

Prediction of Phytoplankton Growth in Response to the Frictional Decay of a Warm-Core Ring

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A modelling study was conducted to examine the question, Is the high phytoplankton biomass which often develops in warm-core rings of the Gulf Stream a consequence of the circulation associated with the frictional decay of the ring? A time-dependent, two-dimensional (r, z, t) model of plankton dynamics in a hypothetical ring similar in features to warm-core ring 82B generates a lens of high phytoplankton biomass at ring center. Phytoplankton grow on nutrients advected into the euphotic zone as the depressed warm water in the ring's core rebounds and spreads out at the surface. This vertical motion induced as the ring's rate of rotation slows may be an important process maintaining the high production in warm-core rings.

INTRODUCTION

Gulf Stream rings are energetic mesoscale eddies formed by the closure of a Gulf Stream meander [Richardson, 1983]. Warm-core rings form to the north of the Gulf Stream and consist of a lens of Sargasso Sea water surrounded by a Gulf Stream remnant, lying on top of colder North Atlantic Slope Water [Saunders, 1971]. Mesoscale eddies are associated with every major boundary current in the ocean, including the Benguela Current, the California Current, the Kuroshio Current, and the East Australian Current [Robinson, 1983].

Otherwise anomalous temporal and spatial distributions of biological variables are associated with the physical signature of rings. Tranter *et al.* [1980] and Tranter *et al.* [1983] have noted high phytoplankton productivity associated with warm-core eddies of the East Australian Current. Tranter *et al.* [1980], Tranter *et al.* [1982], and Yentsch and Phinney [1985] have related production in the center of a warm-core ring to convection and stabilization driven by local heat fluxes. Yentsch and Phinney advanced the hypothesis that growth and abundance of phytoplankton in the high velocity region near the ring's outer boundary are regulated by geostrophic forces providing nutrient enrichment there. An additional hypothesis should also be considered: that the vertical flow due to the frictional decay of the ring is a major source of nutrients driving phytoplankton production in the euphotic zone at ring center.

To examine this hypothesis a time-dependent, two-dimensional (r, z, t) model of plankton dynamics in a warm-core ring was constructed, incorporating a flow field calculated from an empirically derived stream function. The circulation pattern was calibrated with the observed changes in the temperature field of Gulf Stream warm-core ring (WCR) 82B

during the period April to June 1982 [Schmitt and Olson, 1985]. Due to the simplicity of the dynamics included, the model is not a true simulation of this ring. The rudimentary plankton dynamics, including only the prominent biological variables observed in marine ecosystems (phytoplankton, zooplankton, and dissolved nutrient), preclude a quantitative comparison with available data. Rather, the model is a tool used to explore certain physical-biological interactions which may be characteristic of warm-core rings.

FORMULATION OF PHYSICAL DYNAMICS

We assume that warm-core rings are axisymmetric [Schmitz and Vastano, 1976], hence changes in variables around a ring are negligible compared to changes with distance from ring center. Except during episodes of ring-Gulf Stream interaction [Joyce *et al.*, 1983], this is a reasonable approximation. One radial transect through WCR 82B tended to show the same patterns as another radial transect [Olson *et al.*, 1985]. Isolated features such as streamers (entrained filaments of external waters) disrupt this symmetry; however, no attempt is made to include the effect of streamers in this simplified model.

Having assumed azimuthal symmetry in a ring, we may then infer that any radius-depth (r, z) plane through the ring is characteristic of the ring as a whole. The physical model is based on this argument, and we examine changes in a single (r, z) plane of a ring. The radial flows are much less vigorous than the azimuthal flows in a warm-core ring [Joyce and Kennelly, 1985] and are probably due to frictional decay of the ring or topographic and Gulf Stream interactions. As the ring ages, energy is lost due to friction, and the permanent pycnocline relaxes, gradually rising toward the level of the permanent pycnocline in the surrounding waters [Flierl and Mied, 1985]. As this occurs, the volume of the ring decreases, water being forced out along isopycnals. It is this flow which is simulated.

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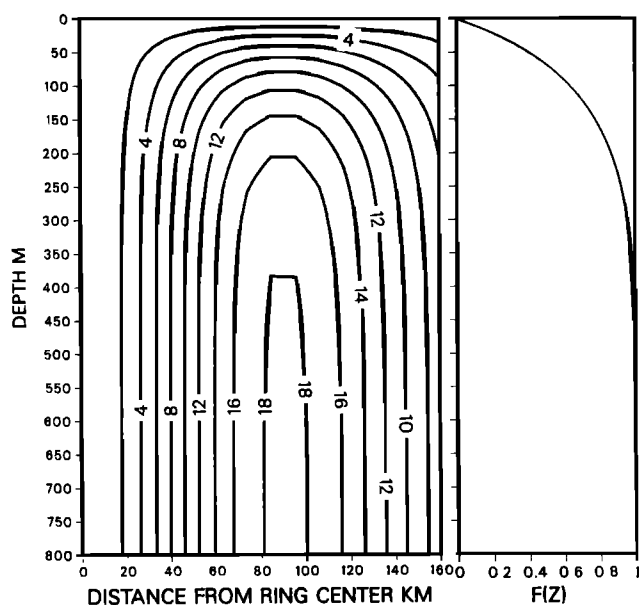


Fig. 1. Streamlines of the flow field used in the (r, z, t) physical-biological model of a warm-core ring. Contours are multiples of $10^3 \text{ m}^3 \text{ s}^{-1}$. The center of the ring is at the far left, and the flow is from left to right. At the right is plotted $F(z) = 1 - e^{-0.01z}$ to show its shape relative to the streamlines.

The stream function proposed to describe the radial flow is

$$\psi = F(z)r^2/2 \exp [(-r^2)/(2r_0^2)] \quad (1)$$

Here r is the distance from ring center, and r_0 the initial radius of the ring. $F(z)$ describes the vertical dependence of the flow and was chosen so that the permanent thermocline rises at approximately 1 m day^{-1} at ring center. The analytical form of $F(z)$ with depth (z) measured in meters is

$$F(z) = 1.4 \times 10^{-5} (1 - e^{-0.01z}) \text{ m s}^{-1}$$

so that at $r = 0$ and $z = 800 \text{ m}$, the vertical velocity, w , is

about 1 m day^{-1} . This was the rate of movement observed in ring 82B between April and July [Olson *et al.*, 1985]. Maximum radial velocities at the surface were assumed to be 200 m day^{-1} . The initial radius of the ring was set at 60 km , approximately the initial radius of warm-core ring 82B [Kennelly, 1983]. The flow field generated by this stream function is shown in Figure 1. The strongest upward water motion is at ring center where the ring relaxation is most evident [e.g., Schmitz and Vastano, 1976; Flierl and Mied, 1985]. The greatest horizontal velocities are at the ring edge near the surface where water escapes the ring along isopycnals.

The velocities calculated from the stream function were laid on a grid with spacings 10 km wide by 10 m deep. In computer runs with the biological processes included, these grid spacings were reduced to 10 km by 2.5 m to obtain more resolution in the vertical direction. In cylindrical coordinates, assuming an incompressible fluid and constant eddy diffusivities, the equation governing the advection and diffusion of phytoplankton (P) is

$$\frac{\partial P}{\partial t} + \frac{u \partial P}{\partial r} + \frac{w \partial P}{\partial z} = K_r \left(\frac{\partial^2 P}{\partial r^2} + \frac{1}{r} \frac{\partial P}{\partial r} \right) + K_v \frac{\partial^2 P}{\partial z^2} \quad (2)$$

In each grid box, the horizontal velocities were calculated analytically from the stream function:

$$u = -\frac{1}{r} \frac{\partial \psi}{\partial z} \\ = -\frac{\partial F(z)}{\partial z} \frac{r}{2} \exp \left(\frac{-r^2}{2r_0^2} \right)$$

The vertical velocities were then calculated using the equation of continuity to ensure mass conservation in the model grid.

Equation (2) was solved numerically using the quadratic-conservative scheme of Piacsek and Williams [1970] for the advective terms and an explicit scheme for the diffusion terms, lagged in time for computational stability (see Wroblewski [1983] for details). At the bottom and sides of the grid region

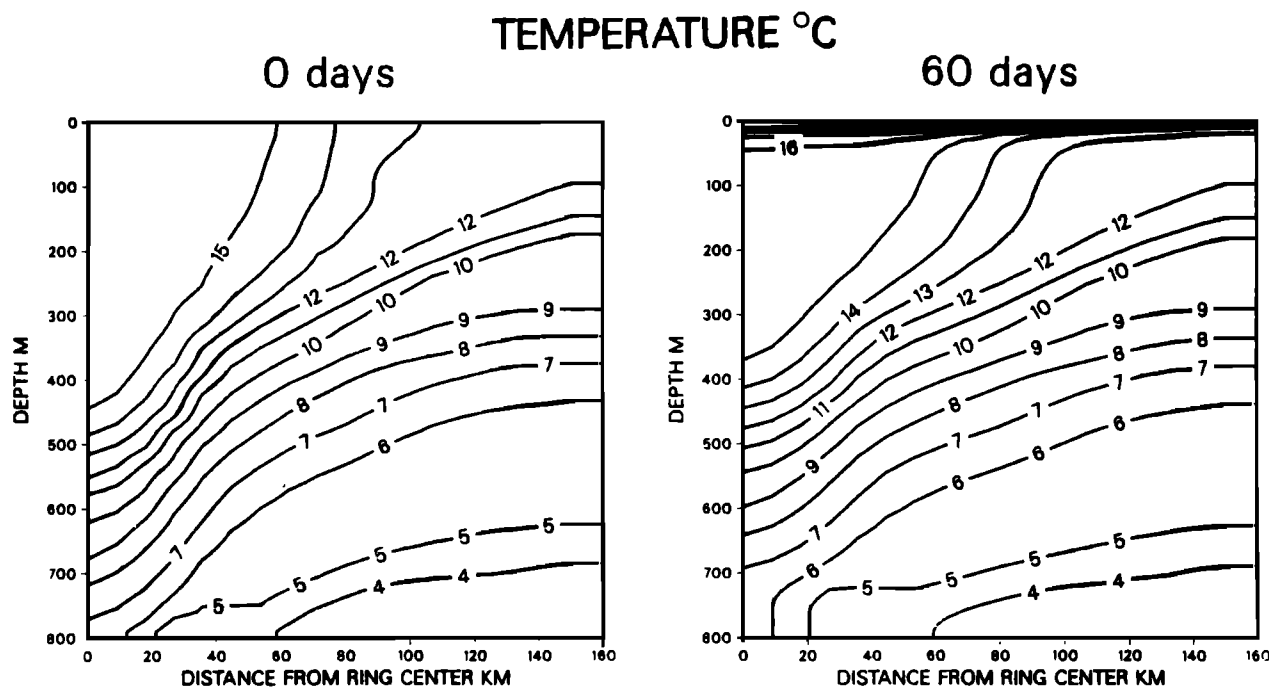


Fig. 2. Evolution of the model temperature field. The contour interval is 1°C .

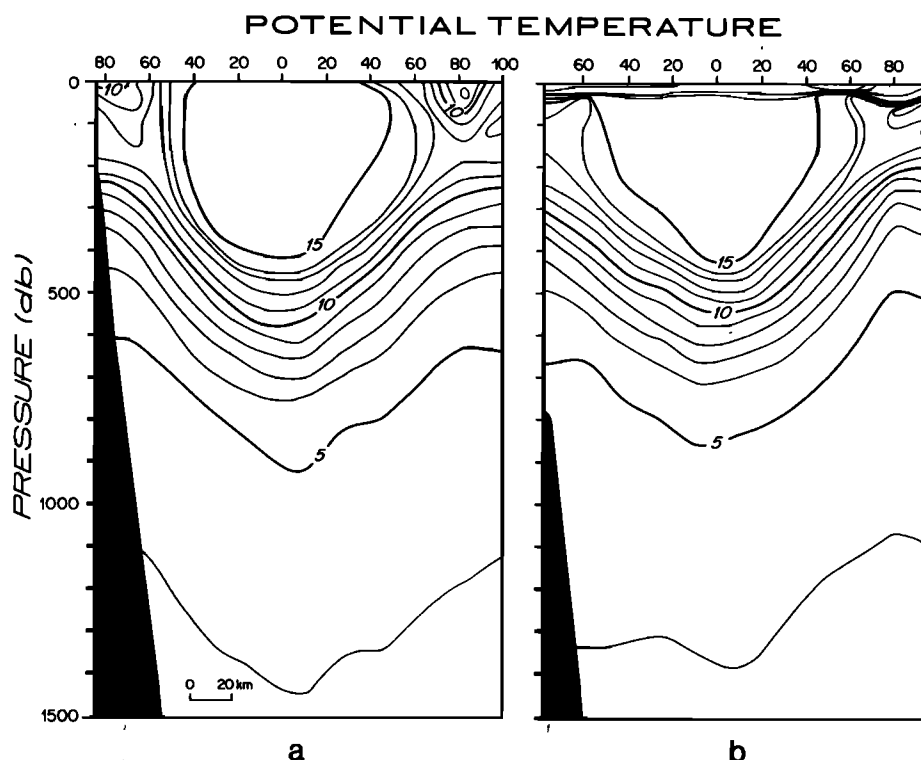


Fig. 3. Radial temperature section of WCR 82B in (a) April and (b) June 1982 (adapted from Joyce and Kennelly [1985]).

(Figure 1), zero gradient boundary conditions were set. Eddy diffusivities were spatially uniform, with $K_h = 5 \times 10^4 \text{ cm}^2 \text{ s}^{-1}$ and $K_v = 0.2 \text{ cm}^2 \text{ s}^{-1}$. For simulation of the temperature field, heat was supplied at the surface at a constant net rate of approximately $20 \text{ J m}^{-2} \text{ s}^{-1}$, and absorbed following equation (2) of Lewis *et al.* [1983], with a constant attenuation coefficient of 0.1 m^{-1} . In the biological simulations the incident light at the surface was assumed constant. Including diel or seasonal variation of incident solar radiation in the model had little effect on the model solutions.

A quasi-simulation of the ring's changing temperature structure was initialized with data taken in ring 82B in April [Joyce and Kennelly, 1985]. The model was integrated for 60 days to test how well the circulation pattern resembled the flow field of 82B. The initial and final model temperature fields are shown in Figure 2. These fields may be compared to temperature data from radial transects through 82B in April and June shown in Figure 3. The model simulation appears to be accurate enough for purposes here. The rise of the permanent thermocline is in agreement with the data, as is the ring shape. However, the model surface temperature structure is not an accurate depiction of the ring, as the thermocline is not sufficiently strong at the ring edge.

FORMULATION OF BIOLOGICAL DYNAMICS

The model framework for the plankton dynamics (Figure 4) is a common one [e.g., Steele, 1974; Parker, 1975; Wroblewski and O'Brien, 1976; Hallam, 1977]. The three state variables considered, phytoplankton (P), zooplankton (Z), and dissolved nutrient (N), are modelled in terms of their nitrogen content, this being the assumed limiting nutrient. The grazing formulation used is a modified version of the function experimentally determined by Mayzaud and Poulet [1978]. It differs from the traditional Ivlev [1961] expression for herbivore

grazing in that there is no asymptotic limit to the grazing rate. The biological equations which contain this grazing function are not oscillatory, or exhibit oscillations which are quickly damped if used with realistic parameter values [Franks *et al.*, in press, 1986]. This allows the modeller to clearly resolve temporal and spatial variation in plankton concentrations which arise as a response of the plankton to physical oceanographic factors.

The equations for the plankton model are

$$dP/dt = V_m NP / (k_s + N) - mP - R_m \Lambda P (1 - e^{-\Lambda P}) Z \quad (3)$$

$$dZ/dt = (1 - \gamma) R_m \Lambda P (1 - e^{-\Lambda P}) Z - gZ \quad (4)$$

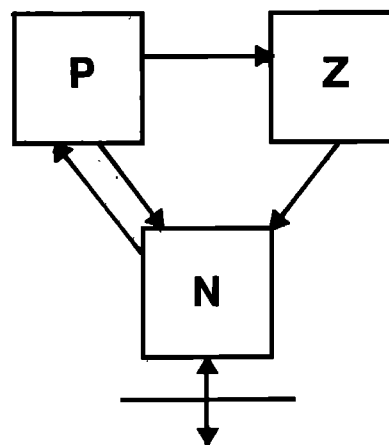


Fig. 4. Conceptual diagram of the plankton dynamics. The model investigates the pathways between P (phytoplankton), Z (zooplankton), and N (nutrient). Fluxes of dissolved nutrient into and out of the euphotic zone are indicated by the crossed horizontal line.

TABLE 1. Biological Parameter Values Used in the Model

Dimensional Quantity	Definition	Value
g	zooplankton death rate	0.2 day^{-1}
k_s	nutrient uptake half saturation constant	$0.1 \mu\text{g at } N \text{ l}^{-1}$
m	phytoplankton death rate	0.1 day^{-1}
R_m	zooplankton maximal grazing rate	0.25 day^{-1}
V_m	phytoplankton maximal growth rate	2.0 day^{-1}
γ	unassimilated grazing fraction	0.3
Λ	Ivlev constant	$0.5 (\mu\text{g at } N \text{ l}^{-1})^{-1}$

$$dN/dt = -V_m NP/(k_s + N) + mP + gZ + \gamma R_m \Lambda P(1 - e^{-\Lambda P})Z \quad (5)$$

and

$$P + Z + N = N_t \quad (6)$$

The phytoplankton, P , grow according to Michaelis-Menten uptake of dissolved nutrient, with a maximal growth rate of V_m and a half-saturation constant of k_s . The loss terms of phytoplankton include a linear death rate of m (day^{-1}), and losses due to grazing. Phytoplankton death is a gross parameterization of many varied processes including physiological death, exudation of organic substances, etc. The zooplankton, Z , dynamics include growth as assimilated ingested ration and a loss rate of g (day^{-1}) due to whatever cause: predation,

physiological death, etc. The unassimilated fraction of ingested phytoplankton, γ , goes immediately into dissolved nutrients, N , as do the dead zooplankton and phytoplankton. The total amount of nitrogen in the system, N_t , is assumed constant. The values of the biological parameters are given in Table 1. A discussion of the parameter values and an analytical sensitivity analysis of the biological equations (3)–(6) can be found in the work by Franks *et al.* [in press, 1986].

COUPLED PHYSICAL-BIOLOGICAL DYNAMICS

For the complete (r, z, t) model, the biological equations were incorporated into the physical framework. For example, the full equation for phytoplankton dynamics was

$$\frac{\partial P}{\partial t} + u \frac{\partial P}{\partial r} + w \frac{\partial P}{\partial z} = K_h \left(\frac{\partial^2 P}{\partial r^2} + \frac{1}{r} \frac{\partial P}{\partial r} \right) + K_v \frac{\partial^2 P}{\partial z^2} + \frac{V_m NP}{k_s + N} - mP - R_m \Lambda P(1 - e^{-\Lambda P})Z$$

Spatial patterns in the biological variables were influenced by light distribution, advection and diffusion, and biological interactions. Where nutrients were not limiting, the growth rate V of the phytoplankton followed the same exponential decrease with depth as the light: $V = V_m e^{-kz}$ with $k = 0.08 \text{ m}^{-1}$ [Phinney *et al.*, 1984a; Phinney *et al.*, 1984b]. No surface inhibition of photosynthesis was stipulated, and the light extinction coefficient was assumed to be constant. The zooplankton were not allowed to vertically migrate, thus making interpretation of the results simpler since fewer processes affecting nitrogen transport were occurring.

The physical-biological model was initialized with a nutrient field derived from data of Fox *et al.* [1984]. The initial phytoplankton and zooplankton fields were assumed homogeneous with $P = 0.3 \mu\text{g at } N \text{ l}^{-1}$ and $Z = 0.12 \mu\text{g at } N \text{ l}^{-1}$. The

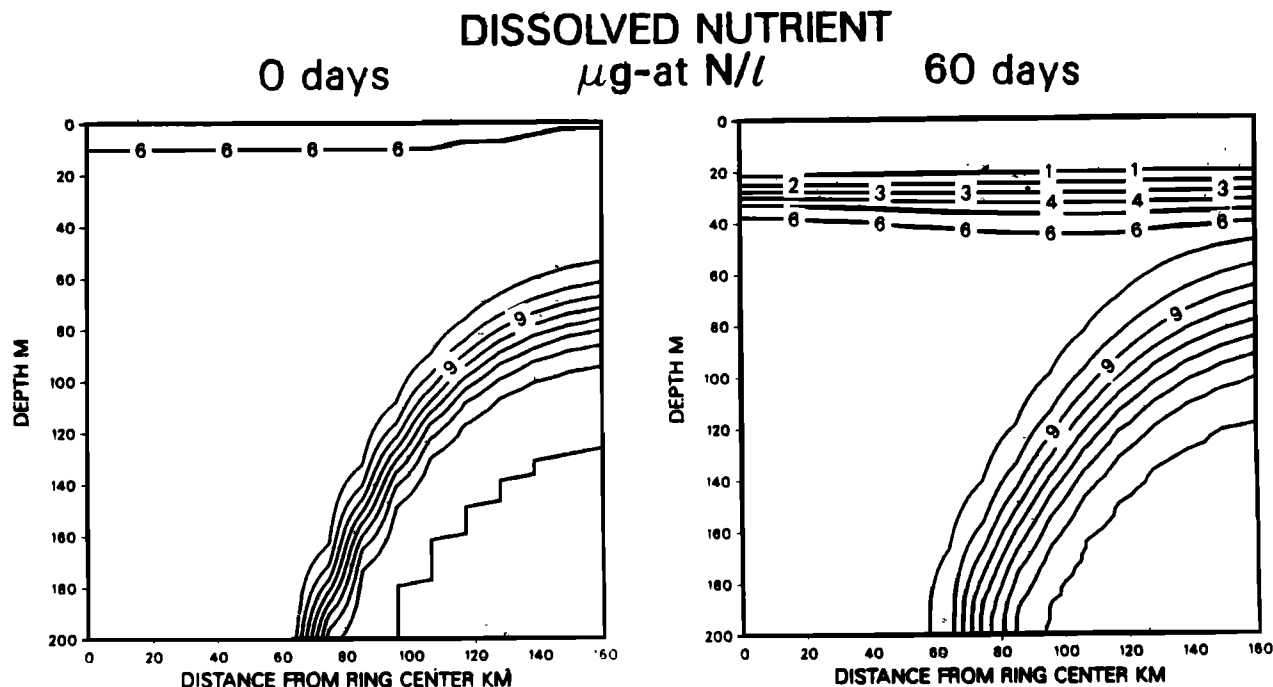


Fig. 5. Evolution of the dissolved nutrient distribution in the (r, z, t) physical-biological model. The initial field is similar to the distribution observed in WCR 82B in April 1982. The waves in the contours are artifacts of the contouring program.

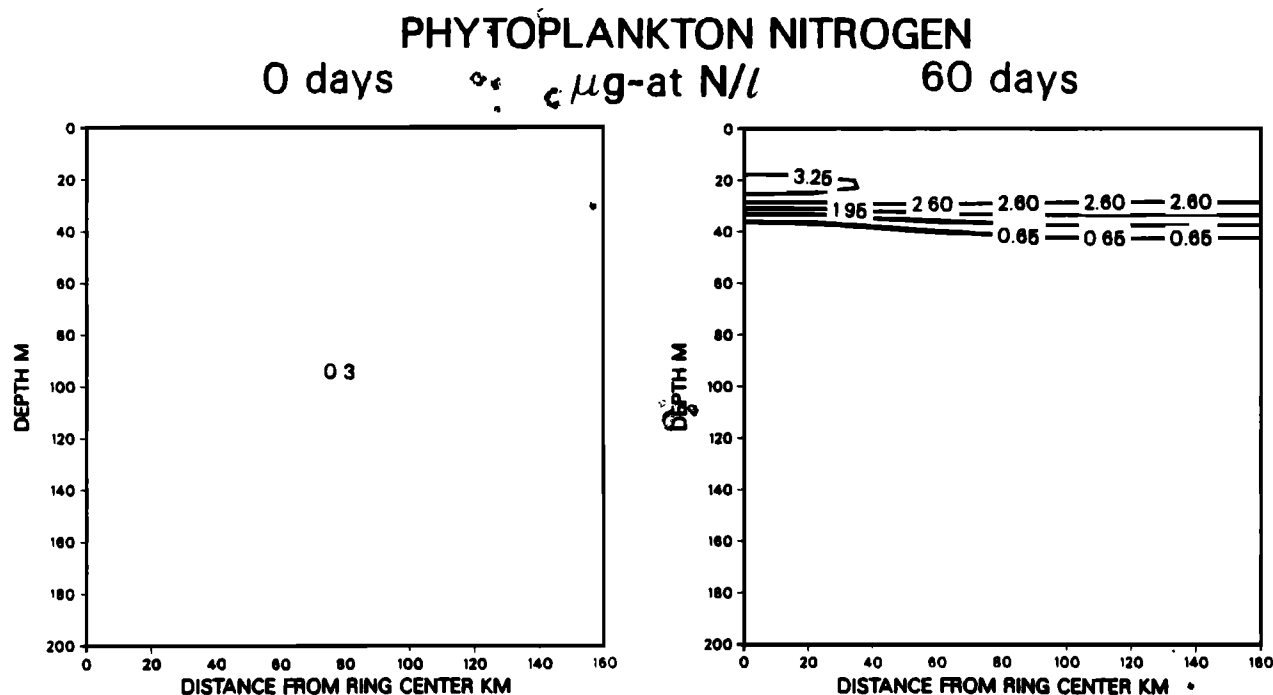


Fig. 6. Evolution of the phytoplankton field in the (r, z, t) physical-biological model. The field is homogeneous at time zero, corresponding to the conditions of a deep, wintertime mixed layer. The model has achieved a steady state by model day 60.

choice of these initial values had little influence on the steady state distributions of P , Z , and N achieved by the model after 60 model days.

RESULTS

As the physical-biological model evolved, the initial fields changed quite radically as they approached steady state (Figures 5 and 6). Uptake of dissolved nutrient by phytoplankton led to surface nutrient concentrations of less than $1 \mu\text{g}$ at $N \text{ l}^{-1}$, and a strong surface nutricline at about 30 m depth (Figure 5). Over the 60 day model run the permanent nutricline (which follows the main thermocline) rose and diffused as the ring structure decayed. The phytoplankton field evolved from being uniform with depth (similar to a deep, well-mixed euphotic zone), to a field generally decreasing with depth (Figure 6). A persistent feature of the phytoplankton distribution was a lens of enhanced phytoplankton biomass centered at 20 m depth at ring center, with a radius of about 35 km. The zooplankton field became approximately radially uniform, with concentrations decreasing with depth (not shown).

It is instructive to examine the processes leading to the formation and maintenance of the lens of high phytoplankton biomass. Figure 7 shows the steady state vertical phytoplankton profile at ring center for various upwelling velocities at ring center. With no upwelling, no region of enhanced biomass was formed: the phytoplankton concentration was constant with depth to the base of the euphotic zone, where the concentration dropped off sharply. As upwelling velocities were increased, higher phytoplankton concentrations were seen in the zone of enhanced biomass. In addition, this zone is located at progressively shoaler depths. Changing the value of the vertical eddy diffusivity caused changes in the vertical gradients of the lens, but vertical diffusion could not, of itself,

generate a lens of enhanced biomass. Decreasing the light extinction coefficient caused a deepening of the lens, accompanied by an increase in its magnitude consistent with the upwelling velocity at that depth.

From various numerical experiments similar to those mentioned above, it became clear that the lens of enhanced phytoplankton biomass was created by phytoplankton uptake of dissolved nutrient advected into the euphotic zone at ring center due to the frictional decay of the ring. Phytoplankton at this depth grew at a very slow rate and consequently were not heavily grazed by the zooplankton [see *Franks et al.*, in press, 1986]. The higher the rate of advection, the higher the phytoplankton biomass which could be supported.

DISCUSSION

The model formulated above is a hypothesis concerning the processes governing phytoplankton production in a warm-core ring. The most appropriate test of this hypothesis is a comparison of the model output with data gathered from warm-core rings. *Yentsch and Phinney* [1985] and *Smith and Baker* [1985] present transects of chlorophyll concentration through WCR 82B in June 1982. To compare the present model output to these data requires converting the phytoplankton concentrations from nitrogen to chlorophyll. To do this, nitrogen was converted to carbon using the Redfield ratio, and carbon converted to chlorophyll using a modified equation (4) of *Falkowski and Wirick* [1981] for the steady state case. The model chlorophyll predictions after 60 model days may be seen in Figure 8a and compared to June chlorophyll data in 82B in Figures 8b, 8c, and 8d. It can be seen that the model predicts concentrations similar to the chlorophyll and phaeopigment concentrations of *Smith and Baker* [1985] and those found by *Yentsch and Phinney* [1985]. In all cases the lens appears at approximately the same depth and is of the same

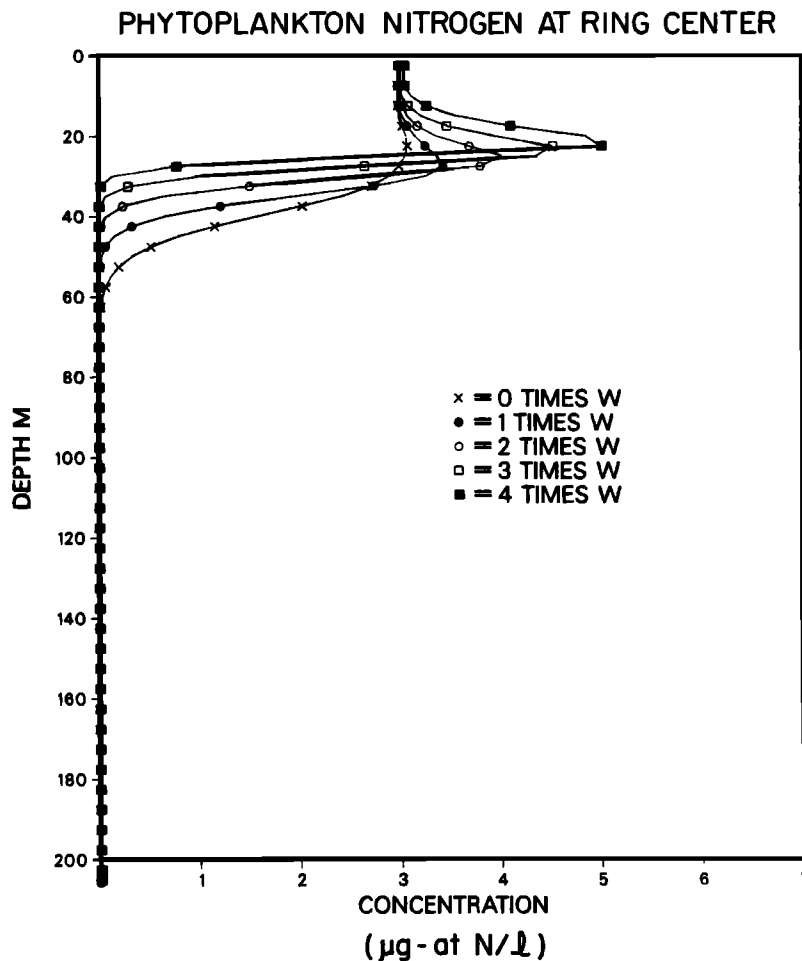


Fig. 7. Profiles of phytoplankton nitrogen at ring center for various multiples of the upwelling velocity profile $F(z)$.

radius. Since the biological parameters of the model were chosen independent of data taken in WCR 82B, we may infer that the processes described above may be a general feature of warm-core rings. The feature seen in Figures 8b, 8c, and 8d at the edge of the ring near the surface is a shelf water streamer [Altabet and McCarthy, 1985], a transient feature which cannot be addressed by the present model. The importance of streamers in altering the physical, chemical, and biological properties of rings is poorly understood.

The evolution of a relatively unproductive warm-core ring into a highly productive water mass has also been described by Tranter *et al.* [1980], Jeffrey and Hallegraeff [1980], Bradford *et al.* [1982], and Tranter *et al.* [1983]. Tranter *et al.* [1980] conclude that the increased production occurred through the mixing of the ring's own nutrient reserves into the euphotic zone. The present model predicts that this takes place through relaxation of the ring, which causes upward motion of nutrient-rich water at ring center.

The resulting production at ring center would be termed 'new production' by Dugdale and Goering [1967] and Eppley and Peterson [1979]. This implies that the phytoplankton utilize nitrate-nitrogen brought into the euphotic zone from below, rather than ammonium and urea which are forms of nitrogen biologically recycled within the euphotic zone. Highly productive areas are known for their high ratio of new production to total production, for example, upwelling regimes [Eppley *et al.*, 1979]. Although production due to am-

monium or nitrate cannot be distinguished with the present model, we can separate the proportions of dissolved nutrient contributed by biological recycling (the last three terms on the right-hand side of equation (5)) and physical processes (advection and diffusion). To create a ratio as similar as possible to Eppley and Peterson's [1979] f ratio, we have calculated the ratio of the physical input to the dissolved nutrient pool (which becomes new production), divided by the biological uptake of dissolved nutrient (total production). This ratio is plotted for an r - z section of the model ring in Figure 9. The region where this ratio is highest (i.e., where the greatest proportion of production is based on physical input of dissolved nutrient) is at ring center at the base of the lens of high phytoplankton biomass. Here a little over 20% of the total production is based on dissolved nutrient made available through physical processes. It remains to be seen whether this prediction will be verified by future observations and experiments in warm-core rings.

From the numerical experiments we predict that any transient or sustained enhancement of the ring decay would lead to increased phytoplankton concentration in the lens at ring center. Since the ring's decay is not a steady process [Olson *et al.*, 1985], we would not expect the phytoplankton in the lens to be in a steady state. Thus large deviations from the predicted chlorophyll concentrations could be expected in a warm-core ring, depending on its recent history.

The model formulated above gives a mechanism for the

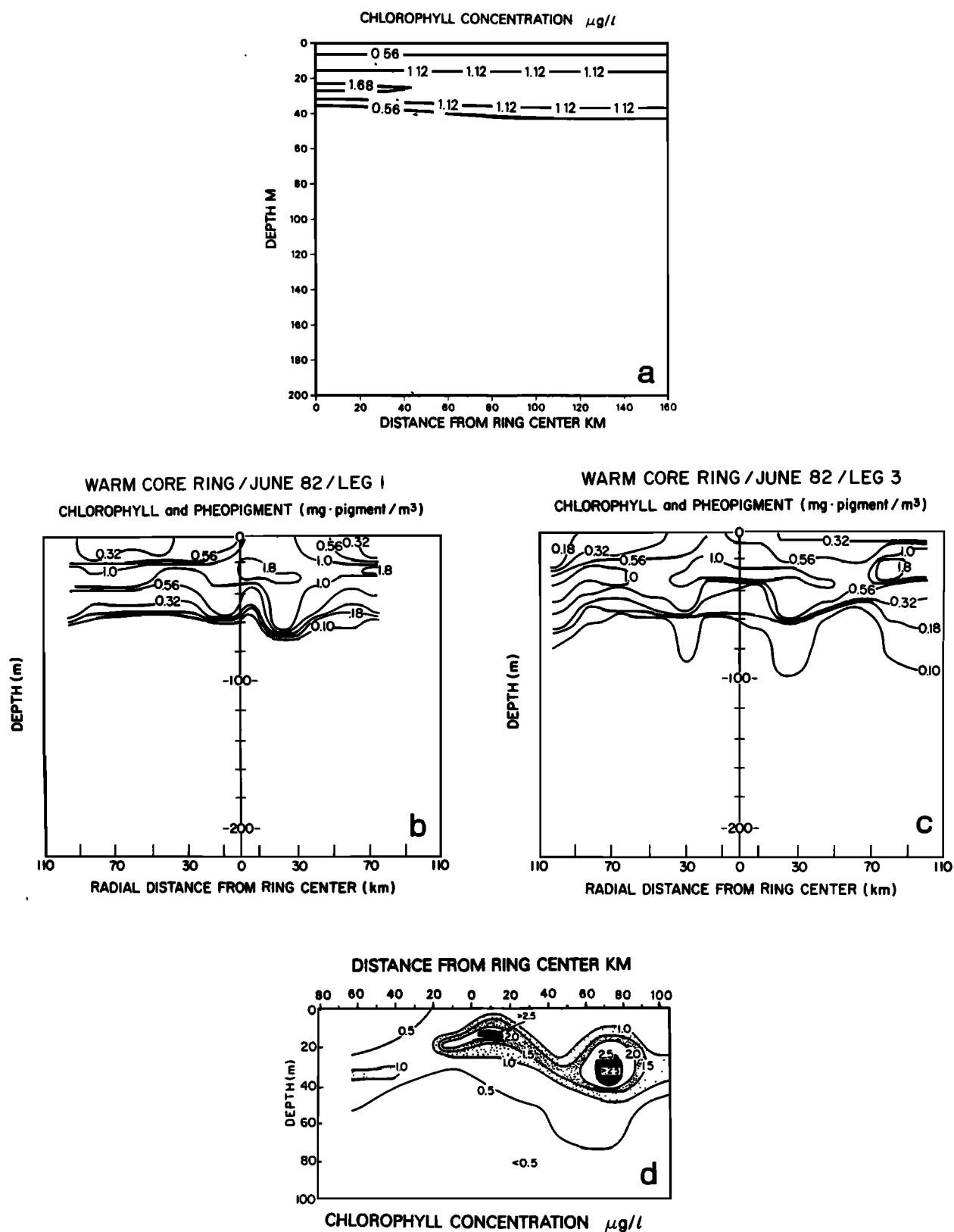


Fig. 8. (a) Model chlorophyll field generated after 60 days. (b, c) Chlorophyll and phaeopigment data of Smith and Baker [1985] from WCR 82B in June, (d) Chlorophyll transect of WCR 82B in June from Yentsch and Phinney [1985].

formation of certain spatial patterns seen in the phytoplankton and nutrient fields of warm-core rings. By including more detailed physical processes (e.g., mixed-layer dynamics) and a more complex biological model (including a detrital pool, ni-

trate and ammonium, and vertical fluxes of nitrogen through fecal pellets or vertical migration), elucidation of the detailed biological structure observed in warm-core rings may be possible.

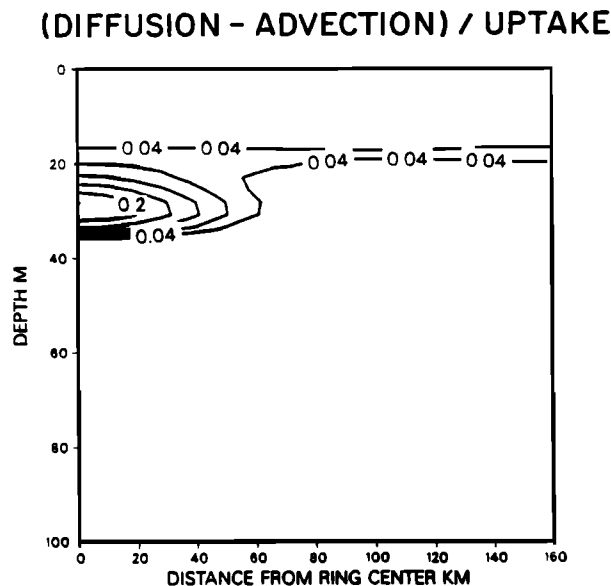


Fig. 9. A section plot of the ratio of the physical input to the dissolved nutrient pool (diffusion of N minus advection of N) over the total production (uptake of N), at steady state. This is similar to Eppley and Peterson's [1979] f ratio.

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