THE POSSIBLE INFLUENCE OF WARM CORE GULF STREAM RINGS UPON SHELF WATER LARVAL FISH DISTRIBUTION

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ABSTRACT

We propose a simple one-dimensional model for examining the impact of warm core rings upon the larval fish distribution and abundance over the continental shelf off the northeastern United States. The model includes (in a cross-shelf averaged sense) the loss of larvae due to biological causes of mortality, the advective transport of larvae due to the mean down-shelf currents, and the changes in larval density produced by the on-shelf or off-shelf flows occurring when a ring approaches the shelf-slope front. The results of this highly idealized model indicate that the decreases in larval abundance caused by cross-shelf flows may be as large as those caused by biological factors and, furthermore, the effects are strongly dependent upon the rate of motion of the ring. A stationary ring may cause a 20 to 50% drop in abundance, depending on the strength and size of the ring and on the longshore velocity in the shelf water. When the ring is slowly moving, the impact can be even greater: a patch of larvae being advected downshelf by the longshore current could, when catching up to the back side of an eddy, essentially be swept off the shelf, decimating the patch.

Model predictions are compared with historical MARMAP data of larval cod and haddock density in the Georges Bank area. There does appear to be a relationship between the frequency of ring interaction with Georges Bank and the subsequent year-class strength of cod and haddock stocks. Thus we suggest that further investigation of the impacts of rings is warranted, both from the observational and the theoretical viewpoints. These studies should include detailed measurements in entrainment features, further analysis of ring-Bank interactions factoring in the closeness of the ring, the strength of its currents and its translation rate, and more detailed modelling of entrainment events and larval fish ecology.

Warm core rings form in the Slope Water region between the North American continental shelf and the Gulf Stream. These rings are eddies 100 to 200 km in diameter which result when a Gulf Stream meander separates from the main current. The potential impact of warm core rings upon the continental shelf ecosystem has become more apparent with routine satellite infrared images of the sea surface. Charts of sea surface temperature prepared from these images, e.g., Figure 1, (Halliwell and Mooers 1979; Chamberlin 1981) frequently show rings entraining cold water from the continental shelf. This interpretation is supported by ship observations and current meter records of water transport onto and off the continental shelf induced by warm core rings (Morgan and Bishop 1977; Smith 1978; Smith and Petrie 1982). Physical and biological oceanographers have long been aware of occasional intrusions of anomalously warm water onto Georges Bank (for a review, see Bolz and Lough 1981), which are now likely to be attributable to warm core ring activity. In 1961 Colton and Temple hypothesized that large numbers of larval fish of shelf species can be drawn off Georges Bank into warmer Slope Water where they succumb to unfavorable environmental conditions (c.f. Laurence and Rogers 1976).

The purpose of this paper is to examine theoretically the possible influence of warm core rings on the abundance and distribution of larval fish in continental shelf waters off the northeastern United States, in particular the shelf region associated with cod and haddock spawning on Georges Bank. Our study makes estimates of the advective losses of larvae because of the entrainment of shelf water by an eddy and predicts changes in larval density (the observable quantity in ichthyoplankton surveys) because of the onshore and offshore flows induced by a ring. We also consider the possible biological causes of mortality (e.g., predation, physiological death). In other words we wish to estimate the relative importance of the physical and biological losses via a mathematical model. While our model does not describe either in great detail, we feel that it does indicate the importance of ring-induced entrainment and the dependence of this effect upon the speed of translation of the ring, the width over which it interacts with the shelf, and the strength of its currents at the shelf break. We compare our model predictions of the spatial and temporal distributions of larval fish

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with the historical MARMAP (Maritime Resources Monitoring, Assessment and Prediction) data of larval cod and haddock distributions in the Georges Bank area (Smith et al. 1979). We also present an apparent relationship between years of low warm core ring activity and strong year classes in the fishery.
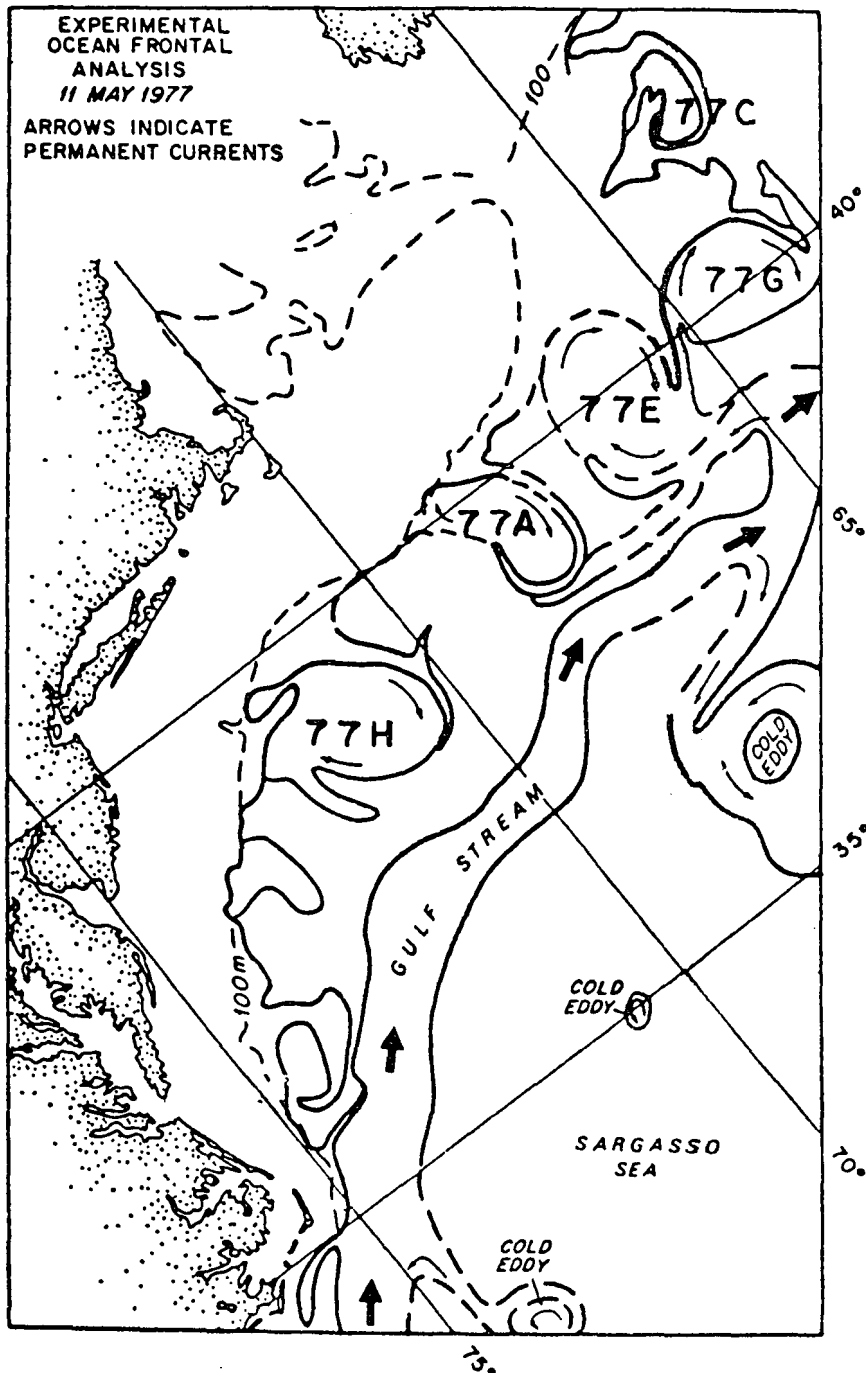

FIGURE 1.—Distribution of warm core rings off the U.S. northeast coast during the week of 11 May 1977. The chart was produced by the U.S. Naval Oceanographic Office from infrared satellite images.

Finally, we make recommendations for further investigations of the influence of warm core rings on the northeast coast marine ecosystem.

Our very simplified modelling approach to the problem of resolving biological distributions in a variable oceanic flow regime could, with proper reparameterizations, be applied to estimating the impact of rings on chemical distributions as well – an example would be determining the distribution of pollutants dumped in deepwater dumpsite 106. For variables which do not behave as passive particles in the flow, the model has limitations. Vertical migration behavior by fish larvae may play an important role in their distribution which is not resolved by our preliminary modelling. Other potentially important details, such as the mechanism for mixing on the shelf, have also not been included in this first, simplified calculation. Nevertheless, we feel that the results are extremely suggestive, indicating ways to examine existing data sets and hypotheses to be tested in future field studies.

THE MODEL

There are many possible approaches to modelling the effects of rings upon fish larvae, ranging from simple order-of-magnitude estimates to complex physical models which predict the mean and varying currents from winds, heating, topography, and coastlines. The water motions could then be coupled with complex biological models of spawning, predation, growth, and mortality. However, we are not yet at the stage where such a full-scale calculation is really justifiable; we do not understand enough about the physics of the shelf-slope region and the rings or enough about larval fish biology to ensure that only important processes are included and that these are being properly represented in our numerical model. In addition, the questions we wish to address are fairly simple ones: How large could the impact of rings upon larval fish populations be and how do these impacts depend upon the flow structure and translational speed of the rings? We, therefore, shall take the simplest approach to the problem of estimating our primary variable, the larval fish density (or abundance). The various processes which affect the population distribution will be represented in the model in an almost schematic form. The actual populations vary in all three dimensions and in time, but we shall include only the downstream and time variations in the model. Likewise, the actual current patterns are quite complicated and we choose only to represent the impact of the ring-induced currents by a specification of the flow at the outer edge of the shelf, with onshore flow ahead of the ring and offshore flow behind the eddy. The mean downshelf drift currents will also be included. The biological processes of predation, physiological mortality, and metamorphosis out of the planktonic larval stage will be represented simply as a loss rate μ which will be assumed to be independent of space or time. With these simplifications, the general equation governing the density $n(x,y,z,t)$ of the planktonic larvae can be reduced to a manageable form

$$\frac{\partial}{\partial t} n + \frac{\partial}{\partial x} un + \frac{\partial}{\partial y} vn + \frac{\partial}{\partial z} wn = -\mu n. \qquad (1)$$

We shall use the geometry shown in Figure 2 with x the downshelf coordinate, y the offshore coordinate,
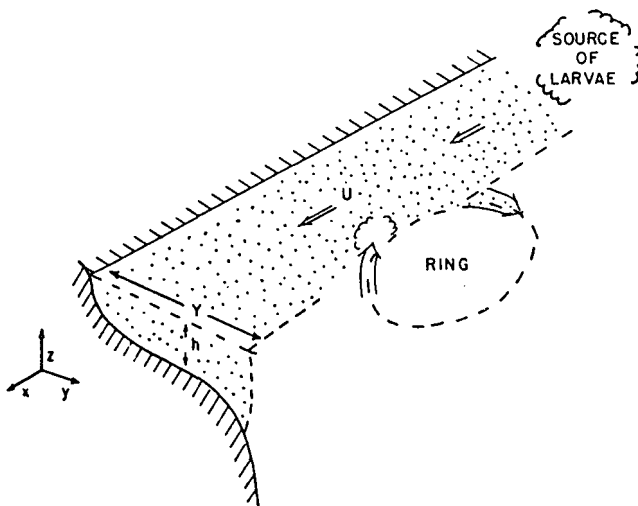

FIGURE 2. – Schematic diagram of the geometry assumed in the mathematical model. Y is the shelf width, h is the average depth, and U is the average longshore velocity of the shelf water.

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and z positive upwards. We shall assume that there is a source of larvae somewhere upstream of $x = 0$, e.g., the spawning grounds on Georges Bank, leading to a specified flux of organisms into the domain at the $x = 0$ boundary. Alternatively, and more conveniently, the upstream spawning can be thought of as leading to a specified abundance of organisms $N_0(t)$ at $x = 0$.

Although we could, in principle, specify the three-dimensional currents and the source function N_0 from either measurements or models, the available data and models are not really adequate for this to be possible. We have chosen, therefore, to simplify the model further by averaging the larval fish density vertically and across the shelf

$$N(x,t) = \frac{1}{hY} \int_0^Y \int_{-h}^0 n(x,y,z,t)\, dz\, dy. \tag{2}$$

Here Y is the width of the shelf and h is the depth (both assumed independent of x). We can find the equation governing this N by averaging Equation (1) over the shelf width and depth, applying boundary conditions of zero flux through the upper and lower surfaces and the continent side of the domain. This gives

$$\frac{\partial}{\partial t} N + \frac{\partial}{\partial x} \left[\frac{1}{hY} \int_0^Y \int_{-h}^0 un\, dz\, dy \right]$$
$$+ \frac{1}{hY} \int_{-h}^0 v(x,Y,z,t)\, n(x,Y,z,t)\, dz = -\mu N. \tag{3}$$

The downstream variation of Y and h has been neglected although it is not too difficult to include it. The term representing downstream advection of larvae will be simplified by assuming that the cross-shelf mixing of larvae is sufficiently intense that n is uniform in y. The along-shelf advection term then becomes

$$\frac{\partial}{\partial x} \frac{1}{hY} \int_0^Y \int_{-h}^0 un\, dz\, dy \cong \frac{\partial}{\partial x} UN;$$

$$U(x,t) = \frac{1}{hY} \int_0^Y \int_{-h}^0 u(x,y,z,t)\, dz\, dy. \tag{4}$$

Similarly, we shall ignore vertical variations in n at the shelf edge so that the flux off the shelf becomes

$$\frac{1}{hY} \int_{-h}^0 v(x,Y,z,t)\, n(x,Y,z,t)\, dz \cong \frac{N_e V_0}{Y};$$

$$V_0(x,t) = \frac{1}{h} \int_{-h}^0 v(x,Y,z,t)\, dz. \tag{5}$$

Here $V_0(x,t)$ is the depth-averaged onshore-offshore flow (positive offshore) and N_e is the depth-averaged larval fish density in the water which is moving onto or off of the shelf. (Vertical migratory behavior which is somehow correlated with vertical shears would alter this parameterization of the outflowing flux of larvae.)

When there is onshore or offshore flow, the averaged velocity along the shelf cannot be constant. The variations in U can be calculated from the conservation of fluid volume integrated across the shelf

$$\frac{\partial}{\partial x} \left[\frac{1}{hY} \int_0^Y \int_{-h}^0 u\, dz\, dy \right] + \frac{V_0}{Y} = 0$$

which implies $\dfrac{\partial U}{\partial x} = -\dfrac{V_0}{Y}$. \qquad (6)

Finally we must introduce a parameterization for the density of larvae carried on or off the shelf at the edge N_e in terms of the average density $N(x,t)$. It is assumed that the Slope Water pushed onto the shelf by the ring is devoid of shelf fish larvae. If we presume that this Slope Water mixes completely with the shelf water, then the water leaving the shelf carries larvae with density N, as sketched in Figure 2. These considerations suggest that the entrainment term can be modelled by

$$N_e = \begin{cases} 0 & \text{for } V_0 < 0 \\ N & \text{for } V_0 > 0 \end{cases}. \tag{7}$$

(Again, we must remark upon the limitations of the present calculation; certainly the shelf water is not thoroughly mixed and the density of the outflowing larvae is much more complicated and perhaps smaller on the whole than this formula would suggest. We hope that our results will spur further modelling and observational efforts to assess the processes we have been forced to represent so crudely.) When all of these simplifications are gathered together, the approximate equations for the average density of larvae $N(x,t)$ become

$$\frac{\partial}{\partial t} N + \frac{\partial}{\partial x} (UN) + \begin{cases} 0 & \text{for } V_0 < 0 \\ \dfrac{V_0 N}{Y} & \text{for } V_0 > 0 \end{cases} = -\mu N$$

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$$\frac{\partial U}{\partial x} = -\frac{V_0}{Y} \qquad (8)$$

with the boundary condition

$$N(0,t) = N_0(t). \qquad (9)$$

STATIONARY EDDIES

In nature, there are pulses of larvae entering the domain as the fish spawn. In addition, the shelf-edge velocities $V_0(x,t)$ are changing as mesoscale eddies and Gulf Stream warm core rings impinge upon the shelf. We shall present in the section on moving eddies several numerical solutions of Equations (8) and (9), simulating this complex situation. However, in order to fully understand the importance of the rings and eddies in determining the fish larvae's spatial distribution, it is first useful to consider some simpler, analytically tractable cases. We shall begin by discussing the distributions which occur when the shelf-edge flows are not changing with time, i.e., the eddies are stationary. This problem also has bearing on the real situation south of Long Island, where rings may often stop for considerable lengths of time.

As a first example, consider the larval fish distribution which would occur in the absence of any biological loss processes ($\mu = 0$) and when the source term N_0 is independent of time. The resulting equations

$$\frac{\partial}{\partial x}(UN) = \begin{cases} -V_0 \dfrac{N}{Y} & \text{for } V_0 > 0 \\[2mm] 0 & \text{for } V_0 < 0 \end{cases},$$

$$\frac{\partial U}{\partial x} = -\frac{V_0}{Y} \qquad (10)$$

can be solved readily

$$N = \begin{cases} N_0 \dfrac{U_0}{U} = \dfrac{N_0 U_0}{U_0 - \displaystyle\int_0^x \dfrac{V_0}{Y}} & \text{if } V_0 < 0 \qquad (11a) \\[4mm] N_0 & \text{if } V_0 > 0 \text{ and } U_0 > \displaystyle\int_0^x \dfrac{V_0}{Y} \qquad (11b) \\[4mm] 0 & \text{if } V_0 > 0 \text{ and } U_0 < \displaystyle\int_0^x \dfrac{V_0}{Y} \qquad (11c) \end{cases}$$

where U_0 is the longshore velocity and N_0 is the (time-independent) population density at the upstream boundary $x = 0$. We can now see explicitly the effects of the physics alone upon the larval fish distribution. In the regions where the flow is onto the shelf (Equation (11a)), the shelf break boundary contribution to Equation (10) is zero. But the effects of the flow field are still felt in that the along-shelf flow is divergent. U increases downstream as water comes onto the shelf, spreading out the larvae and reducing their average density. In contrast, when the flow is offshore (Equations (11b) or (11c)), there are direct loss terms due to larvae being carried off the shelf. Some of the water flowing into a section are diverted offshore while some continues down the shelf, with the larvae separating in the same proportions. Thus, although there is a decreased flux down the shelf, this does not affect the density since there are no biological losses which need to be balanced by this flux. The net effect is that the physics by itself does not change the population density in regions of offshore flow (Equation (11b)). The only exception would occur when the offshore transport ($\int V_0\, dx$) is sufficiently strong so that all of the normal alongshore flow ($U_0\, Y$) is diverted off the shelf. In this case (Equation (11c)), the flow in regions farther down the shelf is reversed and the water moves up the shelf. Since this water is from regions without sources of larvae, the population density is zero.

By putting together these two results, we can construct a picture of the density of larvae in continental shelf water flowing past a stationary ring centered at $x = D$. This is shown in Figure 3. For these calculations we have used

$$V_0 = -A\,\frac{x-D}{L}\,\exp\left[\frac{1}{2} - \frac{1}{2}\frac{(x-D)^2}{L^2}\right] \qquad (12)$$

with $A = 20$ cm/s the peak offshore velocity) and $L = 20$ km (so that roughly 80 km along the shelf is strongly influenced by the ring currents). This figure
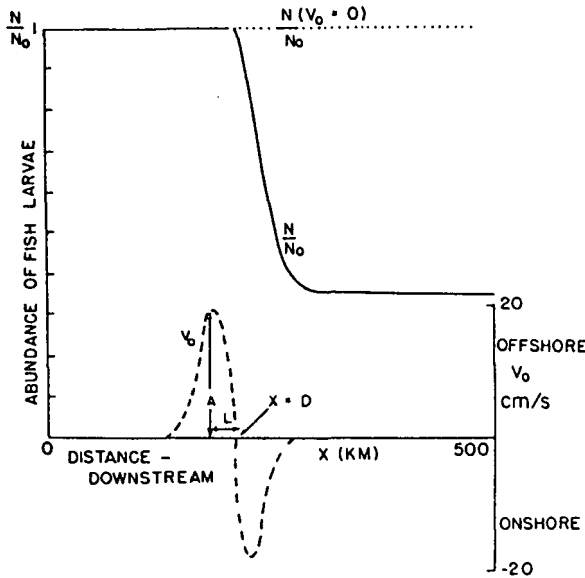
FIGURE 3.—The steady state abundance of fish larvae with distance along the shelf. This abundance is expressed as a fraction of the number of larvae continuously being produced at the spawning site, N_0. There is a 80 km wide, stationary eddy at the shelf edge, inducing onshore and offshore flows of 20 cm/s. The longshore velocity U_0 of the shelf water is 5 cm/s. Biological losses (μ) are set equal to zero. The dotted line shows the steady abundance of fish larvae with distance down the shelf when there is no eddy present.

shows only the spatial distribution of larval density in the water moving down the shelf, as affected by flow convergences or divergences associated with the physics of the ring. The flux of larvae off the shelf (not shown) is given by $V_0 \, hN_0$ in the regions where V_0 is greater than zero and amounts in total to

$$\int_0^D V_0 \, h \, N_0 \, dx \cong A \, h \, L \, N_0 \, e^{\frac{1}{2}}.$$

66% of the flux into the domain ($U_0 N_0 hY$) at $x = 0$. Next, we shall see that the physics and biology actually interact to produce a greater net impact than when either is considered separately.

For this second model problem, we shall still use a steady onshore and offshore flow pattern, but now include the biological loss term and the time-dependence in the source function N_0. When the flow is offshore or zero, the population distribution is given by

$$N(x,t) = N_0(t - \tau) \, e^{-\mu\tau} \qquad (13a)$$

where the variable τ measures the length of time necessary to reach the point x from the upstream edge of the domain. In general τ is given by

$$\tau = \int_0^x \frac{dx'}{U(x')} \qquad (13b)$$

where $U(x)$ can be found by integrating the mass conservation equation

$$U(x) = U_0 - \int_0^x dx' \, \frac{V_0(x')}{Y}. \qquad (13c)$$

In the absence of ring-induced onshore-offshore flows ($V_0 = 0$), however, τ is just equal to x/U_0 and

$$N(x,t) = N_0 \left(t - \frac{x}{U_0} \right) e^{-\mu \, x/U_0}. \qquad (13d)$$

The population at any downstream point lags that at the origin by the travel time x/U_0 and has also decayed exponentially during its travel. This solution is an important base case for understanding the distributions in a spawned patch which has not been impacted by rings.

When water is being drawn off the shelf, the along-shelf decay in concentration is again purely due to travel time, since the effect of losses off the shelf on the density is compensated for by the convergence. However the spatial density of the larvae is still noticeably altered by the offshore flow because the travel time necessary to reach any point is increased. This occurs because U is decreasing with x as a result of the advection of water off the shelf (as shown in Equation (13c)). Since U is less than U_0, the travel time τ in Equation (13b) is necessarily greater than that in the absence of the ring (x/U_0). We have sketched $\tau(x)$ for the three possible signs of V_0 in Figure 4a. These results suggest that there will be an enhanced spatial decay rate of larval density in the regions where the flow is offshore.
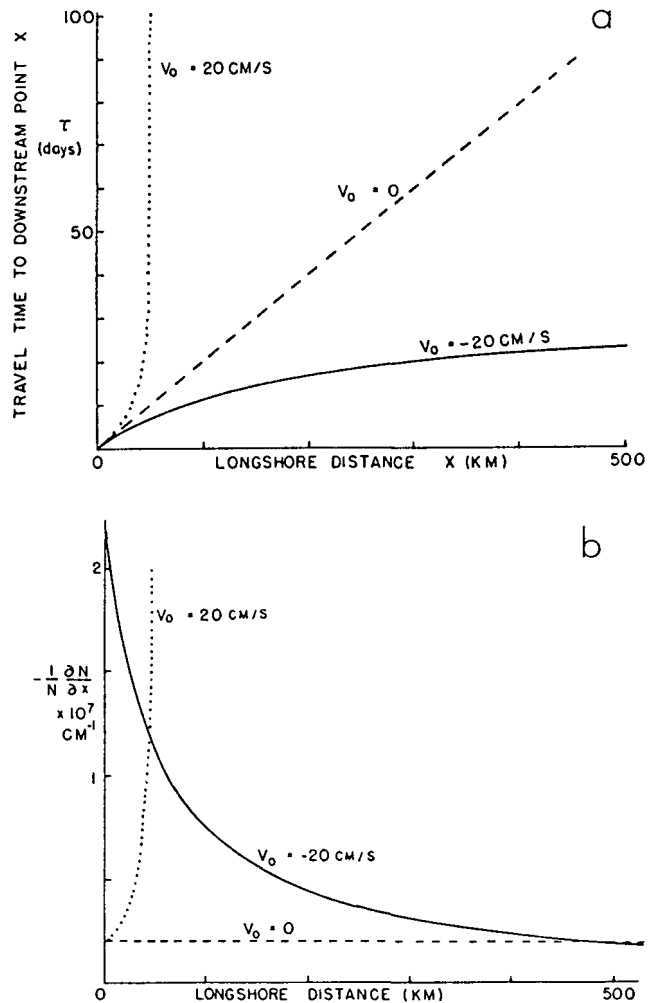
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FIGURE 4.—a) The travel time τ necessary for larvae to reach the point x down the shelf from the spawning site at x = 0. The values of τ are computed in the absence of an eddy (V_0 = 0) and when an eddy induces onshore ($V_0 = -20$ cm/s) and offshore ($V_0 = 20$ cm/s) flows. b) The rate of change in numbers of larvae N with distance down the shelf x, plotted against longshore position for the three values of V_0.

When the flow is onshore ($V_0 < 0$) we can also solve Equations (8) and (9) and find

$$N(x,t) = N_0(t - \tau)\,\frac{U_0}{U(x)}\,e^{-\mu\tau}. \qquad (14)$$

In this case, the timelike variable τ increases less rapidly with x than in the base case. This alone would lead to a slower spatial decay; however, the dilution effect (the U_0/U factor) counters this. In most cases, the dilution will be stronger than the effects of decreased transit time.

Perhaps the simplest way to see this is to consider the downstream decay rates when the source of larvae is constant in time and the onshore or offshore flows are spatially uniform. The spatial decay rates $-(\partial N/\partial x)/N$ for the three flow cases are

$$-\frac{1}{N}\frac{\partial N}{\partial x} = \begin{cases} \dfrac{\mu}{U_0} & \text{for } V_0 = 0 \\[2mm] \dfrac{\mu}{U} & \text{for } V_0 > 0 \\[2mm] \dfrac{\mu}{U} + \dfrac{1}{U}\dfrac{\partial U}{\partial x} & \text{for } V_0 < 0. \end{cases} \qquad (15)$$

We have plotted these as functions of x in Figure 4b using $\mu = 10^{-7}$ s^{-1}, $U_0 = 5$ cm/s, $V_0 = \pm 20$ cm/s, and $Y = 200$ km. With this value for μ, two-thirds of the larvae disappear from the population because of the various biological causes within 4 mo from hatching. Most values of μ in the literature (e.g., Sissenwine et al. 1983) tend to be higher (see, however, Peterson

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and Wroblewski 1984), but it is important to remember that these also include the advective losses. We have therefore chosen a smaller value of μ to reflect only biological processes; alternate values

$$\frac{N}{N_0} = \exp\left(\frac{-\mu x}{U_0}\right) \tag{16}$$

to that with the eddy

$$\frac{N}{N_0} = \begin{cases} \exp(-\mu\tau) & \text{for } 0 < x < D \\ \dfrac{U(D)}{U(x)}\exp(-\mu\tau) & \text{for } D < x < W \end{cases}, \quad \tau = \int_0^x \frac{dx'}{U(x')} \tag{17}$$

of μ will be considered shortly. The graph shows the extreme situation where the inflow or outflow is uniform over the whole downstream distance. The decay rate with distance travelled is always increased for offshore flow. For onshore flow, the decay rate can be reduced below the "no-ring" case but only very far downstream ($x > 500$ km) where the flow rate down the shelf is huge ($U = 30$ cm/s). Since onshore flows of 20 cm/s over a 500 km stretch of shelf are not likely to occur, we can conclude that the spatial decay rate will be enhanced in both the regions of onshore flow and the areas with offshore flow.

The net result, when a stream of larvae moving down the shelf and declining in density due to biological losses encounters a stationary eddy, can be calculated by combining the result for offshore flow in the region $0 < x < D$ with the one for onshore flow in $x > D$ where the ring is centered at the point $x = D$. In Figure 5 we compare the solution without the eddy

where W is the length of the shelf domain, taken to be 500 km. Most of the decrease in population density occurs in the onshore flow regime; the final density is only half of that which would occur in the absence of the eddy. In assessing the causes of the population decrease, it is clear that the physics and the biology play comparable roles: the decrease in density when there is no eddy is a factor of two during the transit down the shelf (Fig. 5). The changes in density which occur predominantly in the region of onshore flow when the currents are present, give another factor of 2.5 decrease. Note that recruitment cannot be inferred directly from these density patterns; we will address the implications for recruitment in the section on Moving Eddies below.

We summarize the impact of stationary rings for various values of the onshore-offshore flow rates and the scale length along the shelf impacted in Figure 6. Here we plot contours of the ratio of the population density far downstream of the eddy (N_∞) to that
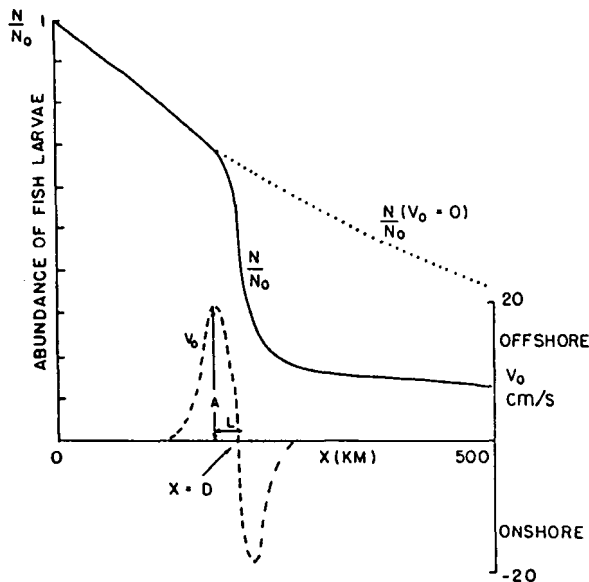

FIGURE 5. – Same as Figure 3 except biological losses ($\mu = 10^{-7}$ s^{-1}) are included.

which would be present without any cross-shelf currents (N_∞, $V_0 = 0$). This figure shows clearly the increasing impact with stronger transports onto or off of the shelf edge. There are slight differences in this ratio if the biological decay is ignored and if the cross-shelf flows occur over large distances, since the longshore flow slows down significantly. We should note that the decrease in larval fish density compared with the no-ring case depends on two nondimensional parameters $P_0 = AL/U_0Y$ and $P_1 = \mu L/U_0$. Thus for values of μ, U_0, or Y other than 10^{-7} s^{-1}, 5 cm/s, and 200 km, the graph can be read with suitable values of A and L to give the desired values for these two nondimensional numbers:

$$L_{\text{graph}} = P_1 \times 500 \text{ km} = \frac{\mu L}{U_0} \times 500 \text{ km}$$

$$A_{\text{graph}} = \frac{P_0}{P_1} \times 2 \text{ cm/s} = \frac{A}{\mu Y} \times 2 \text{ cm/s}.$$

MOVING EDDIES

In the previous examples, we have considered the changes in fish larvae distributions which occur when the shelf water flows by a stationary eddy. But rings frequently translate to the southwest, following a track between the continental slope and the Gulf Stream. The translational speeds vary considerably, ranging from a few cm/s to perhaps 10 cm/s. This along-shelf ring movement has a profound influence on the ring's contribution to decreasing the concentration of larvae – in some cases, they may be swept offshore in the entrainment flow of a slowly translating ring; in other cases the ring may catch up to, dilute, and pass the organisms. Finally, if the ring and shelf water are moving at the same rate, the larvae may never experience the impact of the ring, or alternatively may be in a region under constant influence.

The physical effects of a moving ring upon the larval fish population can be estimated readily from the previous results; it is only necessary to remember that the important quantity is the rate at which the shelf water moves relative to the eddy. If the ring is propagating westward more slowly than the westward drift of the shelf water, the organisms are in contact with the ring for longer periods of time, corresponding to a decreased value for the effective current U_0. But decreasing the effective downstream flow rate while keeping the eddy size constant is equivalent to increasing the length scale of the shelf

region influenced by the ring's cross-shelf flows while the longshore current speed is maintained. Figure 6 shows clearly that such an increase in L will cause a greater reduction in larval density downstream of the eddy. As the eddy translation rate becomes closer and closer to the flow rate on the shelf (effectively increasing L in Figure 6), the effect upon the population becomes larger and larger, until eventually the eddy is drawing all of the larvae off the shelf as it passes. This occurs when the ring's speed is great enough so that the longshore transport of water relative to the ring is smaller than the offshore transport induced by the currents at the shelf edge:

$$U_0 - c < \int_0^x \frac{V_0(x')}{Y} \, dx' \qquad (18)$$

where c is the speed of translation of the ring.

If the ring is moving faster than the shelf currents, the situation is somewhat different; now the eddy catches up to the larvae and they are first influenced by a region of onshore flows and then by offshore currents. We can calculate the impact upon the population using the same methods as were employed in deriving Equation (10). For simplicity, we consider a domain which is infinite in x and compare the population density in regions which have not felt the ring with that in regions which have passed through the ring. For a ring moving at speed c, the equations describing the effects of the currents upon the population are
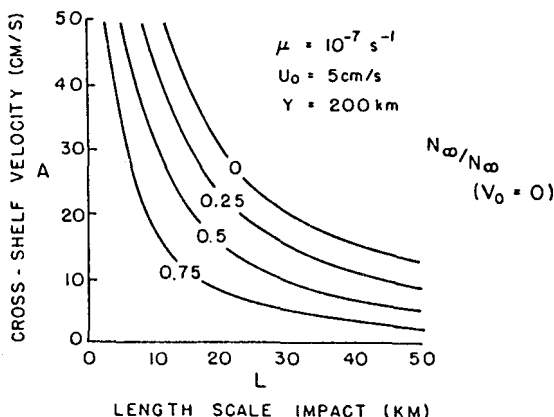

FIGURE 6. – The ratio of the number of larvae present far downstream of the eddy N_∞ to the number present if there were no eddy, $N_\infty(V_0 = 0)$. Contours of the ratio are plotted for different values of eddy size (L) and cross-shelf velocity A.

$$\frac{\partial}{\partial x}\left[(U - c)N\right] = \left\{ \begin{array}{ll} -V_0 \dfrac{N}{Y} & \text{for } V_0 > 0 \\[2ex] 0 & \text{for } V_0 < 0 \end{array} \right\} \tag{19}$$

$$\frac{\partial U}{\partial x} = -\frac{V_0}{Y}$$

and the population change caused by the eddy when the downstream flow is sufficiently faster than the ring's translation rate is

$$\frac{N(\infty) - N(-\infty)}{N(-\infty)} = \frac{1}{Y}\int_{V_0 > 0}\frac{V_0(x,0)}{U_0 - c}\,dx,$$

$$c < U_0 - \frac{1}{Y}\int_{V_0 > 0}V_0\,dx. \tag{20}$$

When the flow stagnates relative to the ring at some point, we have

$$N(\infty) = 0 \qquad U_0 - \frac{1}{Y}\int_{V_0 > 0}V_0\,dx < c < U_0 \tag{21}$$

and when the ring is moving faster than the shelf waters

$$\frac{N(-\infty) - N(\infty)}{N(\infty)} = \frac{\dfrac{1}{Y}\displaystyle\int_{V_0 > 0}V_0\,dx}{c - U_0 + \dfrac{1}{Y}\displaystyle\int_{V_0 > 0}V_0\,dx}$$

$$c > U_0. \tag{22}$$

These are plotted in Figure 7. Notice that the ring may cause substantial losses in the population, especially when its speed is roughly matched to the mean flow on the shelf.

In principle, one could write down an analytical solution to the full problem (Equations (8) and (9)), including a translating ring and a time-dependent source at the upstream edge of the domain. However, this is a rather cumbersome calculation, and we have chosen instead to solve these equations numerically and simply present representative pictures here of the ring induced effects when a cohort —a single patch of larvae spawned roughly simultaneously— moves down the shelf and is disturbed by a ring. Some care is necessary in selecting a numerical scheme, since centered differencing is
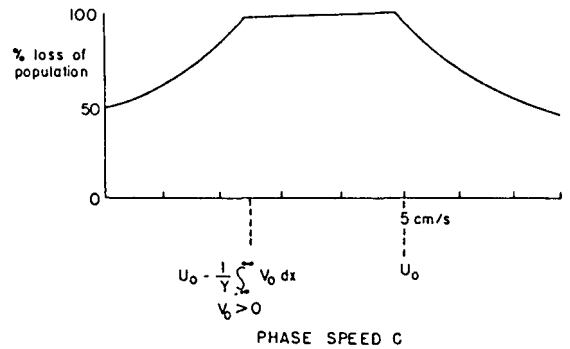

FIGURE 7.—Percent of the total number of larvae produced at the spawning site which are ultimately lost when a moving eddy is present at the shelf edge. When the speed c of the eddy is greater than $U_0 - 1/Y \int^x V_0$, all the larvae advected along the shelf are drawn offshore. When the ring is moving faster than the down-shelf current U_0, the ring catches up to the larvae, which are then diluted before being drawn offshore.

unstable while upstream differencing introduces a numerical diffusivity (Roache 1972). This may not be undesirable, since in reality one would expect some mixing to occur along the shelf; but unfortunately the diffusivity is spatially variable, being lowest in the vicinity of the eddy, and this we do not want in the model. We compromised by choosing a very small grid scale (5 km) so that the effective diffusivity is only 1.2×10^6 cm^2/s. This is not completely negligible, as shown in Figure 8a which plots successive snapshots of the larval fish density at 15-d intervals in the absence of any rings (the time step was one-half day). The population at the beginning of the domain is assumed to enter in a pulse

$$N_0(t) = \exp\left[-\frac{1}{2}\left(\frac{t}{5\ \text{d}}\right)^2\right]. \tag{23}$$

The gradual decrease in the peak abundance and the spread in width is caused by the numerical diffusion. Also included in this figure are the simple cases adding biological decay (Fig. 8b), a stationary ring (Fig. 8c), or both simultaneously (Fig. 8d). Note the large decreases in density induced as the population passes the ring and also the slower advection of the population down the shelf so that the organisms downstream are half a month older than they would otherwise have been (compare Figure 8b and 8d).

Finally, we show in Figure 9 two cases when a moving ring interacts with a patch of larvae. In the first case, the eddy is moving at 7 cm/s (faster than the 5 cm/s drift rate of the shelf water), so that the eddy catches up to the population and passes by it.
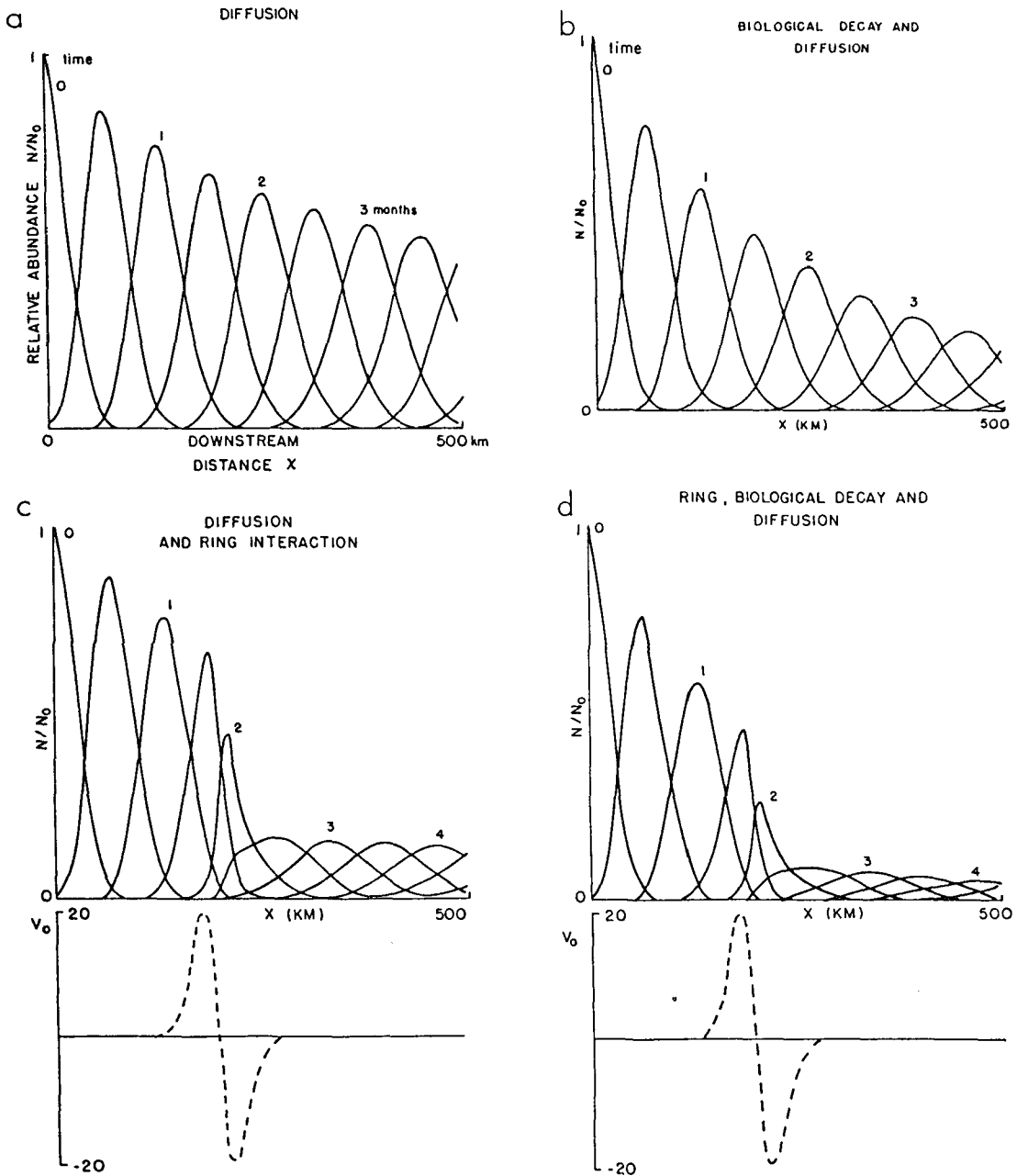
FIGURE 8. – Time-dependent solution of the numerical model which includes   a) the diffusion of a spawning group or cohort of larvae as the patch is advected down the shelf. Snapshots are at 15-d intervals. Parameters $\mu = 0$, $U_0 = 5$ cm/s, $\Delta x = 5$ km, and $\Delta t = 0.5$ d.   b) Same as (a) except $\mu = 10^{-7}$ s^{-1}.   c) Same as (a) except a stationary ring is present at the shelf edge, with parameters A = 20 cm/s and L = 20 km.   d) Same as (c) except $\mu = 10^{-7}$ s^{-1}.

As the ring passes by, the patch of larvae is spread out and distorted. Some losses do occur, but because of the rapidity of the interaction, these are slight. Comparison of this picture with Figure 8d shows that the larval density at 4 mo is higher than that for the stationary ring case. On the other hand, in the case when the shelf flow is faster than the speed of the ring (Fig. 9b), the impact of the ring is tremen-
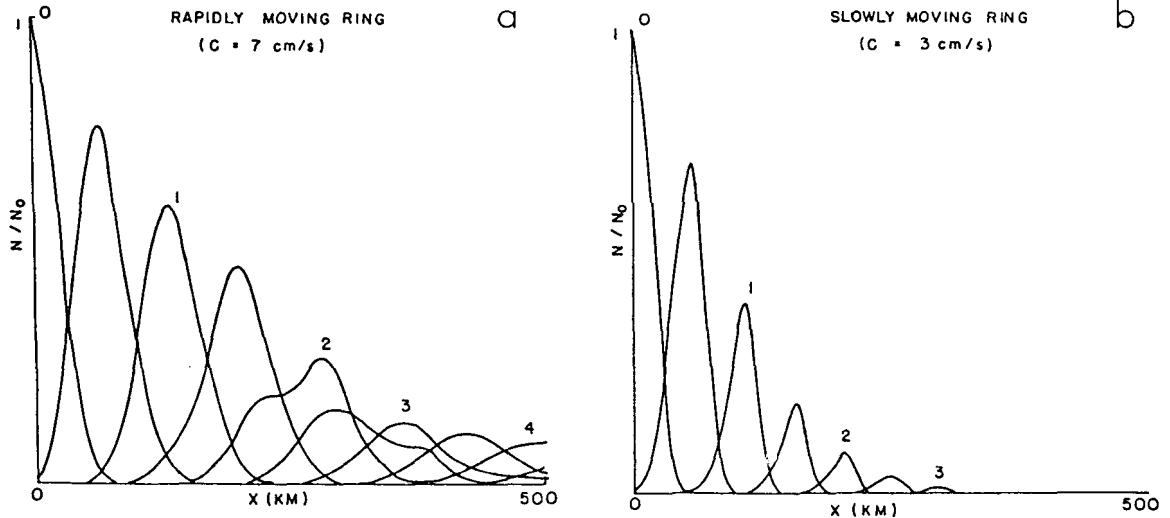
Figure 9.—a) Same as Figure 8d except a moving ring is present at the shelf edge, with parameters A = 20 cm/s, L = 20 km, and c = 7 cm/s.   b) Same as (a) except c = 3 cm/s.

dous. When the population catches up to the back side of the eddy, the relative speed is so slight that all of the organisms are diverted off the shelf and lost from the system.

In addition to the plots of density versus time and along-shelf distance, it is extremely useful to consider the net balances for larvae within the domain. By integrating Equation (8) over x and t, using Equation (9) to evaluate the starting point contribution at $x = 0$, we can calculate the percentages of the total incoming population which are removed from the domain by three processes. First, there are biological decreases of the net population (due to the integrated μN term). It is important at this point to recall that we consider this as representing both larval death and metamorphosis. Therefore the recruitment should be roughly proportional to this term. (We do not consider the development time history of the larvae here; clearly this model could be combined with more detailed and complex larval development models to attempt more sophisticated recruitment predictions.) Secondly, there are losses due to advection off the shelf by the ring currents, and thirdly, larvae can be lost out the downstream end of the domain. The 500 km length of the domain puts the end of the model region near Cape May; exiting larvae may be swept offshore into the Gulf Stream and, like those drawn off by ring currents, presumably be lost.

The magnitude of each of these terms is summarized in Table 1 for the cases plotted in Figures 8b, d and 9a, b. Table 1 shows that the ring-induced advective losses from the population can be as large as or larger than the biological (mortality and metamorphosis) losses. This is most dramatic when the ring is moving slightly slower than the shelf water currents. The recruitment should vary in a fashion similar to the integrated biological causes term in Table 1; thus we expect a strong year class when rings are not interacting with the shelf waters, a reduction when stationary or rapidly moving rings are present, and a very sharp decrease in recruitment if a slowly moving ring is near the edge of the shelf at the time of spawning and larval development.

DISCUSSION

Theoretically, the passage of warm core rings close

TABLE 1.—Percent of total larval fish population entering the domain. WCR = warm core ring.

In the presence of	Biological causes	Advection off the shelf in flows induced by a WCR	Advection out of the downstream end of the domain
No ring $\mu = 10^{-7} s^{-1}$	62	—	38
Stationary ring A = 20 cm/s L = 20 km	42	46	12
Rapidly moving ring c = 7 cm/s	54	29	17
Slowly moving ring c = 3 cm/s	18	82	0

to the continental shelf should have considerable influence on the abundance and distribution of shelf-water larval fish and consequently on their recruitment to the fishery. Our simple mathematical model suggests a major effect of the ring-induced cross-shelf flows is to cause decreases in the larval density ahead of the ring where there is onshore flow. In addition, water being drawn off the shelf in an entrainment feature behind the eddy can carry larvae away, constituting a significant loss to the shelf population.

Research scientists of the National Marine Fisheries Service are currently investigating the frequency of entrainment events and their impact upon the fisheries (A. Friedlander[3]). Here we shall briefly examine the published literature on ring distributions and larval fish surveys. We have used the schematic charts of sea surface temperature produced by NOAA and ONR (Office of Naval Research). All of these records are necessarily incomplete due to cloudiness in the imagery and the difficulties in inferring water motions from the surface features. We therefore will make a somewhat subjective estimate of ring importance by considering the persistence of various eddies and their closeness to the shelf.

Figure 10 is a composite of the observed MARMAP distributions of cod *Gadus morhua*, larvae in the shelf region near Georges Bank during the late winter and spring of 1977 (Smith et al. 1979). We have placed on this figure the approximate locations of the warm core rings shown on the Experimental Ocean Frontal Analysis Chart produced by the U.S. Naval Oceanographic Office for this period. Figure 11 shows the corresponding MARMAP distributions for haddock, *Melanogrammus aeglefinus*, larvae.

Four warm core rings had trajectory paths near enough to Georges Bank during the spring spawning period in early 1977 to have had significant impact upon the larval fish distributions according to the predictions of our model. In front of each ring shown on Figures 10 and 11, the concentration of larvae over the shelf appears to be relatively low, much as our model suggests would occur in areas of ring-induced onshore flow. There even appear to be indications of entrainment of larvae off the shelf behind rings 77E (Figs. 10c, 11c) and 77A (Fig. 11d). Unfortunately the MARMAP station grid does not extend beyond the 200 m contour, so that this cannot

be confirmed from the historical data. Extending the MARMAP grid further offshore would be of great benefit in assessing losses of larvae both by rings and by other offshore transports. It is also not possible to differentiate between patchiness from concentrated spawning upon Georges Bank or other biological causes and ring-induced variations. Again this makes the relationship between theory and data difficult to assess.

Warm core ring 77A (Figs. 10, 11) is an example of a nearly stationary eddy, remaining adjacent to Georges Bank from 30 March to 25 May 1977. But according to our theory, ring 77E is potentially even more dangerous, since it slowly sweeps down the entire Georges Bank edge between 18 May and 6 July, moving at 3-5 cm/s. Drifting groups of larvae could have caught up to the back side of ring 77E and been drawn off the shelf.

The survival of larvae in 1977 was low, and the year class was weak for both cod and haddock (Serchuk and Wood 1981; Clark et al. 1982). In other years also, there appears to be a relationship between the frequency of ring interaction with Georges Bank during the winter and spring spawning season and subsequent year-class strength for both cod and haddock stocks (Table 2). Cod spawn on Georges Bank from December into May and haddock spawn from February into June (Smith et al. 1979). Therefore we have examined the 6-mo period from January to June each year from 1975 to 1979 for ring activity using the charts of Bisagni (1976), Mizenko and Chamberlin (1979a, b), Celone and Chamberlin (1980), and Fitzgerald and Chamberlin

TABLE 2.—Apparent relationship between years of less frequent WCR (warm core ring) interaction with Georges Bank during the winter and spring spawning season and strong recruitment of cod and haddock stocks.

| Year | Recruitment Strength | | No. of WCR's interacting during spawning season (Jan.-June) | Comments |
	Cod	Haddock		
1975	Very good	Very good	1	Eddy 6 present February-April
1976	Weak	Weak	3	WCR 75I, 76A, and 76C detrimental; 76D too far offshore
1977	Weak	Weak	4	WCR 76F, 76G, 77A, and 77E all detrimental
1978	Good	Very good	1	WCR 78A present in May; 78B too far offshore
1979	Weak	Average	3	WCR 78I, 79A, and 79B detrimental

[3]A. Friedlander, Northwest Fisheries Center Narragansett Laboratory, National Marine Fisheries Service, NOAA, R.R. 7A, Box 522A, Narragansett, RI 02882, pers. commun. January 1983.
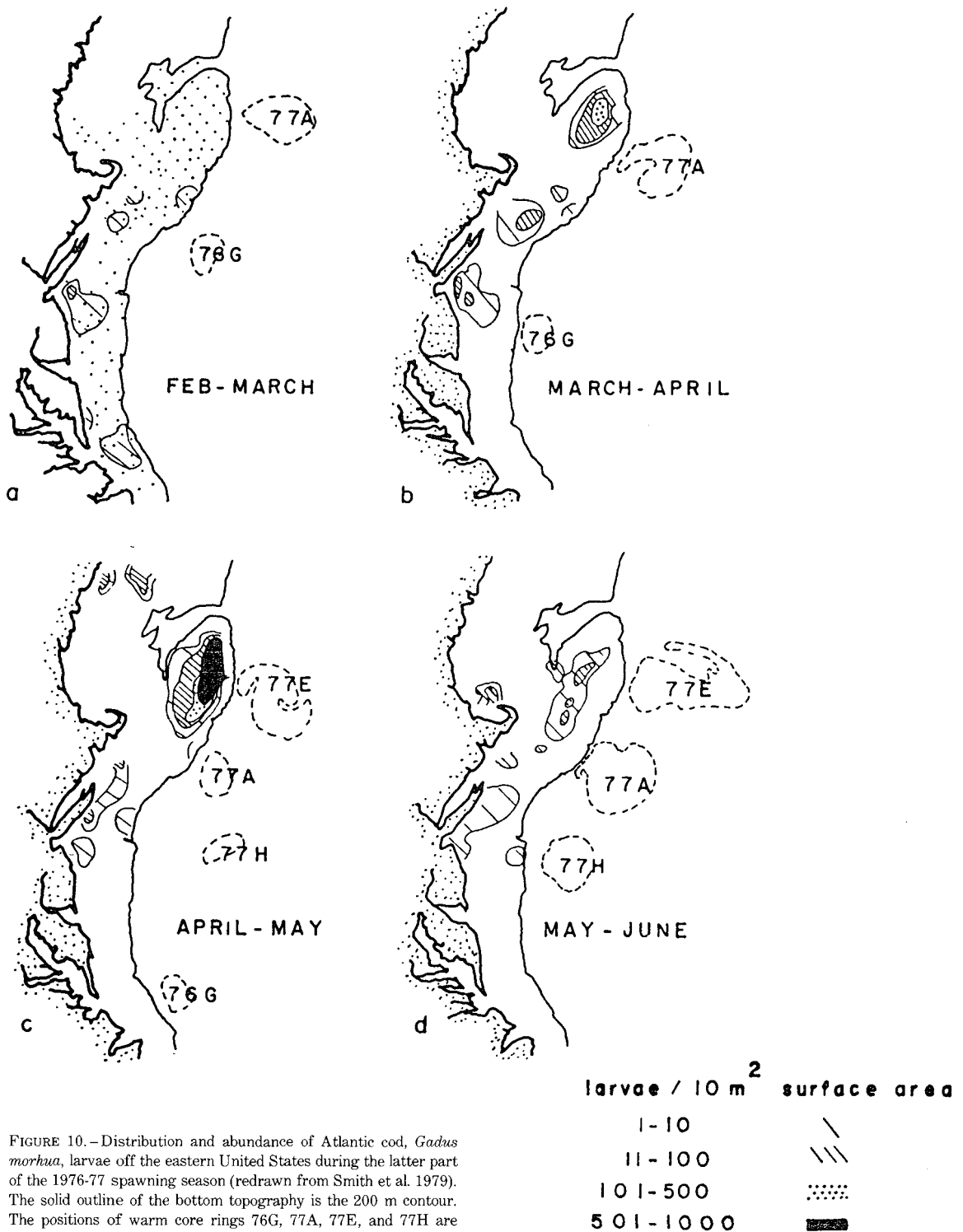
FIGURE 10.—Distribution and abundance of Atlantic cod, *Gadus morhua*, larvae off the eastern United States during the latter part of the 1976-77 spawning season (redrawn from Smith et al. 1979). The solid outline of the bottom topography is the 200 m contour. The positions of warm core rings 76G, 77A, 77E, and 77H are replotted from Experimental Ocean Frontal Analysis Charts produced by the U.S. Naval Oceanographic Office on 25 February (a), 23 March (b), 27 April (c), and 25 May (d) in 1977. The dots on (10a) show the sampling locations.
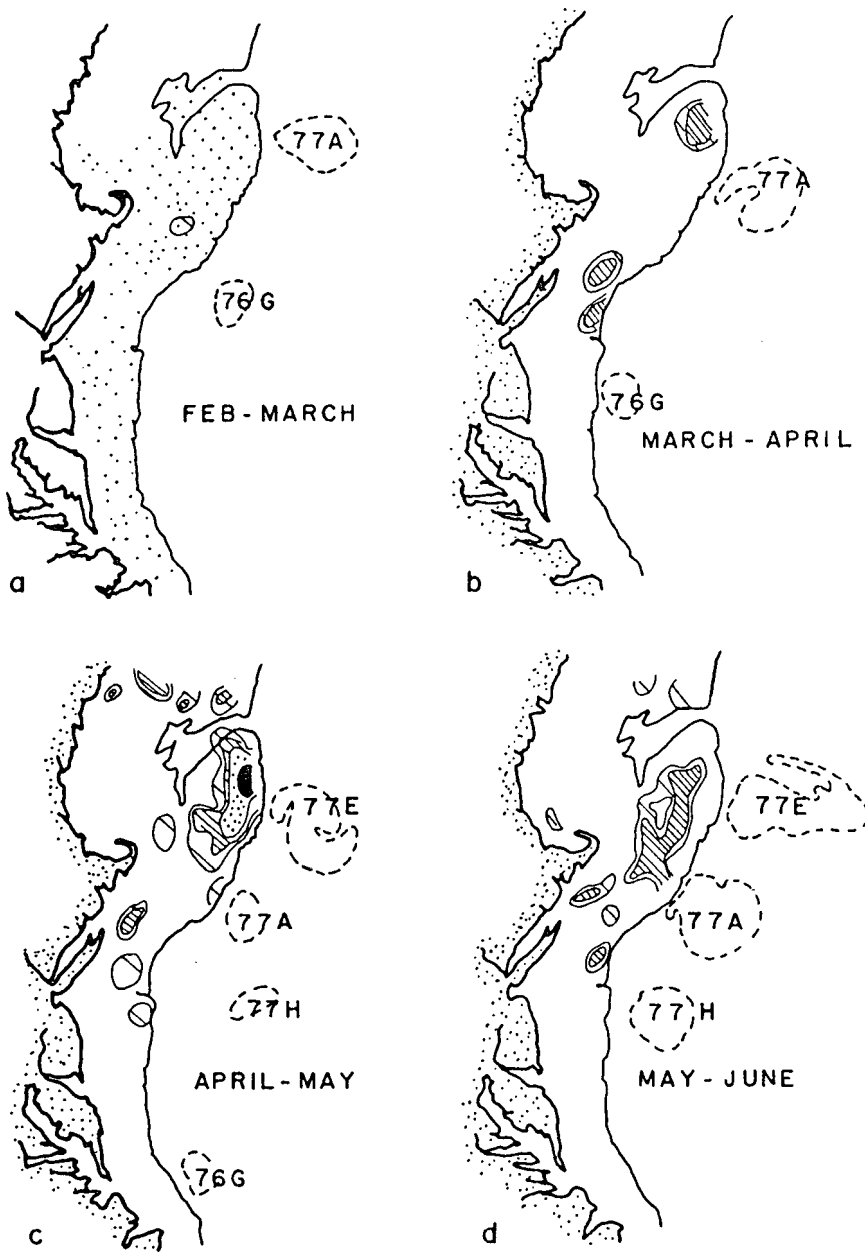
FIGURE 11.—Distribution and abundance of Atlantic haddock, *Melanogrammus aeglefinus*, larvae off the eastern United States during the latter part of the 1976-77 spawning season (redrawn from Smith et al. 1979). The positions of the warm core rings are the same as in Figure 10.

(1981). The number of rings present in the Slope Water is less important than the trajectories of the rings. If they pass too far offshore or appear too early or too late in the spawning season, they may have little impact. It is difficult to measure the magnitude of the onshore-offshore flows from the remote sensing data, but we have tried to consider the size of the shelf edge affected and the longshore speed of the eddy when judging the strength of a particular interaction. Unfortunately, we have no information for the years considered on the timing or location of spawning which undoubtably is important in determining the impact of individual rings.

The spring of 1975 was a time of low warm core ring activity (Table 2), and both cod and haddock produced good year classes, essentially the best since the 1960's (Smith et al. 1979). This high recruitment was not due to large numbers of larvae being spawned; indeed, the abundance of cod and haddock larvae was at a 5-yr low (Smith et al. 1979). Apparently, the few larvae present on Georges Bank experienced exceptionally high survival. There was only one ring (designated eddy 6 by Bisagni 1976) which by our model predictions could have influenced recruitment. Eddy 6 was in the vicinity of Georges Bank from February through April but did not seem to be entraining shelf water for this entire period.

During the spring of 1976 there were three, possibly four, warm core rings interacting with Georges Bank between January and May. Mizenko and Chamberlin (1979a) presented the track lines for eddies 75I (which later possibly became 76B), 76A, and 76C. Rings with these trajectories had the potential to affect recruitment. The 1976 year class strength for both cod and haddock stocks was weak (Smith et al. 1979).

The spring of 1977 was a year of unusually high ring activity. Figure 1 shows five rings (77A, 77C, 77E, 77G, and 77H) simultaneously present in the Slope Water region on 11 May 1977. Mizenko and Chamberlin (1979b) presented trajectories for all the eddies observed in 1977. Of these rings, 76F, 76G, 77A, and 77E appear to be most detrimental. The 1977 year-class strength for both cod and haddock stocks was again weak (Serchuk and Wood 1981; Clark et al. 1982).

The relationship of low ring activity and high recruitment observed in 1975 holds true again for 1978. This was a good year for cod and a very good year for haddock recruitment (Serchuk and Wood 1981; Clark et al. 1982). Examining the trajectories of warm core rings present during 1978 (Celone and Chamberlin 1980), we find no rings interacting with Georges Bank until late May or June. During the

60-d period from mid-February to mid-April, no anticyclonic eddies were apparent off the northeast coast. In late April and May, there were two rings (78A and 78B), but they occurred too far south or too far offshore to affect the Bank.

Finally in 1979, the most recent year for which there are both fisheries recruitment data and trajectory records, we find three potentially dangerous rings: 78I, impinging upon Georges Bank from March to July (Fitzgerald and Chamberlin 1981) and two eddies, 79A and 79B, lingering southwest of the Bank from February through May. The 1979 year class was weak for cod and only average for haddock (Serchuk and Wood 1981; Clark et al. 1982).

CRITIQUE

According to our calculations, warm core rings may have considerable influence on the distribution and ultimate survival of cod and haddock larvae spawned on Georges Bank. Our simple mathematical model demonstrates the possible effects of cross-shelf flows induced by a ring upon larval fish distributions and abundance. The ring's size, strength, and translation speed are critical in determining its potential impact. A stationary ring may cause a 20 to 50% loss of larvae by inducing advective transport off the shelf. If a ring is moving, the impact can be even greater, especially for an eddy travelling longshore at a slightly slower speed than the shelf water. In this most catastrophic case, a group of larvae can catch up to the back side of the eddy and be entirely swept off the shelf.

In briefly examining the published literature on ring trajectories and fisheries recruitment statistics, we have found what appears to be a relationship between years of frequent ring interaction with Georges Bank during the late winter and early spring spawning season and weak year classes of cod and haddock. Our analysis can be criticized as cursory and incomplete since we had no detailed information on entrainment features or on many important biological factors such as the timing and location of spawning. Future studies may show this relationship was fortuitous; however, our results certainly indicate that future study is warranted.

An implicit assumption in our analysis of ring events and fisheries recruitment data is that advective losses can affect year-class success. This has not yet been demonstrated for the Northwest Atlantic; however, Parrish et al. (1981) presented convincing arguments that the dominant exploitable fishes off the west coast have adopted spawning behaviors which minimize losses due to offshore transport.

They suggested that deviations from normal transport conditions may be a cause of the very large recruitment variations observed in the fisheries for sardine and anchovy. Whether warm core rings represent anomalous conditions or whether the shelf fishes of the Northwest Atlantic have adopted spawning patterns which minimize the losses by entrainment is yet to be discovered.

G. Laurence[4] has suggested that in some instances vertical migratory behavior may prevent significant numbers of larvae from being advected offshore. If the entrainment feature is shallow and the fish larvae avoid the surface layer, then the offshore transport could be much less than predicted by our model. The National Marine Fisheries Service is currently surveying entrainment features associated with warm core rings to assess the losses occurring off the shelf. Recently, Wroblewski and Cheney (1984) reported finding significant numbers of the white hake, *Urophycis tenuis*, larvae 140 km seaward of the Scotian Shelf break in Slope Water which had been entrained by a warm core ring. *Urophycis tenuis* spawn on the Scotian Shelf and upper continental slope. Wroblewski and Cheney concluded that the ring altered the usual larval drift pattern along the shelf edge. Curiously, no larvae of cod or haddock, which also spawn on the shelf during spring and summer, were found in the ichthyoplankton net tows. It remains to be demonstrated whether sufficient numbers of shelf-spawned larvae are transported offshore by rings to affect recruitment of shelf stocks.

The advective losses predicted by our model may be overestimates if only larvae present near the shelf edge are susceptible to entrainment and if their density is much lower than that further inshore. The influence of the ring may not reach the shallower regions where many larvae are found. Also, biological losses may be larger than assumed in the model, so that the relative importance of ring-induced losses may be less.

Warm core ring entrainments are not the sole mechanism by which fish larvae can be transported off the shelf. In 1955, Chase found a relationship between haddock recruitment and the strength of the wind-driven current normal to the southern side of Georges Bank. We also recognize that there could even be beneficial effects to the Georges Bank ecosystem if the ring-induced cross-shelf flows push nutrient-rich Slope Water onto the Bank and fertilize

the system (G. A. Riley[5]). Rather than exploring all mechanisms, we have chosen to assess one particular source of variability which may contribute to fluctuations in year-class strength for the fish stocks spawning on Georges Bank.

We have also assumed that the fish larvae are well mixed across the shelf, although we know that they are generally distributed in patches. Thus our model solutions may be comparable with field data only if one integrates the field data over x and z as we have done in our simplified model. Fisheries recruitment data naturally reflects this integration over large spatial scales and we are encouraged by the apparent relationships in Table 2. However, loss during the larval period is only one factor affecting recruitment. Events during the postlarval stages are also significant; Sissenwine et al. (1983) showed that predation in these later stages is an important factor in year class success.

Our model has given quantitative but crude estimates of the importance of ring events for larval survival and suggested that the impact of the ring depends strongly upon its motion; investigations with more highly resolved and more complex models and further survey work for assessing both ring and mesoscale eddy influences on larval fish distributions and subsequent recruitment are the next steps.

ACKNOWLEDGMENTS

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