Analytical correction for oversampled Atlantic mackerel *Scomber scombrus* eggs collected with oblique plankton tows

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Atlantic mackerel *Scomber scombrus* is a pelagic species spawning on both sides of the North Atlantic ocean. In the east, mackerel spawn off the British Isles and in the North Sea (as reviewed by Lockwood 1988 and Daan et al. 1990). In the west, mackerel spawn in the Middle Atlantic Bight (Berrien 1978) and in the Gulf of St. Lawrence (Ware 1977). Atlantic mackerel is a moderately prolific species (Bigelow and Schroeder 1953); its fecundity has been estimated at 255,000 eggs for a medium-size female (30 cm FL) in the northeast Atlantic (Lockwood et al. 1981), and at 243,000 eggs for a similar-size female in the Middle Atlantic Bight (Morse 1980).

Mackerel eggs are concentrated near the surface when the water column is thermally stratified during spawning (Coombs et al. 1983, Ware and Lambert 1985). Sette's (1943) data from the Middle Atlantic Bight indicated that 80% of mackerel eggs were in the top 10 m. In the North Sea, Coombs et al. (1981) reported that 91% of mackerel eggs were above 26 m, and that more than 85% were between 0 and 16 m. In the Gulf of St. Lawrence, de Lafontaine and Gascon (1989) indicated that 89% of mackerel eggs were within 15 m of the surface. The distribution of mackerel eggs is thus characteristically non-homogeneous in the vertical plane.

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In the Gulf of St. Lawrence and Middle Atlantic Bight, mackerel eggs are routinely surveyed for stock assessment purposes (e.g., Castonguay and Grégoire 1989, Berrien 1990). Surveys are carried out with oblique plankton tows, with bongo nets as described by Posgay and Marak (1980). However, accuracy of oblique plankton tows is known to be sensitive to nonhomogeneous vertical distribution of the sampled organisms (Smith and Richardson 1977). Ideally, there should be no hesitation at the surface when retrieving the net, as it would lead to a severe oversampling of the surface layer where the eggs are concentrated (Posgay and Marak 1980, Smith et al. 1985). In practice, it is difficult not to drag the plankton net at the surface for at least a few seconds; when the net is retrieved, it reaches the surface several meters behind the block, and is dragged at the surface until directly under the block, where it can be lifted out. During such dragging at the surface, the mouth of the net is typically nearly all submerged and samples the surface layer. It is usually assumed that such oversampling at the surface leads to a negligible bias in estimates of abundance.

In this paper, the bias caused by an oversampling of surface water on the calculated abundance of mackerel eggs is analyzed. An analytical correction for this bias is derived and applied to empirical data from a mackerel egg survey held in the Gulf of St. Lawrence in 1990 to reevaluate the annual production of eggs. Also, some potential effects of oversampling surface water are evaluated when computing total abundance and mortality rates of near surface organisms.

Bias in computed egg abundance caused by oversampled surface water

Distribution of mackerel eggs

Concentrations of mackerel eggs are highest near the surface and decrease rapidly with depth. Sundby (1983) reported that under assumptions applicable in the present study, a negative exponential model (as Eq. 1, below) was appropriate to describe the vertical distribution of mackerel eggs. Ware and Lambert (1985) also concluded that the vertical distribution of mackerel eggs was best described by a negative exponential model. Data on the vertical distribution of mackerel eggs presented by Sette (1943) and by de Lafontaine and Gascon (1989) were fitted to negative exponential models; in both cases, over 90% of the variance in the egg distribution was explained. Therefore, a negative exponential model is appropriate to describe the distribution of mackerel eggs in the vertical plane.

Sampling mackerel eggs

Let the abundance of a population of eggs in a body of water decrease from the surface following an exponential model:

$$\frac{dN(z)}{dz} = -kN(z) \qquad (1)$$

where $N(z)$ = concentration of eggs in number per volume at depth z, and k = rate constant. Upon integration of Eq. 1, the concentration of eggs at depth z is given by

$$N(z) = N_0\, e^{-kz}, \tag{2}$$

where N_0 = concentration of eggs at the surface. When integrating Eq. 2, the total number of eggs (N_a) in number per surface area in this body of water is given by

$$N_a = \int_0^{\infty} N_0\, e^{-kz}\, dz = \frac{N_0}{k}. \tag{3}$$

If an oblique plankton tow (Fig. 1A) is made through this distribution of eggs with a net of radius a, and a centered depth of α, the total number of eggs collected (N_H) will be equal to

$$N_H = \tag{4}$$

$$\int_0^{L_1} \int_{\alpha-a}^{\alpha+a} \int_{-\sqrt{a^2-(z-\alpha)^2}}^{+\sqrt{a^2-(z-\alpha)^2}} N(z)\, dydzdx_1$$

$$+ \int_0^{L_2} \int_{\alpha-a}^{\alpha+a} \int_{-\sqrt{a^2-(z-\alpha)^2}}^{+\sqrt{a^2-(z-\alpha)^2}} N(z)\, dydzdx_2,$$

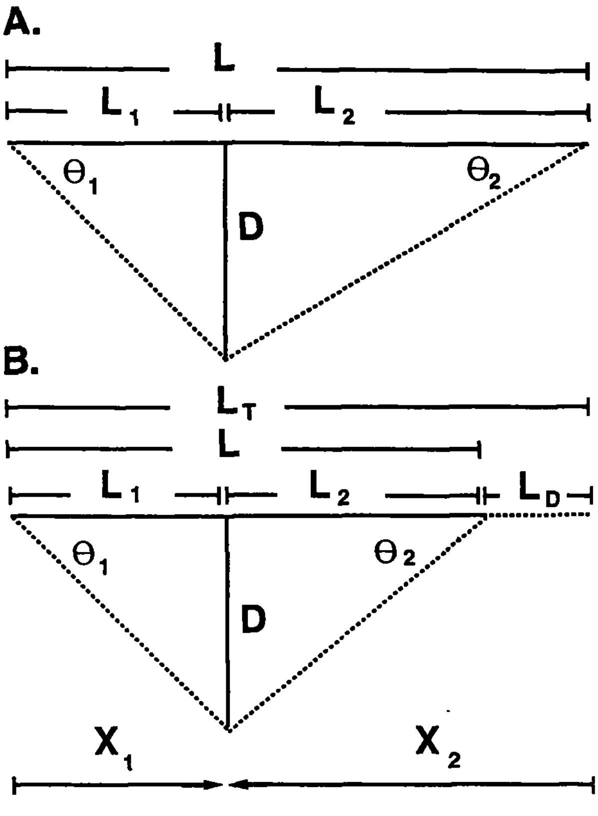

Figure 1

Path (broken line) of net during an oblique plankton tow: L's represent length components of the tow along horizontal references x_1 and x_2; D is the maximum depth of sampling, and θ's represent angles between path of net and horizon. In (A), the net is recovered upon reaching the surface; in (B), the net is dragged at the surface along L_D before recovery.

where x_1 is the horizontal distance from the start of the tow and x_2 is the horizontal distance from the end of the tow (Fig. 1A), and where z and y represent the vertical and horizontal openings of the net, respectively. Integrating Eq. 4 over the limits on z and y (as in D'Amours 1988),

$$N_H \approx \left[1 + \frac{(ka)^2}{8}\right] \left(\int_0^{L_1} N_0\, e^{-kz}\, dx_1 + \int_0^{L_2} N_0\, e^{-kz}\, dx_2\right). \tag{5}$$

The term ka originates from the slight difference between the position of the geometric center of the net and the position of the center of abundance of the eggs within its opening (D'Amours 1988). Defining, $\tan\theta_i = \frac{D}{L_i}$, where D is the maximum depth of the tow, Eq. 5 can be rewritten as

$$N_H \approx \left[1 + \frac{(ka)^2}{8}\right] \left(\int_0^{L_1} N_0\, e^{-k \tan\theta_1 x_1}\, dx_1 + \int_0^{L_2} N_0\, e^{-k \tan\theta_2 x_2}\, dx_2\right), \tag{6}$$

Evaluating Eq. 6 for kD>>0,

$$N_H \approx \frac{N_o}{k}\left(\frac{L}{D}\right)\left[1 + \frac{(ka)^2}{8}\right], \qquad (7)$$

where $L = L_1 + L_2$, and is the total horizontal length of the tow (Fig. 1A). It can now be seen that when the number of eggs collected in an oblique plankton tow (Eq. 7) is multiplied by the ratio D/L, and when the product ka is small, an approximation of Eq. 3 is obtained, which is a measure of the local abundance of eggs in number per surface area. The procedure of multiplying the total number of eggs collected in the oblique tow (equation 7) by the ratio of its maximum depth to its total horizontal length (D/L), is equivalent to the standardization procedure described by Smith and Richardson (1977). To obtain estimates of abundance in number per surface area, the standardization procedure consists of multiplying the number of eggs collected by the ratio of the maximun depth attained during the tow to the volume of water filtered. This standardization procedure is valid if all depth strata are sampled equally.

Now assume the same population of eggs, but where the net is dragged at the surface while being readied for recovery at the end of the tow. The length of drag at the surface is represented by L_D in Figure 1B. Along L_D, the mouth of the net is centered at depth α, which is equal to its radius a; i.e., oversampling occurs in the layer of water immediately below the surface, as deeply as the diameter of the net. Over L_D, the net will collect a number of eggs (N_S) equal to

$$N_S \approx L_D \int_{\alpha - a}^{\alpha + a} \int_{-\sqrt{a^2 - (z-\alpha)^2}}^{+\sqrt{a^2 - (z-\alpha)^2}} N(z)\, dydz, \qquad (8)$$

which is approximated by (as in D'Amours 1988)

$$N_S \approx N_o\, e^{-k\alpha} L_D \left[1 + \frac{(ka)^2}{8}\right]. \qquad (9)$$

The total number of eggs (N_T) collected during an oblique tow, where the net is dragged at the surface at the end, will then be equal to the sum of N_H (Eq. 7) and N_S (Eq. 9):

$$N_T \approx \frac{N_o}{k}\left(\frac{L}{D}\right)\left[1 + \frac{(ka)^2}{8}\right] + N_o\, e^{-k\alpha} L_D \left[1 + \frac{(ka)^2}{8}\right]. \qquad (10)$$

The component N_S will add to the number of eggs collected, and its inclusion in the standardization procedure will result in a systematic overestimation of the abundance of eggs per surface area. When Eq. 10 is standardized with L_D included in the total length of the tow (L_T in Fig. 1B), and the result divided by the true theoretical abundance of eggs (Eq. 3), an expression is obtained which is the ratio (B) of the biased abundance to the true abundance of eggs:

$$B \approx L + D\left(k\, e^{-k\alpha} L_D \left[1 + \frac{(ka)^2}{8}\right]\right). \qquad (11)$$

Removal of bias from computed abundance of mackerel eggs

Assumption of constant filtration efficiency

In Eq. 11, L and L_D can be replaced by the proportion of the total duration of the tow they represent, under the assumption of constant filtration efficiency. This assumption is required to use tow time as a measure directly proportionnal to amount of water filtered, so as to separate L and L_D in Eq. 11. However, as pointed out by Smith and Richardson (1977), the filtration efficiency of a plankton tow declines typically with the duration of the tow, as the accumulated plankton reduces the porosity of the net. They warned that the diminishing efficiency of a net could result in an undersampling of surface water. To verify whether such undersampling of surface water occurred, which would offset oversampling at the end of the tow, the time-course of the efficiency of the plankton net must be assessed.

If filtration efficiency diminishes with time, the volume filtered per unit time will diminish with increasing tow duration. The residuals about a straight line fitted on the values of volume filtered against tow duration would then show a decreasing pattern of departure from linearity. The volumes filtered for the tows in the Gulf of St. Lawrence in 1990 were regressed against their respective total duration. The residuals of this regression did not indicate a decreasing de-

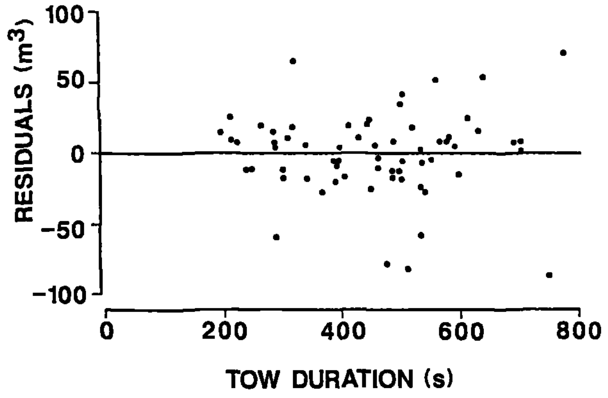

Figure 2

Residuals of a linear regression of volume filtered against tow duration of oblique plankton tows, from a mackerel egg survey held in the Gulf of St. Lawrence in 1990.

parture from linearity; somewhat unexpectedly, a tendency towards an increasing departure from linearity could be detected (Fig. 2). Therefore, it can be concluded that no surface undersampling occurred as a result of diminishing filtration efficiency. The apparent increasing departure from linearity can be explained by the fact that long tows (e.g., duration of 10 minutes) are deeper, i.e., well below the stratum where mackerel eggs are abundant. During short tows (e.g., duration of 6 minutes), the net is towed mainly in the stratum were eggs are present, and the filtration efficiency is less, though stationary, than in water devoid of eggs. During long, deep tows, more time is spent below the stratum containing mackerel eggs, and proportionally more free-flowing water is filtered there.

Correction of survey data

In Eq. 11, a rate constant k must be introduced to describe the distribution of the sampled organisms in the vertical plane. For the purpose of the demonstration, a rate constant $k = 0.15/m$ was selected as representative of all mackerel egg stages at all stations; as discussed below, this rate constant is a representative value extracted from the literature on mackerel egg distribution. During the mackerel egg survey carried out in the Gulf of St. Lawrence in late-June and early-July 1990, the total duration of each oblique tow was measured, as well as the duration of the period during which the Bongo net was dragged at the surface before recovey (F. Grégoire, unpubl. data). The period of drag at the surface started when the net was visually spotted at the surface and ended when the net was lifted out of the water. From those measurements, values of L and L_D were calculated in percent of total tow time. With a rate constant $k = 0.15/m$, a net radius $a = 0.305$ m, a centered depth $\alpha = 0.305$ m along L_D, and a measured maximum depth D, a value of the degree of bias B was calculated for each tow as per Eq. 11. The corrected abundance of eggs was obtained by multiplying the computed biased abundance by [100%/B]. Using uncorrected and corrected abundances of eggs at each station, two total annual productions of mackerel eggs were computed for the Gulf of St. Lawrence in 1990 following the procedures of Ouellet (1987). The totals were 6.77×10^{14} eggs with uncorrected abundance, and 5.63×10^{14} eggs with corrected abundance. The difference of 1.14×10^{14} eggs, with a mean fecundity of 300,000 eggs and a sex ratio of 1:1, amounted to 7.6×10^8 mature mackerel.

The parameter D used in the above calculations was measured accurately with a bathymeter mounted on the plankton net. If triangulation had been used, where D is estimated by the amount of wire paid out and the angle subtended at the block, another source of bias would have been introduced owing to the approximative nature of the method. Assume a population of mackerel eggs in a body of water where $k = 0.15$ and $N_0 = 750$; if sampled to a depth D of 50 m with a net of radius $a = 0.305$ on a transect where $L = 1000$ m, a total of 100,000 eggs will be collected (Eq. 7). Standardization of this result by the ratio of D to L shows that the abundance of eggs is 5000 eggs/m^2. Had D been underestimated by 10% at 45 m, the abundance of eggs would have been underestimated also by 10% at 4500 eggs/m^2. If the same tow is repeated, but with $L_D = 75$ m and $\alpha = 0.305$ m, a total of 153,775 eggs will be collected. Standardization of this result with D correctly evaluated at 50 m indicates an abundance of 7152 eggs/m^2; with D underestimated by 10% at 45 m, standardization indicates an abundance of 6437 eggs/m^2. These examples show how an underestimation of 10% of D results in an abundance of eggs equal to 90% of the real value, and how a 7% (75 m/1075 m) oversampling at the surface results in an abundance of eggs equal to 143% of real value. Also, they show that when both an underestimation of D and an oversampling of the surface layer occur during a tow, the effects of both biases on the estimate of abundance are opposite, but not symmetrical, with the effect of the oversampling at the surface much more important than that from the underestimation in D.

A degree of bias (B in Eq. 11) was computed for various combinations of L_D (with $L = 100\% - L_D$) and rate constant k, with $a = \alpha = 0.305$ m, and $D = 50$ m (Fig. 3A). The degree of bias caused by an oversampling of surface water is a function of the time of sampling at the surface, and of the degree of contagion of the eggs near the surface, as described by the parameter k. For

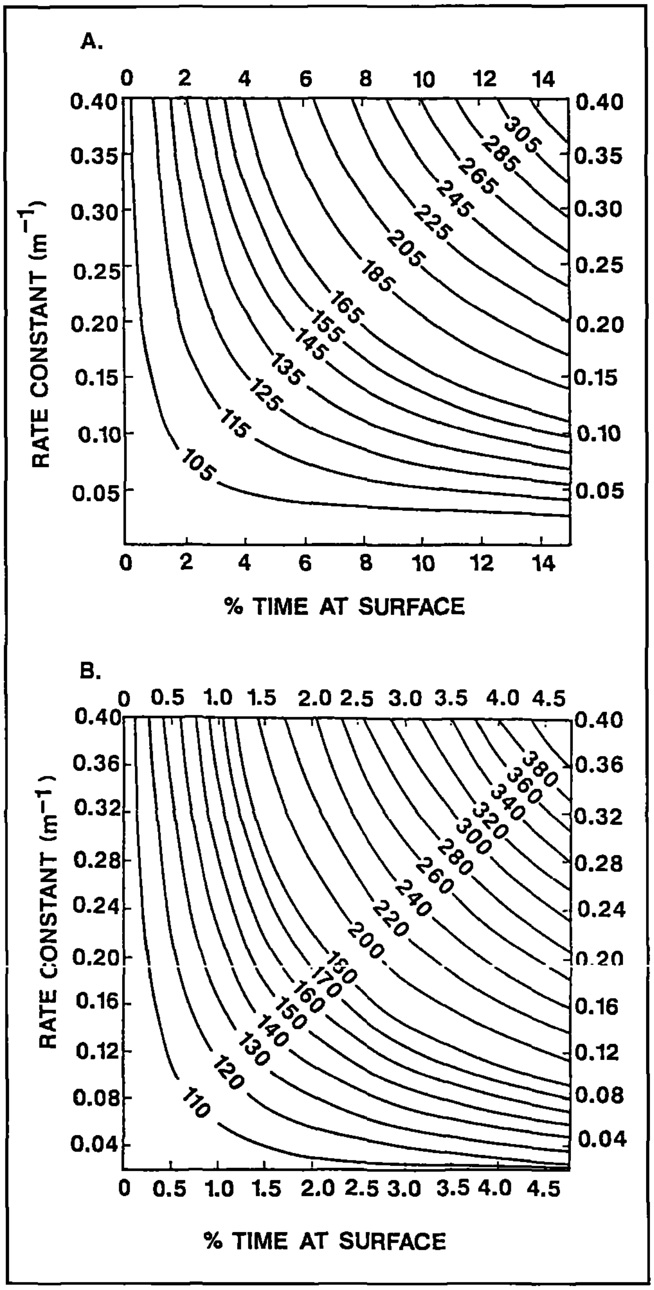

Figure 3

Isopleths (in %) of the ratio of biased abundance to true abundance per surface area of a theoretical population of fish eggs. The isopleths were computed for variable rate constants k of a negative exponential model describing the vertical distribution of the eggs, and for varying degree of oversampling surface water during an oblique plankton tow, L_D, expressed as percent of the total duration of the tow. In (A), the maximum sampling depth was set at 50 m; in (B), the maximum sampling depth was set at 200 m. All other parameters equal in (A) and (B).

example, with a sampling time at the surface representing 7% of the total duration of the tow, and with a rate constant of 0.15/m, the calculated abundance will be 140% of the real value. With eggs highly concentrated near the surface, that is with high values of k, even briefer towing times at the surface will still result in severe bias.

The degree of bias B was also computed for similarily varying k and L_D, again with $a=\alpha=0.305$ m, but with maximum depth D increased to 200 m (Fig. 3B). For a rate constant of 0.15/m as in the previous example, but with towing time at the surface representing only 2% of the total duration (e.g., 12 seconds at the surface for a total tow time of 10 minutes), the calculated abundance of eggs will again be 140% of the real value. This somewhat counterintuitive result stems from the fact that by sampling deep strata, the fraction of the tow occurring in the stratum where eggs are present is proportionally smaller. As a result, brief times of oversampling at the surface have proportionally more effect on the calculated abundances of eggs than when the tow extends only to shallow strata.

Effects of oversampling surface water on variance of total abundance and on mortality rate

Effect on variance

Since the length of dragging at the surface is likely to vary (as a function of weather, crew handling of the net, etc.), a variance will be introduced in the computation of the total abundance of eggs over the studied body of water. It was assumed that the abundance of eggs (5000 eggs/m^2) was constant over the surface of a theoretical body of water where numerical experiments were carried out. Ten oblique tows were made in this theoretical body of water, with $L=1000$ m, $a=\alpha=0.564$ m, and $k=0.2$/m, which are convenient values for illustrative purposes. A different length of drag at the surface (L_D) was assigned randomly to each tow; ten random numbers were multiplied by an arbitrary length of 6 m and the resulting L_D's were 6 (×2), 12, 24 (×3), 30, 36, 48, and 54 m. Ten estimates of abundance of eggs per unit surface area were calculated, and the mean was 5994 eggs/m^2, with 95% confidence intervals of 5646–6342 eggs/m^2. This illustrates that small and variable lengths of drag at the surface bias the estimated abundance over the whole body of water, and add a substantial margin of uncertainty to the estimate of local abundance.

In another numerical experiment, the abundance of eggs was again assumed constant throughout at 5000 eggs/m^2, except this time the degree of contagion near the surface was made variable, i.e., the rate constant k varied randomly within bounds. Ten transects were carried out through these distributions of eggs, with $L=1000$ m, $a=\alpha=0.564$ m, and the length of drag at the surface (L_D) was held constant at 50 m. For each tow, a random value was assigned to the rate constant k: ten random numbers were multiplied by 0.1/m, and added to 0.15. The resulting values were 0.15, 0.16, 0.17 (×2), 0.20 (×2), 0.21 (×2), 0.22, 0.23 (×2), and the corresponding values of N_0 were adjusted so that $N_0/k=5000$ eggs/m^2. Ten estimates of abundance of eggs per unit surface area were calculated, and the mean was 6876/m^2, with 95% confidence interval of 6713–7039 eggs/m^2. This indicates that even when maintaining a constant length of drag at the surface, similar problems of bias and variance still arise when the degree of contagion of the eggs varies.

Effect on mortality rates

Again for numerical experiments, the abundance of eggs at a theoretical station was assumed to be 5000 eggs/m^2, with $N_0=475/\mathrm{m}^3$, and $k=0.095$/m (i.e., $475/0.095=5000$). An oblique tow with $L=1000$ m, $D=50$ m, $L_D=50$ m, and $a=\alpha=0.564$ m, was made through this concentration of eggs at time t_0, and the biased abundance was calculated to be 5873/m^2. For the purpose of the demonstration, it was assumed that the eggs suffered no mortality. Some time later at time t_1, the abundance of eggs was still the same, but they were closer to the surface, with $N_0=950/\mathrm{m}^3$ and $k=0.19$/m (i.e., $950/0.19=5000$). The same oblique tow in this slightly rearranged concentration of eggs yielded a biased estimate of abundance of 6806/m^2, a relative increase of nearly 16% compared with the value at t_0, and an absolute bias of over 36%. In real situations, then, an increase in the degree of vertical contagion of the eggs over a sampling period could lead to an underestimation of the mortality rate if the surface water is oversampled, or to an overestimation if the degree of contagion decreases.

Conclusion

The oblique tow is a convenient method to obtain an estimate of abundance of eggs over a body of water. However, in actual operating conditions, it is rarely possible to carry out an oblique tow without dragging the net at the surface for some period of time, which may introduce a large bias in the estimate of abundance. The first practical recommendation to avoid such bias is to evaluate the assumption that a brief drag time at the surface will cause only a small bias in the estimation of abundance. If eggs are equally distributed over considerable depth, or concentrated in deeper water, this assumption is valid. If not, action should be taken to avoid dragging the net at the surface. If this is impossible, a measure of the amount of oversampling at the surface, and of the rate constant k, should be used to remove the bias from the data following Eq. 11.

In this study, the percent time of the tow spent at the surface was used as a measure of the amount of oversampling at the surface; this information is readily recorded in the field. However, the constant k describing the distribution of eggs had to be approximated from data available in the literature. Ware and Lambert (1985) reported values of k ranging from 0.1 to 1.1; they further indicated that variations in k were related to the steepness of the thermal gradient in the water column, the development stage of the eggs, and the degree of wind-induced mixing. Data on mackerel egg distribution by deLafontaine and Gascon (1989) indicated a mean value $k=0.1$, with the lowest values for the most recently spawned eggs. Data on mackerel egg distribution by Sette (1943) indicated a higher mean value $k=0.17$, but with the highest values for the most recently spawned eggs. Differences in mean values of k as well as development-stage specific values may result from differences in local wind conditions as well as in differences in local water density. As discussed by Sundby (1983), the shape of a vertical distribution of mackerel eggs will be determined by the difference of density between the egg and the surrounding water, and by the degree of wind-induced mixing. The relationship reported by Sundby (1983) between wind velocity and vertical eddy diffusivity coefficient of mackerel eggs indicates that the rate constant k should diminish as the state of the sea increases. The definite application of the analytical correction proposed herein will require more site-specific studies on the factors affecting the vertical distribution of mackerel eggs and determining the value of k. Nonetheless, the value $k=0.15$ used in this study is representative of realistic conditions in the field, and can be considered as a conservative estimate of the degree of vertical contagion of mackerel eggs. With more reliable values of k, the simple correction procedure suggested in this study could help increase the accuracy of biological parameters based on data from fish egg surveys where the technique of the oblique plankton tow has been used.

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