sprat stock increased to record levels during the 1990s, which still persists to date (Köster *et al.*, 2003). Consequently, sprat has a large potential of inducing high cod egg mortality.

The goal of this work was to develop a process-oriented model for the mortality of cod eggs in the Bornholm Basin due to climatically regulated hydrographic conditions. We consider explicitly the effect of cod spawning time, egg density and predation. Using this operational model we show *i*) the direct effect of low salinity and oxygen conditions on cod egg sur-

Table 2: List of the parameters entering the model, their standard values and the sensitivity of the model to the value of the parameters.

| Parameter                  | Value                          | Sensitivity   |
|----------------------------|--------------------------------|---------------|
| Environment                |                                |               |
| Mean density of eggs       | $s_{egg} = 13$ psu             | low           |
| Standard deviation of eggs | $\sigma_{egg} = 2$ psu         | high          |
| Minimum salinity           | $s_{min} = 11$ psu             | low           |
| Spawning time              |                                |               |
| Peak spawning time         | $t_{spawn} = \text{July 1st}$  | medium        |
| Spawning period            | $\sigma_{spawn} = 35$ days     | low           |
| Predation                  |                                |               |
| Strength of predation      | $\alpha_p = 50\,000$           | <b>high</b>   |
| Minimum oxygen for sprat   | $o_{sprat} = 3$ ml/l           | medium to low |
| Distribution over depth    | $\sigma_{sprat.z} = 5$ m       | medium to low |
| Sprat spawning             |                                |               |
| Peak spawning time         | $t_{sprat} = \text{April 1st}$ | medium        |
| Spawning period            | $\sigma_{sprat} = 35$ days     | low           |

vival, but *ii*) also how the physical environment indirectly regulates egg mortality through a biological interaction: predation by sprat.

## 2 Methods

The goal of this model is to estimate the probability that a spawned egg will survive until hatching. The probability of survival  $p_s$  is related to the integrated mortality  $m$  from the time the egg is spawned to hatching as:  $m = 1/p_s$ . The sources of egg mortality are detrimental physical environment, i.e. low levels of salinity and oxygen, and predation by sprat. The different sub-models deal with *i*) spawning time, *ii*) egg buoyancy, *iii*) the direct mortality through hydrography, as well as *iii*) predation by sprat. The equations and parameters in the model are summarized in Tables 1 and 2.

### 2.1 Spawning time

Cod is a multiple batch spawner, with an adult cod spawning about 20 batches during the spawning period (Kjesbu *et al.*, 1996). The peak spawning time of Central Baltic cod has varied between April and August. In the beginning of the previous century the peak spawning was late in the summer (Bagge *et al.*, 1994), then in the middle and late part of the century it shifted to earlier spawning, while after the crash of the stock in the early 1990ies it again shifted to late spawning (Bagge *et al.*, 1994; Wieland *et al.*, 2000). Wieland *et al.* (2000) estimated the peak spawning time by fitting a normal distribution over time to measured egg abundances. They did not quote the values for the standard deviations of their fitted normal distributions, but they seem to vary from 30 to 60 days. We adopt their procedure and model the spawning time as being normally distributed in time. The peak

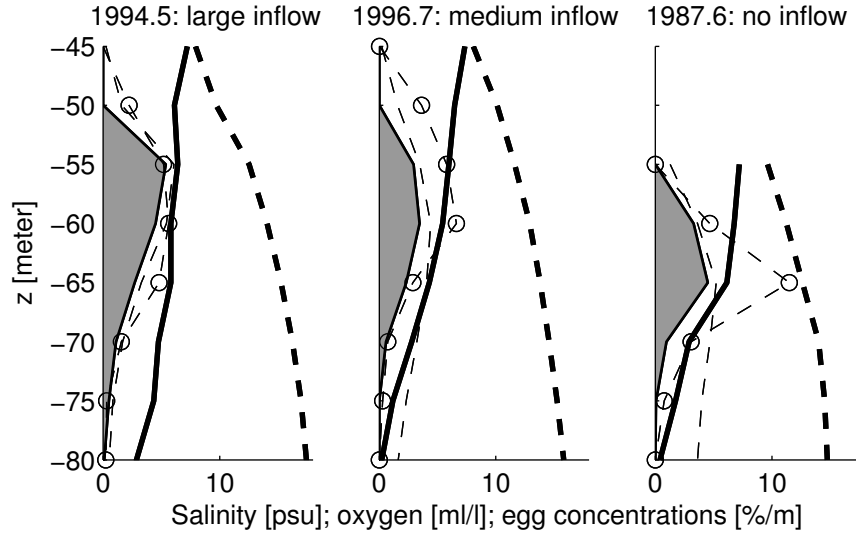


Figure 1: A comparison between the measured vertical egg distribution (circles), the initial egg distribution from the model (thin dashed line) and the final egg distribution from the model (hatched area). The measured and the initial distributions are in units of  $\%/m$  and normalized. The thick lines show measured salinity (dashed) and oxygen (solid). The measured total concentrations for the three years were: 6.0, 139.0 and 257.2 eggs/ $m^2$ . The data are from (Wieland and Jarre-Teichmann, 1997).

spawning time is set at  $t_{spawn} = \text{June 1st}$  and standard deviation  $\sigma_{spawn} = 35$  days. The influence of the exact values for these (and the following) parameters will be addressed in the sensitivity analysis.

## 2.2 Egg buoyancy

A crucial element of the model is the determination of where in the water column the eggs reside. To know this, the buoyancy of the eggs has to be determined. The temperature variation of the buoyancy of the eggs is supposed to be similar to that of the sea water, so the buoyancy can be measured in terms of the effective salinity of the eggs. The buoyancy of eggs from different cod stocks varies significantly and seems tuned to be close to the ambient salinity. Eggs from Atlantic cod have densities larger than 30 psu (e.g. Sundnes *et al.* (1964)) and consequently float slowly towards the sur-

face. The Central Baltic cod stock has lighter eggs; between 11 and 16 psu (Wieland and Jarre-Teichmann, 1997).

We have chosen to model the buoyancy of the eggs simply by assuming that the density is normally distributed with a mean value of  $s_{egg} = 13$  psu and a standard deviation of  $\sigma_{egg} = 2$  psu. The variation in the buoyancy reflects the variation due to the age of the mother fish, batch number, variation during the development etc.

An additional complication is that the buoyancy of the egg is known to vary during the development (Nissling and Vallin, 1995) and due to the age of the mother fish as well as the batch number (Vallin and Nissling, 2000). Vallin and Nissling (2000) made a model of the density of the eggs as a function of the length of the female and the batch number. A problem with the model is that it is based on a very

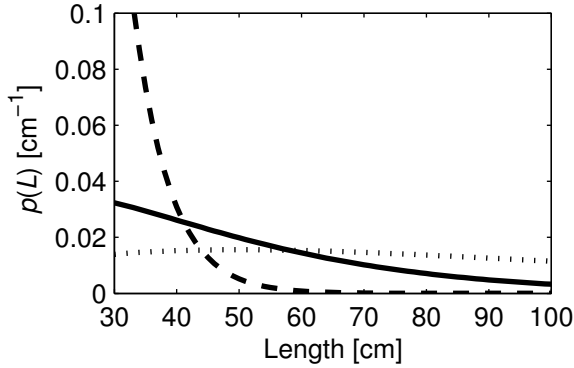


Figure 2: Distribution of lengths of spawning female cod with  $\beta = 0.2$  (dashed line),  $\beta = 0.05$  (solid line) and  $\beta = 0.02$  (dotted line).

small number of fish. An additional cause for caution is that the mechanisms regulating the buoyancy of the eggs are not completely understood. Nevertheless we included the model as an option, as it gives some indication of the importance of the maternal effect on egg buoyancy. We used the relationship for repeat spawners to give  $s_{egg}$  (the average density of the egg) as a function of length of the mother and time of spawning, where it was assumed that the 20 batches were equally distributed over the spawning period. The lengths of the females was drawn from a distribution with the shape  $p(L) = L/\beta^2 \exp(-\beta L)$ , with  $\beta$  varying between 0.02 to 0.20  $\text{cm}^{-1}$  (see Fig. 2). The distribution with  $\beta = 0.2 \text{ cm}^{-1}$  is representative of the situation from the 1990ies and until now where the stock is very depleted, while the distribution with  $\beta = 0.05 \text{ cm}^{-1}$  corresponds to the situation before the stock was over fished.

### 2.3 Direct mortality through hydrography

When the eggs are placed in a water column with a salinity gradient the resulting vertical distribution is a distorted version of the nor-

mal distribution (See hatched areas in Fig. 1). In low salinities the eggs are prone to perish either due to malfunction or to not being fertilized. At a salinity between 6.8 and 10.25 psu the blastula cell burst (Davenport *et al.*, 1981), probably due to a breakdown of the osmoregulation. (Westin and Nissling, 1991) examined the survival of sperm and the development of eggs for varying salinities. They found that for salinities below 11 psu the fertilization of the eggs suffered, however a few eggs were fertilized at salinities as low as 5 psu. When they investigated the development of the eggs, they found that at salinities above 12 psu all eggs showed normal development, while most (around 85 %) at 11 psu showed abnormal development. At lower salinities no eggs were developing normally. Here we suppose that eggs residing in a salinity lower than  $s_{min} = 11$  psu will die.

In addition to being exposed to low salinities, the eggs may also encounter low oxygen levels. The survival of eggs as a function of the oxygen saturation was measured quite accurately by (Rohlf, 1999), and a 50 % survival was found around 4.5 ml/l, with the lower limit for survival being around 2.0 ml/l. The measured survival probability was fitted to a combination of an exponential and a power law. The fit was adjusted for the present article, as the original one resulted in a survival larger than one for high values of oxygen (Table 1).

### 2.4 Predation

In spring, sprat enters the deep part of the Bornholm Basin to spawn (Aro, 1989). Köster and Schnack (1994) and Köster and Möllmann (2000) estimated the predation on cod eggs by the sprat from the analysis of stomach data. In some years they found very strong predation, while in others the predation was less dominant, even though there was a large abundance of sprat. One explanation for the

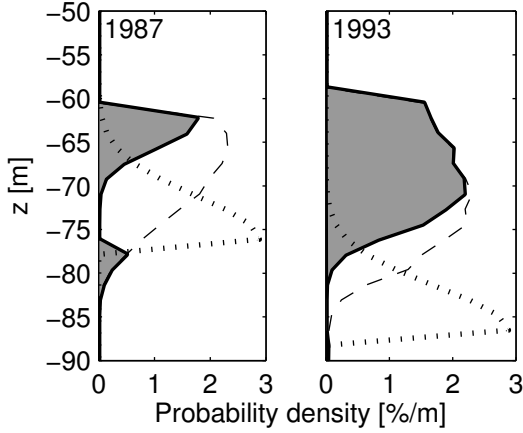


Figure 3: Illustration of the effect of the spatial overlap between cod eggs for two years; one without inflow (left) and one with a strong inflow (right). The cod eggs before predation is shown with the dashed line and the thick line is the distribution of sprat.

variation in predation is the degree of spatial overlap between sprat and the cod eggs. To model the predation by sprat there are two steps: *i*) the encounter problem and *ii*) the spatial and temporal overlap between the eggs and the sprat.

We will first tackle the encounter problem. We will not dive into processes like switching, variable turbulence levels etc., but use the simplest possible hypothesis, namely that the predation is proportional to the density of sprat  $\rho_s(t, z)$  and cod eggs  $\rho_e(t, z)$  (numbers pr. volume):

$$\frac{\partial \rho_e}{\partial t} = -\alpha \rho_e \rho_s, \quad (1)$$

where  $\alpha$  is a parameter determining the efficiency of the predation. Assuming that  $\rho_e$  and  $\rho_s$  are approximately constant during the development time of an egg ( $\tau_{egg} \approx 2$  weeks (Wieland *et al.*, 1994)), (1) can be integrated to give the relative change in the density of cod

eggs during the development period:

$$\frac{\Delta \rho_e}{\rho_e} = 1 - e^{-\alpha \rho_s \tau_{egg}}. \quad (2)$$

The density of cod eggs can be written as:

$$\rho_e(t, z) = p_e(t, z) \bar{\rho}_e, \quad (3)$$

where  $\bar{\rho}_e$  is the seasonal average density and  $p(t, z)$  is the probability density of finding an egg at a given depth and time. Introducing this in (2) for  $\rho_e$  and similarly for  $\rho_s$ :

$$\frac{\Delta p_e(t, z)}{p_e(t, z)} = 1 - e^{-\alpha p_s(t, z)}, \quad (4)$$

which is the mortality controlled by the new dimension less predation parameter  $\alpha_p = \alpha \bar{\rho}_s \tau_{egg}$ .

Next the temporal and vertical distribution of the sprat  $p_s(t, s)$  has to be determined. The spawning period of the sprat is modelled similarly to that of the cod, namely as a normal distribution with peak time  $t_{sprat} = \text{April 1st}$  and standard deviation  $\sigma_{sprat}$  (35 days) (REF!). While spawning in spring, sprat are mainly preying upon older developmental stages of the copepod *Pseudocalanus* sp. (Möllmann and Köster, 2002), which lives in the halocline of the Central Baltic deep basins, in oxygen concentrations down to 0.7 ml/l (Schmidt *et al.*, 2003). To reach the copepods, the sprat have to go as deep as they can, which in general is limited by the available oxygen. Under inflow conditions, the sprat can go very deep, due to favourable oxygen conditions. At the same time the salinities are higher, which means that the cod eggs will float higher in the water column. In this case the vertical overlap between sprat and cod eggs will be small. Conversely, in an oxygen-depleted situation, the sprat will not be able to go deep, and there will be a vertical overlap between sprat and cod eggs leading to high predation rates. Here it is assumed that

the sprat go as far down as they can with respect to oxygen (to  $o_{sprat} \approx 3$  ml/l) to prey on *Pseudocalanus* sp.. Above that lower level they are distributed as half a normal distribution with a width over depth of  $\sigma_{sprat.z}$ , here set to 5 m. This is in fairly good agreement with the fits to observations of vertical distributions made by (Neuenfeld and Beyer, 2003), see their Fig. 5. Combining this with the temporal distribution  $p_{sprat}(z, t)$  is determined. The effect of the spatial overlap between the cod eggs and the sprat is illustrated in Fig. 3. Here it is seen how in a bad year there is strong overlap between the cod eggs which has survived the environment, and the sprat. In a good year, the cod eggs are wider distributed in the water column, and they are also further up, thus avoiding the fatal overlap with the sprat.

## 2.5 Background mortality

In addition to the mortality driven by the environment and the predation, one could add a “background” mortality. This would be the fraction of eggs dying even under perfect conditions. Studying the oxygen related mortality, Waller *et al.* (1993) found a 70 % mortality even when the oxygen saturation was high. A constant background mortality would just mean a scaling of all the calculated mortalities, and as we are mostly interested in comparing different effects here, we will not include such a mortality.

## 3 Results

First the predicted vertical distribution of the eggs will be validated with observations from ichthyoplankton surveys. The main results of the model is presented through a sensitivity analysis, where each of the parameters in the model is varied. Finally, we explore what the model can tell us about the future development in survival of the Central Baltic cod eggs with

respect to likely scenarios of *i*) the absence or presence of inflows; *ii*) the size of the sprat stock and *iii*) variability in peak spawning.

### 3.1 Validation

Fig. 1 shows the influence of the salinity and oxygen on the egg distribution in three years, characterized by different strength of inflows. In 1994, a year with a strong inflow, the eggs were not influenced by the environment, and most of them survived. This is evident from the figure, as the initial calculated egg distribution (thin dashed line) is very similar to the surviving eggs (grey area). In 1996 conditions, in particular for oxygen, were less advantageous as in 1994. The distribution of the surviving eggs is therefore pushed a bit further up in the water column compared to 1994, and fewer survive. 1987 is a example of a fairly unfavourable situation, with both low concentrations of oxygen (confining the distribution from below) and salinity (confining the distribution from above). Comparing with the measured distributions, the profiles of the surviving eggs match fairly well. However, the comparison between the initial distribution and the measured one is not perfect when the hydrographic conditions are unfavourable. This is seen in particular in 1987, where a considerable amount of eggs is predicted to be spawned far down in the water column. This does not seem to be realistic, as the cod would not be able to swim down in the oxygen depleted water to spawn. The reason why this happens in the model is due to the standard deviation in the density of the eggs. If this is made smaller, the vertical distribution will be more confined. This would lead to a better fit with the measured egg distribution in the unfavourable years, but for the inflow years, the fit would deteriorate.

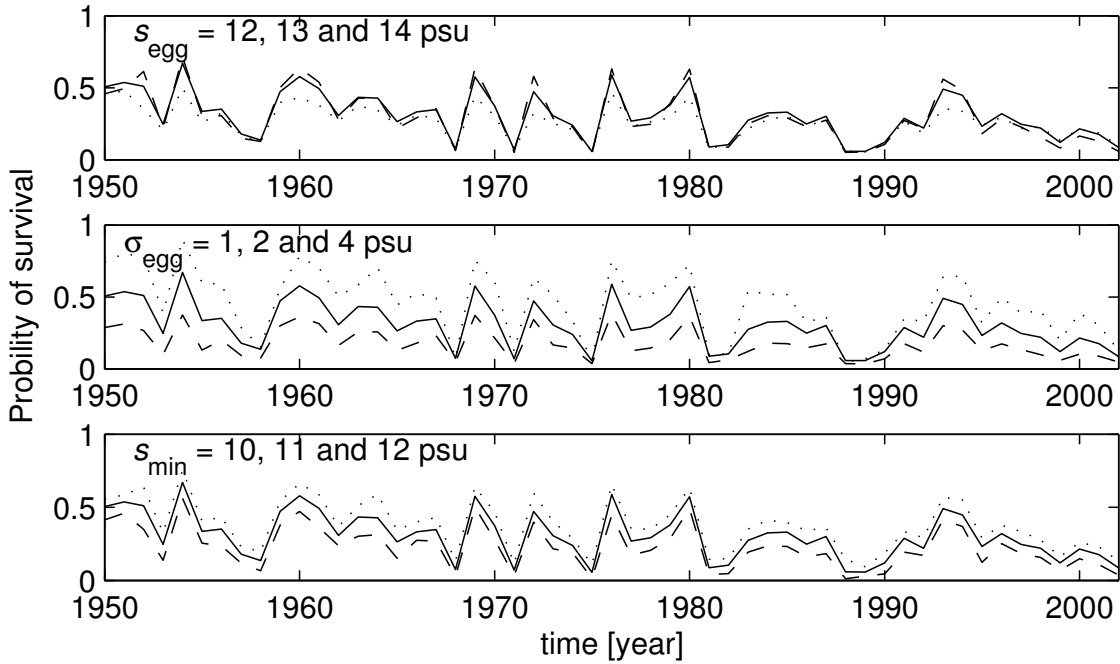


Figure 4: Effect of changing the parameters related to the environment: the mean egg density  $s_{egg}$ , the standard deviation in the egg density  $\sigma_{egg}$  and the minimum salinity where the eggs can survive  $s_{min}$ . The dotted line corresponds to the lower limit, the solid line is using the “standard” parameter values, and the dashed line is the higher limit of the parameter.

### 3.2 Sensitivity analysis

To assess the importance of the different parameters entering into the model, a sensitivity analysis has been performed. The data entering into the model are monthly, horizontal averaged profiles of oxygen and salinity in the Bornholm Basin for the period 1950 to 2002. By using averaged profiles we have assumed that the conditions in the basin are horizontally homogeneous. For each year of the data series of salinity and oxygen, the survival probability has been calculated, first for the “standard” values (Table 1), and then varying each of them in a interval which was deemed reasonable. This was done for the parameters governing the environment, the spawning time and the predation. Finally the effect of using the Vallin-Nissling model to calculate the egg

buoyancy was tested.

In Fig. 4 the probability of survival is given varying the parameters related to the environment. The solid lines correspond to standard values of the parameters and the dotted (dashed) lines to the higher (lower) values of the parameters.

Focusing first at the results for the standard values, a high year-to-year variation in the survival is observed. It is interesting to note that there is still a close to average survival of the eggs during the long stagnation period in the 80ies. The effect of the stagnation will be more evident when the predation is also considered. It is also of interest to note that even in the “good” periods there is very low survival in some single years, like 1971 and 1975.

Varying  $s_{egg}$  (the mean egg density) changes



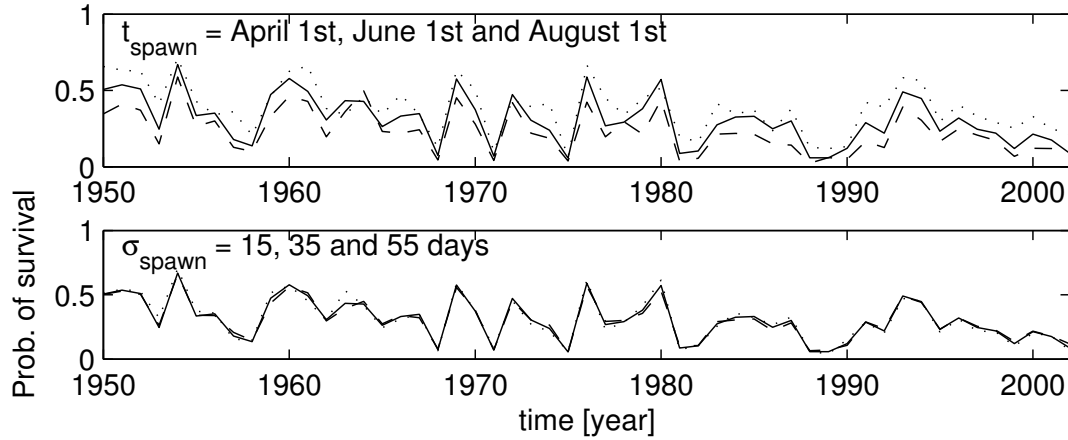


Figure 5: Effect of changing the peak spawning time (top) and the extent of the spawning period (bottom).

the survival probability remarkably little. Changing the standard deviation of the egg density  $\sigma_{\text{egg}}$  however has a large influence. A larger standard deviation means that a larger fraction of eggs enter into the low oxygen or low salinity zones and perish. The influence appears to be mainly as a constant factor, which means that it does not change the relative year-to-year survival. The lower limit of salinity where the eggs can survive,  $s_{\text{min}}$ , has a relatively small influence, and like  $\sigma_{\text{egg}}$  it is a constant factor.

In Fig. 5 the effect of changing the peak spawning time and extent is explored. Even though the year-to-year variation is more complex than for the previous figure, it is generally clear that it is an advantage to spawn early compared to late. However the difference between late and early spawning is not very pronounced. Changing the extent of the spawning time  $\sigma_{\text{spawn}}$  between 15 and 45 days does not change the probability of survival significantly.

In Fig. 6 the influence of changing the parameters related to predation is examined. The interesting plot is the third one, where  $\alpha_p$  is varied. Predation has a strong effect, how-

ever the strength of the effect varies from year to year. It is particularly interesting to note that the predation seems to be most effective in years with stagnation, e.g. the 80ies. In good years like 1993 and 1994, even strong predation does not influence the eggs a lot.

From Fig. 7 it is seen that using the Vallin-Nissling model is not much different from just using a fixed density. However using the Vallin-Nissling model it is possible to explore the effect of changing the stock structure. In good years changing the stock structure does not have a significant effect on the survival probability, but in bad years there is some influence. Overall, the influence of the stock structure seems to be weak.

### 3.3 Application of the model to 2004

As an illustration of how the model can be used real-time, it has been run using profiles measured during a cruise in late April 2004 (Fig. 8). It is early in the season, but even then the oxygen conditions are not the best. Still around 42 % of the eggs survive (filled area in the figure). However, there appear to be a strong overlap between the sprat and the cod eggs,

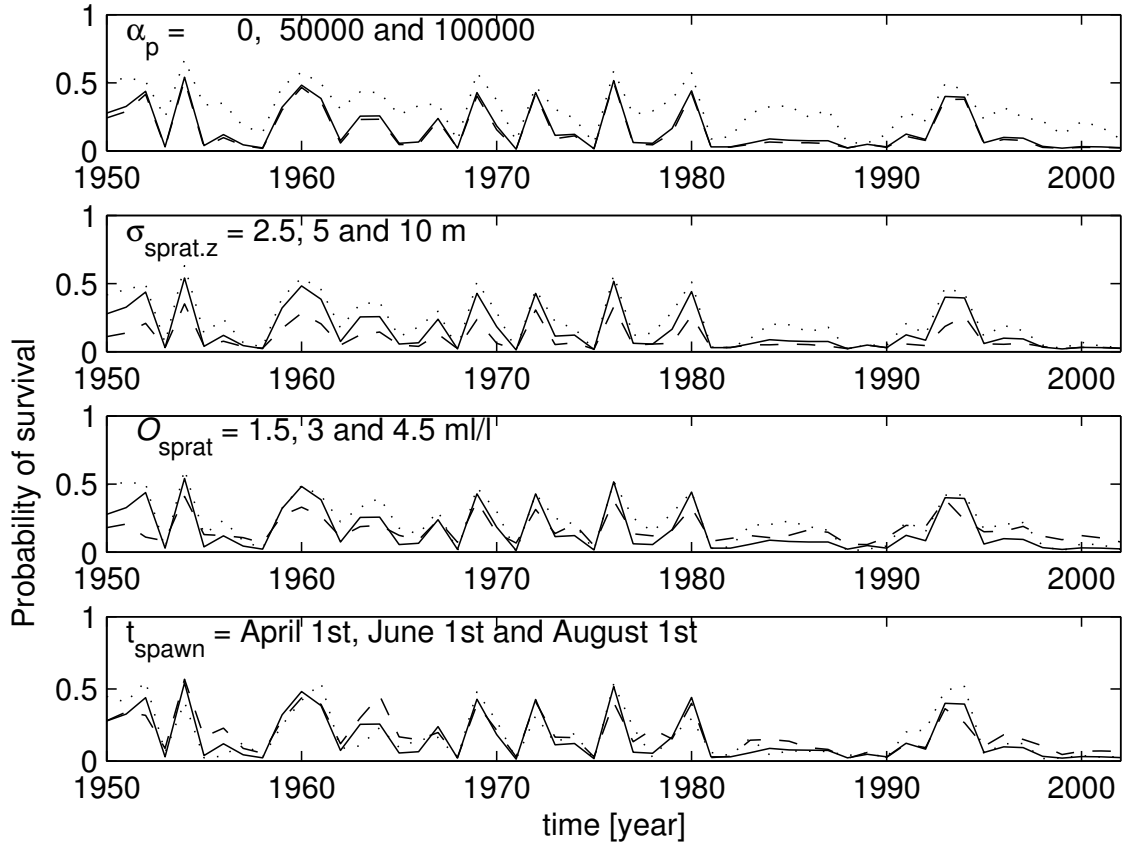


Figure 6: The probability of survival given changes in the parameters governing predation. The predation has been set to  $\alpha_p = 50000$  for all plots, except the top one.

which makes the eggs vulnerable to predation, depending upon the number of sprat present. In the right panel of Fig. 8 is shown the survival if predation is added. For this case, it is clear that even a small amount of predation will do away with a large fraction of the eggs. This results therefore suggests that in the early 2004 season, the amount of surviving eggs is limited not by the environmental conditions, but by the amount of predation.

During the cruise the profiles of salinity and oxygen were measured at 45 stations around the Bornholm Basin. These were averaged, and the average profile was used in the above calculation. The variation from station to sta-

tion did not appear to be large; the standard deviation for the oxygen was around 0.8 ml/l and for the salinity 0.6 psu. However, if the survival (due to environment only) is calculated for each individual profile, survivals ranging from 0 to 70 % are found, and the distribution of survivals is very broad indeed (Fig. 9). The mean is 36 %, not far from the value calculated using the mean profiles. This result however indicates that even though the variability in the basin appears small, it might have a large influence on the survival of the eggs.

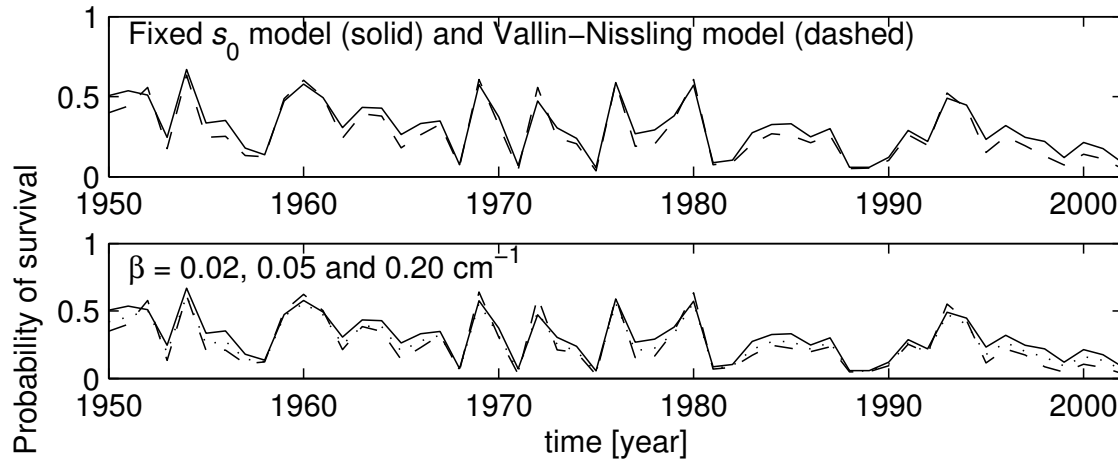


Figure 7: Top: comparison between the results from using a constant egg density and using the Vallin-Nissling model. Bottom: Effect of changing the stock structure in the Vallin-Nissling model.

## 4 Discussion

We have developed a simple process oriented model of the survival of cod eggs, based on existing extensive knowledge. The survival is calculated given vertical profiles of salinity and oxygen, together with a specification of the peak spawning time and the size of the sprat stock. The advantage of a process-oriented model is that each process affecting the eggs is isolated and can be validated using observations or experiments. Using the model it has been possible to make a quantitative comparison of the relevance of various effect.

### Main results

The inclusion of predation by sprat is strongly enhancing the detrimental effects of the hydrography. It is in fact a very good example of an indirect physical-biological interaction, as the predation is governed by the vertical overlap between the eggs and the sprat, ruled by the physical hydrography.

The effect of the stock structure through maternal effects on the egg buoyancy seems to be

only secondary. These effects are therefore not suited as indicators of recruitment success or failure.

Spawning time matters in good (inflow) years, with early spawning being favourable. In stagnation years where the influence of predation is strong, late spawning can be a strategy for avoiding predation. However, by being spawned late, the eggs are subject to exposure to detrimental hydrographic conditions, which seems to balance the advantage of avoiding predation. It can therefore not be used as an explanation for the recent shift in spawning time.

### Performance of the model

Through the comparison with measured vertical egg distributions, it was clear that the model of the initial egg distribution is not completely correct in stagnation situations. As the determination of the egg buoyancy is at the core of the model, this part could be improved. Such an improvement would have to rely on a better understanding of the physiological mechanisms behind the regulation of the egg buoyancy. Even though the complete

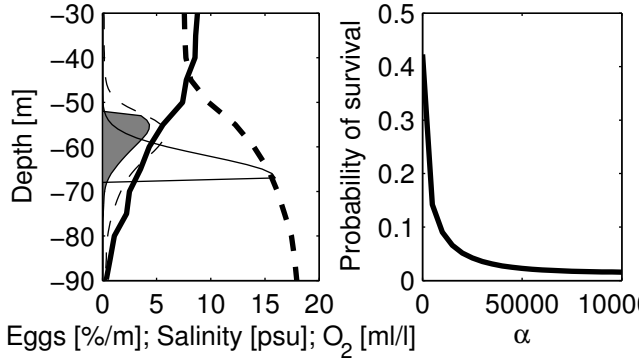


Figure 8: The survival of the eggs, run with measured profiles of salinity (thick dashed) and oxygen (thick solid) ultimo April 2004. The dashed line is the initial egg distribution and the filled area is the eggs which survive the environmental conditions (42 %). The solid line is the predicted distribution of sprat. To the left is shown the probability of survival if the predation by sprat is included, as a function of the predation parameter  $\alpha$ .

story of what determines the buoyancy of the eggs has not been uncovered, some things are well known (Davenport *et al.*, 1981; Craik and Harvey, 1987; Mangor-Jensen, 1987). The egg consists of a central ovoplasm floating in the perivitelline space surrounded by the chorion. Because the chorion is permeable to seawater, the perivitelline space is filled with sea water and thus contributes to regulate the overall buoyancy of the egg toward that of the ambient water. The ovoplasm appears to be able to do osmoregulation to regulate the salinity (Davenport *et al.*, 1981), and thereby actively regulates the buoyancy of the egg. However, it is not clear how the ovoplasm chooses its target salinity, but a possible explanation could be that it is the same as the blood plasma of the mother fish (Davenport *et al.*, 1981), set by the salinity of water with which the eggs are flushed before spawning or genetically determined.

Figure 9: The distribution of survival due to environment on the 45 stations where profiles of salinity and oxygen were measured in 2004.

When the predation is considered, one should in principle take the variation of the development time of the eggs with temperature into account. The temperature in the layer where the peak of the distribution of the cod eggs reside vary between 3° and 9°, resulting in a development time from 10–23 days (Wieland *et al.*, 1994). A long development time means that the eggs are vulnerable to predation for a longer time. We have tried to use this in the calculation of the predation, by letting  $\alpha_p$  in Equation (4) be proportional to the development time. The inclusion of this effect did not change the final survival probability appreciably, and it was therefore omitted.

Absolute mortality rates from the model are not accurate as the background mortality has not been included. In addition some of the parameters are difficult to determine, like the standard deviation in the egg buoyancy. However, the year to year variation in the mortality, and the comparison of the relative importance of different effects appears to be quite more reliable.

## Usage of the model

It is tempting to use the model to make a prediction of the recruitment. It is important to remember, that a model of egg mortality can only predict years where there is problems with the recruitment (high mortality). If there is a low egg mortality, it does not necessarily mean a high recruitment, as the larvae or juveniles could still run into trouble and perish. Low egg mortality only means that there is a *possibility* for a high recruitment.

The model can be run in a real-time mode, as soon as hydrographic data for the season become available. It can also be coupled to a circulation model, and if the accuracy of modelling the oxygen concentration in the Bornholm Basin is improved, it can even be run prognostically.

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