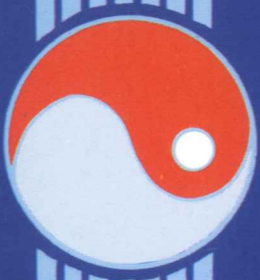


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HAVFORSKNINGSINSTITUTTETS EGG- OG LARVEPROGRAM (HELP)

FACTORS AFFECTING THE VERTICAL DISTRIBUTION OF EGGS

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ABSTRACT

The spatial distribution of eggs and larvae is a function of the properties of the ambient water, i.e. the density, current and turbulent diffusion, and of the physical properties of the eggs, i.e. the buoyancy and dimension. The study of the vertical distribution is the first step to understanding the horizontal transport of eggs and larvae. Two models for the vertical distribution of eggs are applied to demonstrate how the physical and biological conditions influence the vertical distribution for the three main categories of eggs, here defined as pelagic, bathypelagic and bottom eggs. In particular, the physical conditions affecting the distribution of bathypelagic eggs are studied. The wind induced turbulence is the most important ambient factor for the vertical distribution of pelagic eggs and larvae. It contributes to mixing the buoyant eggs and larvae through the wind mixed layer. The vertical spreading of bathypelagic eggs depends mainly on the buoyancy distribution of the eggs. It is demonstrated from the model results that non-adhesive demersal eggs will be partly mixed into the water column. This mechanism contributes to the horizontal transport of demersal eggs.

INTRODUCTION

The spatial distribution of eggs and larvae is influenced by a set of biological and physical processes, which together contribute to determine the fate of the year class. The importance of the distribution and transport of the early stages for recruitment of fish stocks has been pointed out by many authors: It has been suggested that unfavorable drift of eggs and larvae beyond the appropriate distributional area will cause permanent loss from the population (Hjort, 1914). On the other hand it has been shown that anomalous transport from one region to another may transfer recruits from one stock to another. This was described by Hansen and Buch (1986) who found that export of cod larvae from the Iceland to the Greenland area increased the Greenland cod stock. The importance of larval retention within specific geographical regions during critical periods has been outlined by Iles and Sinclair (1982). Considering the large vertical variations of the horizontal flow field, it is evident that the vertical distribution of eggs and larvae is important for their horizontal transport and spreading and their fate with respect to survival. Cushing (1982) gave an example of how the vertical distribution itself directly influenced the recruitment: The rising halocline in the Baltic brought up cod eggs and larvae closer to the productive layers where their food is produced. Consequently, one important step towards understanding the recruitment processes is to describe and understand the vertical distribution of eggs and larvae. This paper demonstrates how the physical properties of eggs and the ambient physical forces influence the vertical distribution. Two models for the vertical distribution of eggs (Sundby, 1983; Westgård, 1989) are applied to demonstrate the three main types of vertical distribution: pelagic, bathypelagic and bottom distributions. The physical conditions for each type of distribution are analysed.

RESULTS AND DISCUSSION

Basic Equation

The vertical processes which influence distribution of eggs, are here studied, and it is assumed that all horizontal gradients are zero. The basic equation is then reduced to the vertical component of the diffusion equation:

$$\frac{\partial C(z,t)}{\partial t} - \frac{\partial [w(z,t)C(z,t)]}{\partial z} = \frac{\partial}{\partial z} \left[K(z,t) \frac{\partial C(z,t)}{\partial z} \right] + S(z,t) + M(z,t) \quad (1)$$

where

$C(z,t)$ is the concentration of eggs in numbers per unit volume

$w(z,t)$ is the vertical velocity of the eggs

$K(z,t)$ is the vertical eddy diffusivity coefficient

$S(z,t)$ is the spawning production of eggs

$M(z,t)$ is the egg mortality

z is the vertical component, positive towards increasing depth

t is time.

To solve the equation, the vertical velocity of the eggs, $w(z,t)$, and the vertical eddy diffusivity coefficient, $K(z,t)$, must be known. The vertical velocity is expressed $w = f(d, \Delta \rho, \nu)$, where d is the diameter of the egg, $\Delta \rho$ is the difference in density (buoyancy) between the egg, ρ_e , and the ambient water, ρ_w , and ν is the molecular viscosity of the water. Hence, the two physical properties of the eggs, the buoyancy and the diameter are key parameters to model the vertical distribution.

In the following sections it will be shown that changes of the buoyancy, $\Delta \rho = \rho_w - \rho_e$, results in the most pronounced changes to the solutions of the basic equation (1). For this reason it is useful to classify eggs into three main groups (See Figure 1):

A. $\Delta \rho > 0$

B. $\Delta \rho = 0$

C. $\Delta \rho < 0$

In this paper group A will be defined as "pelagic" eggs, group B as "bathypelagic" and group C as "bottom" eggs. Since there are few descriptions of the vertical distribution of eggs in relation to their buoyancy, much of the literature is not consistent in this question. It seems that eggs are often called "pelagic" if they are found in the water column and "demersal" if they are found on the bottom. However, the solution to equation (1) will show that all the three groups, defined above, are found in the water column. Even demersal eggs, given they are non-adhesive, will be mixed into the water column. In addition to the three main types of eggs in Figure 1, there are also

mixed types. In particular, species with a buoyancy distribution between pelagic and bathypelagic have been reported by Coombs *et al.* (1985).

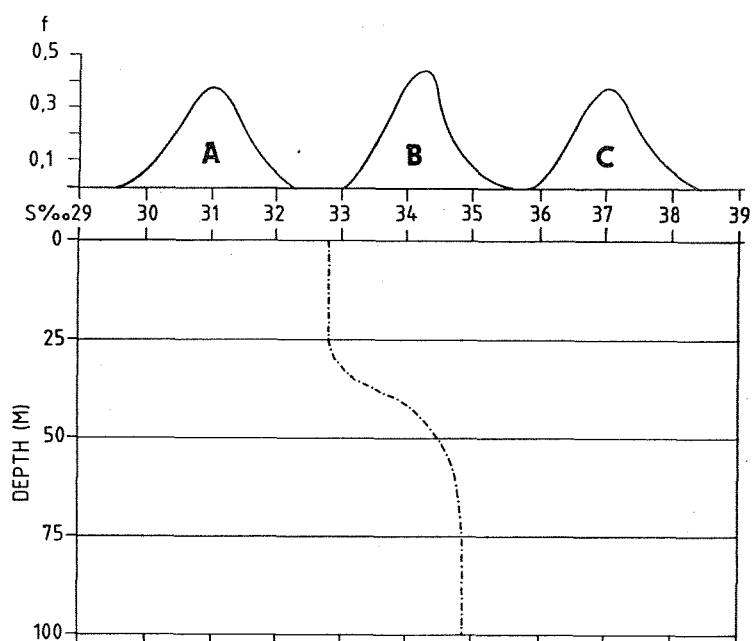


Figure 1. Buoyancy distribution of three categories of eggs (upper part of the figure) in relation to the salinity profile (lower part of the figure). A: pelagic eggs, B: bathypelagic eggs, C: bottom eggs.

Egg buoyancy

The general knowledge of fish eggs' buoyancy has increased substantially during recent years, in particular after the density gradient column was introduced by Coombs (1981). This instrument enables us to measure the specific gravity of individual eggs with a high accuracy and resolution. The physiological causes of buoyancy in marine fish eggs have been studied by Craik and Harvey (1987).

Pelagic eggs have a specific density which is lower than the density of the upper mixed layer of the sea. Hence they tend to rise towards the surface. Only a small fraction of such eggs, however, is found at the very surface, because the turbulent forces of the mixed layer counteract the buoyant forces of the eggs. Depending on the magnitude of the counteracting forces the eggs will be more or less concentrated towards the surface. Examples of eggs with such distributions are the North Sea plaice eggs (Pommeranz, 1973), the North Sea mackerel eggs (Iversen, 1973; Coombs, 1981) and North-east arctic cod eggs (Solemdal and Sundby, 1981). The vertical distributions of these species were

modeled by Sundby (1983).

Bathypelagic eggs have a higher specific density than the density of the upper mixed layer of the sea, but lower than the density of the bottom layer. Hence they are distributed at mid-depths and quite frequently in the pycnocline. Examples of species having this type of egg distributions are Pacific halibut (Hippoglossus stenolepis) (Thompson and van Cleve, 1936), the Baltic cod (Kändler, 1949) and the Atlantic halibut (Hippoglossus hippoglossus L.) found in Norwegian fjords and coastal waters (Haug et al., 1984, 1986). Kendall and Kim (1989) demonstrated how the bathypelagic eggs from the walleye pollock (Theragra chalcogramma) substantially changed their vertical distribution mainly due to changes in the buoyancy during the development.

Bottom eggs have a specific density which is higher than the density of the bottom layer. In principle, demersal eggs is one kind of bottom eggs. However, it is essential to distinguish between adhesive and non-adhesive eggs. With respect to the nature of the vertical forces acting on the eggs, there is no difference between non-adhesive demersal eggs and pelagic eggs. Non-adhesive demersal eggs, unless they are buried in the sea bed, will be more or less mixed into the water column depending on the magnitude of the bottom turbulent mixing. One species having non-adhesive demersal eggs is the saffron cod (Eleginus gracilis) in the north-east Pacific Ocean (Dunn and Matarese, 1986). Even adhesive eggs may break loose from each other and the sea bed and be mixed into the bottom layers and transported away. This has been reported for the Barents Sea capelin eggs (Bakke and Bjørke, 1973).

The density distribution of an egg population can often be described by a Gaussian distribution function. The eggs from the North-east arctic cod are neutrally buoyant at an average salinity of 31.0 and the standard deviation is 0.55 (Solemdal and Sundby, 1981). Eggs from the Atlantic halibut are neutrally buoyant at an average salinity of 34.2 with a standard deviation of 0.52 (Haug et al., 1986). The buoyancy of sprat eggs off the southern coast of Great Britain ranged over about 8 salinity units during the end of the egg stage (Coombs et al., 1985). Consequently, it is expected that there is a large difference of the vertical distribution of the heaviest and the lightest fractions of an egg population. In Figure 1 the neutral

buoyancy distributions of three different egg population are drawn together with a vertical salinity profile. Distribution A, which is consistent with the eggs of North-east arctic cod, will appear as pelagic eggs. Distribution B, which is identical with the Atlantic halibut eggs, will appear as bathypelagic eggs and distribution C will appear as bottom eggs. The latter is a hypothetical distribution, since no reports of quantitative density measurements of non-adhesive bottom eggs are available.

There are, however, examples of species which is a mixture of the main types described above. Coombs et al., 1985 investigated buoyancy and vertical distribution of eggs from sprat (Sprattus sprattus) and pilchard (Sardina pilchardus) off the south coast of Great Britain. These eggs were a mixture of pelagic and bathypelagic eggs. In addition, the specific gravity of the eggs changed through development, and the ambient salinity varied through spawning season. This will result in a variety of possible vertical distributions, partly with peak concentrations in the surface, and partly in the pycnocline.

Vertical eddy diffusivity coefficient

The other parameter which influences the vertical distribution of eggs is the vertical eddy diffusivity coefficient. Depending on the depth, wind velocity, stratification, tidal energy and bottom stress it varies over approximately 5 orders of magnitude. It is largest in the mixed layer and decreases to a minimum in the pycnocline due to the stratification which reduces the vertical transport of turbulent energy. A slight increase occurs below the pycnocline due to the weaker stratification followed by a pronounced increase in the bottom layer due to bottom friction. Figure 2 shows qualitatively how the vertical eddy diffusivity coefficient may vary through a water column.

Estimates of the mixed layer eddy viscosity coefficient are difficult partly due to the great problems of resolving wave motion from turbulence. Sverdrup et al. (1942) derived estimates of the eddy viscosity coefficient from the Ekman theory. Sundby (1983) estimated over-all eddy diffusivity coefficients for the mixed layer from a model on the vertical distribution of pelagic eggs. Thorpe (1984) made estimates of the eddy diffusivity coefficient in the surface layers based on a model for the vertical distribution of air bubbles in the

sea. Although their results to some extent differ, it may be concluded that the eddy diffusivity coefficient ranges from about $10 \text{ cm}^2 \text{ s}^{-1}$ at wind speed near zero to about $10^3 \text{ cm}^2 \text{ s}^{-1}$ at wind speed of approximately 20 ms^{-1} .

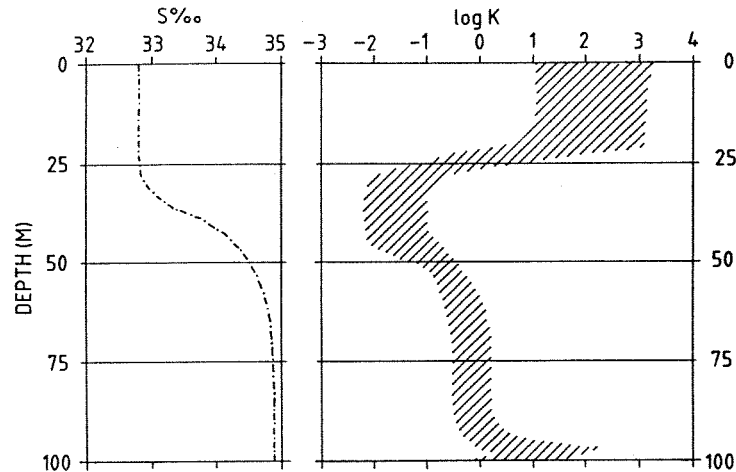


Figure 2. Ranges of the vertical distribution of the eddy diffusivity coefficient, K , in $\text{cm}^2 \text{ s}^{-1}$ (right part) for a hydrographic profile (left part) identical with the profile in Figure 1.

In the pycnocline the eddy diffusivity coefficient is inversely related to the stratification and directly dependent on the energy input. However, the functional relationship to those parameters is still unknown. Several authors have estimated the vertical eddy diffusivity in different fjords and coastal waters e.g. Gade (1970) for Oslofjorden, Kullenberg (1971) for shallow coastal waters, Svensson (1980) for a Swedish fjord and Buch (1982) for two-layered Scandinavian fjords. Gargett (1984) reviewed the literature on the vertical diffusivity coefficient in stratified systems. Depending on the degree of stratification, the eddy diffusivity coefficient ranges from $0.5 \times 10^{-2} \text{ cm}^2 \text{ s}^{-1}$ to about $1 - 4 \text{ cm}^2 \text{ s}^{-1}$.

The bottom turbulence, which normally extends several meters above the bottom, is mainly dependent on the boundary layer velocity and the bottom roughness. Bowden (1962) reported values from several authors. In areas of strong tidal mixing the eddy diffusivity coefficient may exceed $100 \text{ cm}^2 \text{ s}^{-1}$, although $1 \text{ cm}^2 \text{ s}^{-1}$ is more common above the sea bed in deep oceanic areas.

Vertical distribution of eggs

If the terms spawning production, $S(z,t)$, and mortality, $M(z,t)$, are neglected in equation (1), and stationary conditions are considered, the diffusion equation reduces to:

$$- w(z) \cdot C(z) = K(z) \frac{\partial C(z)}{\partial z} \quad (2)$$

Equation (2) applies to the fraction eggs which has reached the steady state distribution after being spawned at some depth. We assume the buoyancy distributions shown in Figure 1 and a variation of the eddy diffusivity coefficient as shown in Figure 2 and apply the models for the vertical distribution (Sundby, 1983; Westgård, 1989). The three categories of eggs, pelagic (A), bathypelagic (B) and bottom eggs (C), will appear as shown in Figures 3a and 3b.

Figure 3a shows the distribution for a situation of low eddy diffusivity coefficients in the water column, corresponding to the lower range of eddy diffusivity profile in Figure 2. The value of the mixed layer is $75 \text{ cm}^2 \text{ s}^{-1}$ corresponding to wind speed of 0 ms^{-1} (according to Sundby (1983)). In the pycnocline the minimum eddy diffusivity coefficient is $0.01 \text{ cm}^2 \text{ s}^{-1}$, and the value of the bottom layer is $6 \text{ cm}^2 \text{ s}^{-1}$.

Figure 3b shows the distribution for a situation of high eddy diffusivity coefficient, corresponding to the higher range of eddy diffusivity profile in Figure 2. The mixed layer eddy diffusivity coefficient is $585 \text{ cm}^2 \text{ s}^{-1}$ corresponding to wind speed of 15 ms^{-1} (according to Sundby (1983)). The minimum value of the pycnocline is $0.5 \text{ cm}^2 \text{ s}^{-1}$, and the value for the bottom layer coefficient is $90 \text{ cm}^2 \text{ s}^{-1}$.

Figures 3a and 3b show that the vertical distribution of pelagic eggs (A) is very sensitive to variations in the wind induced turbulence, as also demonstrated by Sundby (1983). The figures also show that varying bottom turbulence levels influences the vertical distribution of bottom eggs (C). However, the vertical distribution of bathypelagic eggs (B) confined to the pycnocline is rather insensitive to variations in the pycnocline turbulence. The pycnocline eddy diffusivity coefficient is increased by a factor of 50 from Figures 3a to 3b, but the vertical spreading is not substantially changed.

Consequently, the vertical spreading in the pycnocline depends mainly on the density distribution of the eggs and the density profile, and not very much on the level of turbulence.

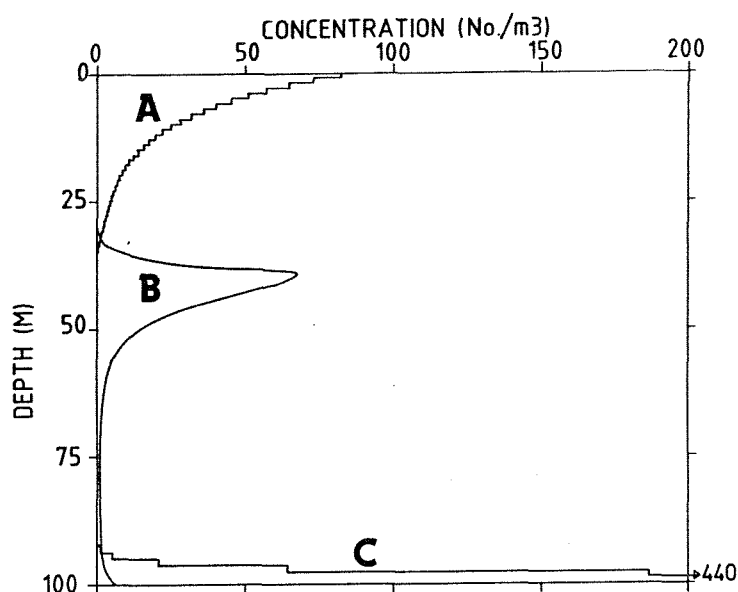


Figure 3 a. Vertical distribution of pelagic (A), bathypelagic (B) and bottom eggs (C) during low turbulence (See numerical values in the text). The neutral buoyancy distributions, salinity profile and eddy diffusion profile as shown in Figures 1 and 2.

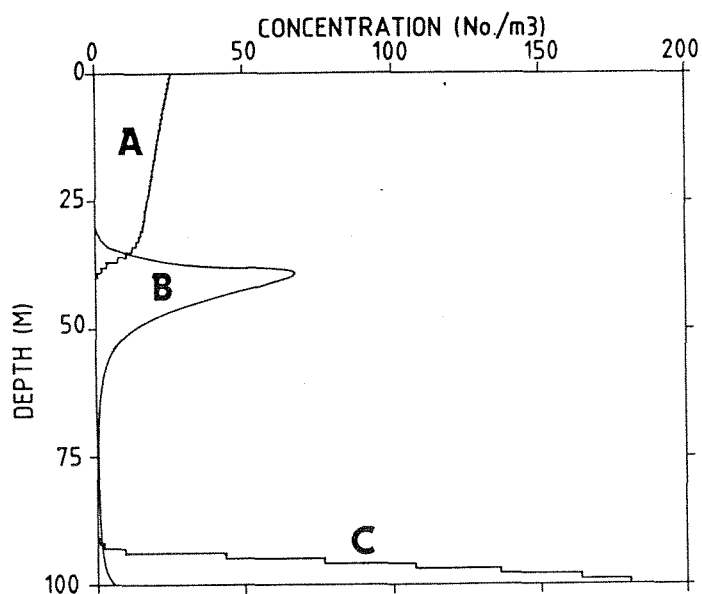


Figure 3 b. Vertical distribution of pelagic (A), bathypelagic (B) and bottom eggs (C) during high turbulence (See numerical values in the text). The neutral buoyancy distributions, salinity profile and eddy diffusion profile as shown in Figures 1 and 2.

To show this we solve the diffusion equation for eggs of a given density in a linear pycnocline. The eddy diffusivity coefficient can

then be considered as constant with respect to depth. In a linear pycnocline, $\rho(z) = k z + b$, the vertical velocity, $w(z)$, varies linearly within the Stokes regime. The vertical velocity may therefore be written:

$$w(z) = m (z - z_A) \quad (3)$$

where m is a constant, and z_A is the level where $\Delta\rho(z) = 0$, i.e. the level of neutral buoyancy of the egg. Equation (3) is inserted into equation (2):

$$- m (z - z_A) \cdot C(z) = K \frac{\delta C(z)}{\delta z} \quad (4)$$

The solution to equation (4) is:

$$C(z) = C_A \cdot \exp - \frac{m}{2 K} (z - z_A)^2 \quad (5)$$

where C_A is the concentration of eggs at the depth of neutral buoyancy, z_A . According to eq. (5) the eggs are vertically distributed as a normal distribution, where the standard deviation:

$$\sigma = \sqrt{K/m} \quad (6)$$

When the velocity of the eggs is confined within the Stokes regime, the Stokes equation for the terminal velocity is valid and the expression for m becomes:

$$m = 1/18 d^2 v^{-1} \rho_w N^2 \quad (7)$$

where d is the diameter of the egg and N is the Brunt-Väisälä frequency. The value of the molecular viscosity, v , is tabulated by Riley and Skirrow (1975) (e.g. at 5 °C and salinity 30 the molecular viscosity is $0.016 \text{ gcm}^{-1} \text{ s}^{-1}$).

We take, as an example, the vertical distribution of Atlantic halibut in the pycnocline of northern Norway fjords described by Haug et al. (1986), where the squared Brunt-Väisälä frequency, N^2 , ranged from 0.5×10^{-4} to $2.0 \times 10^{-4} \text{ s}^{-2}$. From the above mentioned literature on the influence of stratification on the turbulence, the eddy diffusivity

coefficient range from 0.1 to $0.5 \text{ cm}^2 \text{ s}^{-1}$. When these values are inserted into eq. 6 and 7, the standard deviation, σ , of the vertical spreading of one buoyancy group of halibut eggs will range from 0.4 to 1.6 meters. According to Haug *et al.* (1986) the older eggs (which definitely have come to a steady state vertical distribution) extend over a 150 - 250 m water column. Consequently the large vertical spreading of halibut eggs in the water column is due to the neutral buoyancy distribution of the eggs alone and not due to the vertical turbulence.

The vertical distribution of eggs with a density higher than the bottom water layer, here defined as bottom eggs (distribution C in Figs. 3a, 3b), has the inverse distribution of that of pelagic eggs. Since the bottom turbulence generally is much lower than the turbulence in the upper mixed layer, the bottom eggs will be more concentrated towards the boundary than the pelagic eggs. For low levels of bottom turbulence (Fig. 3a), less than 3 % of the eggs are mixed more than 3 m above the sea bed. However, in shallow regions where the tidal induced bottom turbulence is high, and where the mixed layer may even extend to the bottom, the bottom turbulence coefficient may exceed $100 \text{ cm}^2 \text{ s}^{-1}$, and the eggs will be distributed as C in Figure 3b. Here 40 % of the eggs are more than 3 m above the sea bed.

Development of steady state egg profiles

In the previous section distributions based on balance between the buoyancy force of the eggs and the vertical turbulence forces were studied, i.e. when $\delta C / \delta t = 0$ (steady state). The time it takes to reach steady state distribution, depends on the spawning depth, the buoyancy and the turbulence. Figure 4 illustrates how the mixed layer turbulence influence the time to reach the steady state profile for pelagic cod eggs spawned at 120 m depth. The buoyancy distribution of these eggs equals those of the cod eggs shown in Figure 1. The figure shows the concentration profile for every 6th hour after spawning near the bottom. It takes 48 hours to reach the steady state distribution during calm wind conditions, while it takes only 30 hours to reach steady state at wind speed of 15 m/s. It can also be shown that there are large variations in the time to reach steady state for the heavy fraction and the light fraction of the eggs. While the buoyancy of pelagic eggs is constant as they rise through the mixed layer, the buoyancy of bathypelagic eggs decreases as they move toward the depth

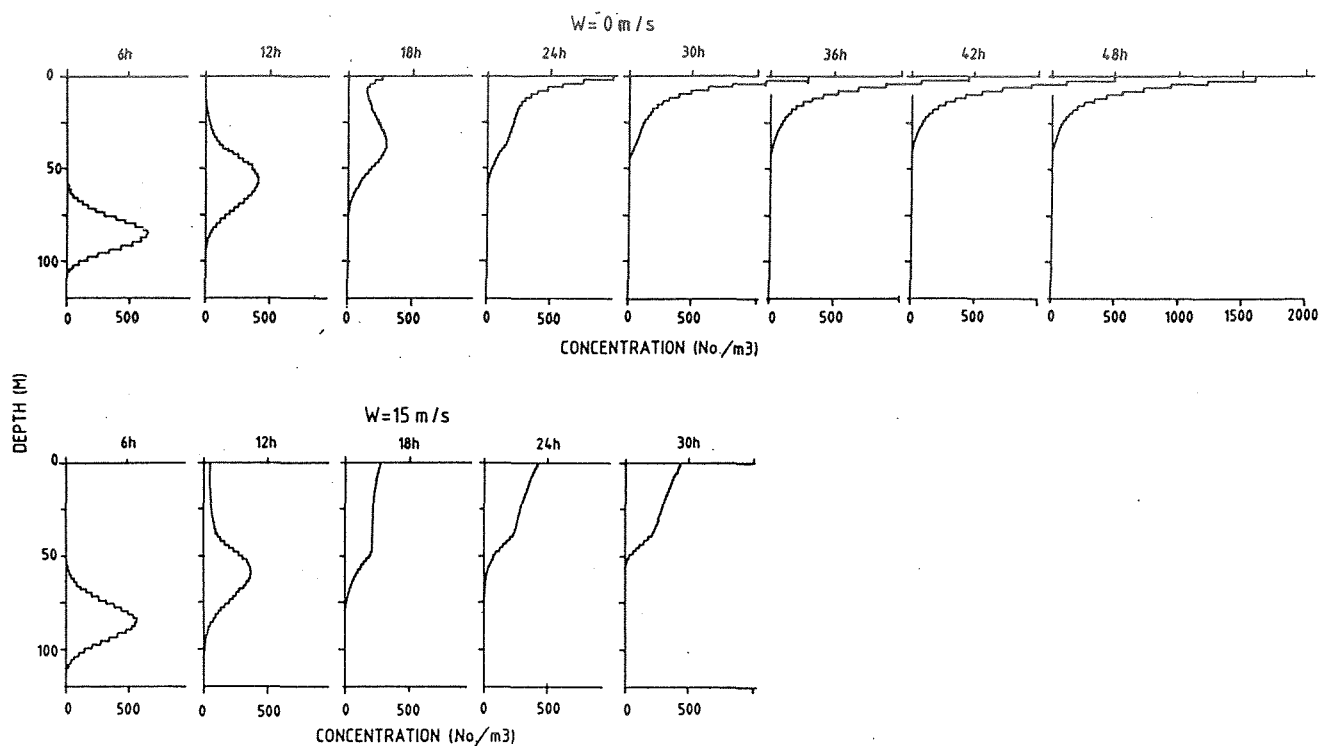


Figure 4. Development of the vertical profile of pelagic eggs (A) from an initial distribution, i.e. spawning near the bottom, to steady state for two events of mixed layer turbulence. Upper part: wind velocity, $W = 0 \text{ ms}^{-1}$. Lower part: wind velocity, $W = 15 \text{ ms}^{-1}$.

of equilibrium. It implies that the vertical velocity also decreases, and it takes a relatively long time to reach steady state for bathypelagic eggs.

CONCLUSION

The vertical distribution of pelagic eggs is mainly influenced by the wind induced mixing. The buoyancy distribution determines the vertical distribution of bathypelagic eggs, while the vertical spreading in the pycnocline of these eggs is essential insensitive to vertical mixing. Model results show that non-adhesive demersal eggs partly will be found in the water column. This will contribute to advection of demersal eggs. The time it takes to reach a steady state vertical egg distribution depends on the spawning depth, buoyancy distribution of the eggs and the vertical mixing.

REFERENCES

- Bakke, S. and Bjørke H. 1973. Diving observations on Barents Sea capelin at the spawning grounds off northern Norway. *FiskDir. Skr. Ser. HavUnders.*, 16: 140-147
- Bowden, K. F. 1962. Turbulence. In *The Sea. Ideas and observations on Progress in the study of the Seas. Volume 1. Physical Oceanography.* pp. 802 - 825. Ed. by M. W. Hill. Interscience Publishers. John Wiley & Sons.
- Buch, E. 1982. An investigation of the mixing in two-layered fjords. Københavns Universitet. Institut for fysisk oceanografi. Report no 43 1982. 79 pp.
- Coombs, S.H. 1981. A density-gradient column for determining the specific gravity of fish eggs, with particular reference to eggs of mackerel *Scomber scombrus*. *Mar. Biol.*, 63: 101-106.
- Coombs, S. H., Fosh, C. A. and Keen, M. A. 1985. The buoyancy and vertical distribution of eggs of sprat (*Sprattus sprattus*) and pilchard (*Sardina pilchardus*). *J. mar. biol. Ass. U.K.*, 65: 461-474.
- Craik, J. C. A. and Harvey, S. M. 1987. The causes of buoyancy in eggs of marine teleosts. *J. mar. biol. Ass. U.K.*, 67: 169-182.
- Cushing, D. H. 1982. *Climate and fisheries.* Academic Press. London. pp. 246-266.
- Dunn, J. R. and Matarese, A. C. 1986. A review of the early life history of northeast Pacific Gadoid fishes. In *Workshop on comparative biology, assessment, and management of gadoids from the Pacific and Atlantic oceans.* Seattle, 24-28 June 1985. pp. 589-628. Compiled by M. Alton. Northwest and Alaska Fisheries Center.
- Gade, H. G. 1970. Hydrographic investigation in the Oslo fjord, a study of water circulation and exchange processes. Geophysical institute, University of Bergen, Norway, report no. 24, 1970. 193 pp.
- Gargett, A. E. 1984. Vertical eddy diffusivity in the ocean interior. *J. Mar. Res.*, 42: 359-393.

- Hansen, H. and Buch, E. 1986. Prediction of year-class strength of atlantic cod (Gadus morhua) off West Greenland. NAFO Sci. Coun. Studies, 10:7-11.
- Haug, T., E. Kjørsvik, and S. Solemdal 1984. Vertical distribution of Atlantic Halibut (Hippoglossus hippoglossus) eggs. Can. J. Fish. Aquat. Sci., 41, 798-804.
- Haug, T., E. Kjørsvik, and S. Solemdal 1986. Influence of some physical and biological factors on the density and vertical distribution of Atlantic halibut (Hippoglossus hippoglossus) eggs. Mar. Ecol. Prog. Ser., 33, 207-216.
- Hjort, J. 1914. Fluctuations in the great fisheries of northern Europa viewed in the light of biological research. Rapp. P.-v. Reun. Cons. int. Explor. Mer, 20:1-228.
- Iles, T.D. and Sinclair, M.M. 1982. Atlantic herring: Stock discreteness and abundance. Science, 215:627-633.
- Iversen, S. A. 1973. Utbredelse og mengde av makrellegg (Scomber scombrus) og zooplankton i den nordlige delen av Nordsjøen i årene 1968-1972. (Distribution and abundance of mackerel eggs (Scomber scombrus) and zooplankton in the Skagerrak and northern parts of the North Sea during the years 1968-1972.) Cand.Real-thesis, University of Bergen, 71 pp. (In Norwegian)
- Kändler, R. 1949. Untersuchungen über den Ostseedorsch warend der Forschungsfahrten mit dem R.F.D. "Poseidon" in den Jahren 1925-1938. Berichte der Deutschen Wissenschaftlichen Kommission für Meeresforschung, Neue Folge 11: 162-168.
- Kendall, A. W. Jr. and Kim, S. 1989. Buoyancy of walleye pollock (Theragra chalcogramma) eggs in relation to water properties and movement in Shelikof Strait, Gulf of Alaska. In Effects of ocean variability on recruitment and an evaluation of parameters used in stock assessment models. Ed. by R.J. Beamish and G.A. McFarlane. Can. Spec. Publ. Fish. Aquat. Sci., 108: 169-180.

Kullenberg, G. 1971. Vertical diffusion in shallow waters. *Tellus*, 23, 129-135.

Pommeranz, T. 1973. Das Vorkommen von Fischeiern, in besonders von Eiern der Scholle (Pleuronectes platessa L.) in den oberflächennahen Wasserschichten der südlichen Nordsee. *Berichte der Deutschen Wissenschaftlichen Kommission für Meeresforschung*, 22: 427-444.

Riley, J. P. and Skirrow, G. 1975. *Chemical Oceanography*. Vol. 2., 2nd edition. Academic Press. London 647 pp.

Solemdal, P. and Sundby, S. 1981. Vertical distribution of pelagic fish eggs in relation to species, spawning behavior and wind conditions. *ICES CM 1981/G:77*. 27 pp.

Sundby, S. 1983. A one-dimensional model for the vertical distribution of pelagic fish eggs in the mixed layer. *Deep-Sea Research*, 30, 645-661.

Svensson, T. 1980. Tracer measurement of mixing in the deep water of a small, stratified sill fjord. *In Fjord Oceanography*, pp. 233-240. Ed. by H. J. Freeland, D. M. Farmer and C. D. Levings. NATO ASI Series. Series_IV: Marine sciences, 4,

Sverdrup, H. U., Johnson, M. W. and Fleming, R. H. 1942. *The oceans, their physics, chemistry and general biology*. Prentice-Hall, New York, pp. 481-484.

Thompson, W. F. and van Cleve, R. 1936. Life history of the Pacific halibut. (2) Distribution and early life history. *Rep. Int. Fish. Comm.* 9: 1-184

Thorpe, S. A. 1984. A model of the turbulent diffusion of bubbles below the sea surface. *J. Phys. Oceanogr.*, 14:841-854.

Westgård, T. 1989. A model of the vertical distribution of pelagic fish eggs in the turbulent upper layers of the ocean. *Rapp. P.-v. Reun. Cons. int. Explor Mer*, 191: 195-200.

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