Impact of Dynamic Light and Nutrient Environments on Phytoplankton Communities in the Coastal Ocean

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When we try to pick out anything by itself, we find it hitched to everything else in the Universe.

John Muir (1838–1914)

In this chapter you will be able to explore:

- Responses of phytoplankton growth to light fields and nutrient concentrations;
- Effects of eutrophication on the structure of phytoplankton communities.

8.1. Introduction

Phytoplankton represent the base of the food web in marine ecosystems. Changes in the structure and composition of these phytoplankton communities will, therefore, have a direct effect on the amount of carbon available to higher trophic levels. In the absence of significant grazing, light and nutrients are the primary factors regulating phytoplankton **photosynthesis** and productivity in marine environments. As the requirements for light and nutrients differ between species, phytoplankton community structure is also sensitive to dynamic optical and chemical conditions in the water column.

Nutrient loading in coastal regions from agricultural runoff and urbanization has been documented on a global scale. Nitrogen (N) and phosphorous (P) inputs into coastal seas have increased four-fold, leading to considerable **eutrophication** (Martin et al. 1981; Nixon 1995). These nutrient additions result in significant shifts in the ratios of macronutrients in the coastal margins. Shifts in nutrient ratios can alter phytoplankton community structure, changing the timing and abundance of dominant phytoplankton species in coastal areas (Sommer 1989; Admiraal et al. 1990; Smayda 1990; Officer and Ryther 1980; Conley et al. 1993; Turner and Rabalais 1994). Increases in N and P concentrations relative to silicate (Si) concentrations have been shown to favor the dominance of non-siliceous phytoplankton over siliceous di-

atom species (Humborg et al. 1997). These non-siliceous phytoplankton are predominantly flagellates, often dinoflagellates, forming dense blooms along the coast. The occurrence of these blooms has raised concern as they are increasing in frequency and are often toxic (see Anderson and Garrison 1997). These toxic blooms are associated with massive mortalities in fish (both farmed and wild), shellfish, birds, and marine mammals. Although there are no global estimates of economic losses due to harmful algal blooms, estimates from isolated individual events provide some indication of the scale of the problem. In Alaska alone, it is estimated that losses from the shellfish industry are \$50 million annually (Neve and Reichardt 1984). The Gulf coast of Florida experiences frequent red tides, often accompanied by dead fish washing up on beaches, contaminated shellfish, and human respiratory problems owing to toxics aerosolized by the surf. Habas and Gilbert (1974) estimated a loss of \$20 million for each event in 1974.

Increased sediment loading and changing bloom composition also modify the relative light fields to which phytoplankton are exposed. As with nutrients, different phytoplankton groups and species respond differently to light intensity with respect to photosynthesis and growth. This exerts an additional selective mechanism on the phytoplankton community structure that may influence the coastal food web. Recent significant changes in environmental conditions select against species that have narrow tolerance ranges with respect to nutrients and light.

8.2. Model Formulation

Here we demonstrate the dynamics and multiple feedback mechanisms between phytoplankton abundance, light and nutrients. The model integrates the concepts of nutrient uptake kinetics, light utilization and photosynthesis with respect to changing environmental conditions. Given these interactions, the impacts of changing nutrient ratios, the effects of water-column mixing and light propagation on phytoplankton abundance and community structure can be predicted. The model is designed to help elucidate some potential anthropogenic impacts on phytoplankton communities in coastal ocean environments.

8.2.1. *Physical Environment*

The physical portion of the model follows a 1 m³ parcel of water (Lagrangian) in one dimension (vertical) over time. Following a single parcel of water is appropriate because the objective of the model is to examine a large-scale phenomenon, where it is assumed that similar processes are occurring in adjacent water masses. This parcel of water is then mixed, expressed as a simplified description of circular motion, which leads to a sin-shaped variation of the depth (Z) similar to Pahl-Wostl (1992).

$$Z(t) = \text{Mixed Layer Depth} / 2 * (1 + \sin(2 * \pi * \text{TIME} / \text{Length of Rotation Period})), \quad (7)$$

Both the Mixed Layer Depth and the Length of Rotation Period can be varied with time to reflect different mixing regimes. The Length of Rotation Period must be an integer in the model as it is relative to Julian date (TIME). The module of Figure 8.1 captures the calculations of Mixed Layer Depth, Length of Rotation Period, and $Z(t)$.

8.2.2. In Situ Light Field

The light field impinging on the parcel of water at any given time is specified as a function of the incident light field at the surface, the depth of the parcel of water and the attenuation of light through the water column. The surface incident light field at a given time over the year ($I_o(t)$) is quantified as a cubic sin function according Marra (1978):

$$I_o(t) = I_{\max} * \sin(\pi * \text{TIME} / 365)^3 + I_{\min}, \quad (8)$$

where $I_{\max}$ is the maximum irradiance (moles photons/m²/d). $I_{\min}$ sets a minimum value during the winter solstice. The value of 2 moles photons/m²/d is used as an estimate for the Baltic Sea, where the effect of nutrient runoff on phytoplankton communities has been shown and where this model will be demonstrated (Conley et al. 1993). The *in situ* light field affecting the parcel of water (I_z) is therefore a fraction of Equation 2,

$$I_z(t) = I_o(t) * \exp(-1 * \text{ATT} * Z), \quad (9)$$

where light attenuates exponentially with depth and where ATT is the attenuation coefficient (Kirk 1994). The attenuation coefficient is a function of the attenuation owing to water and dissolved material (0.3 is used as an

FIGURE 8.1

FIGURE 8.2

average value; Kirk 1994) and the attenuation owing to the accumulation of phytoplankton cells, creating a dynamic feedback over time (Figure 8.2).

8.2.3. Phytoplankton Groups

Two phytoplankton groups are used in this model to illustrate the competitive interaction resulting from nutrient loading in coastal regions. **Diatoms** are historically the dominant bloom-forming phytoplankton, responsible for the majority of the biomass reaching higher trophic levels. **Dinoflagellates** are flagellated single-celled algae that have more recently been found to form significant, and occasionally toxic, blooms.

Phytoplankton from both groups are able to respond differentially to light according to the photosynthesis-irradiance relationship given by the hyperbolic tangent model of Neale and Richerson (1987), such that

$$\text{Phytoplankton Growth} = \text{Growth Nutrient} * \text{TANH}(Iz/Ik),$$

where either the diatom or dinoflagellate growth rate is a fraction of the maximum growth rate, scaled to the nutrient-dependent growth rate (see Figure 8.3 and 8.4, and below).

The fraction of the maximum growth rate is dependent on the ratio of the *in situ* light level, specified in equation (3), and I_k , the irradiance level at which photosynthesis (and growth) is saturated. The hyperbolic tangent (TANH) is not a built-in function of STELLA and therefore requires trigonometric formulation. The final growth rate is used to calculate the number of new cells per DT (1 day), based on the number of cells in the previous time step. In order to maintain cells beyond a single time step, cells in the model

FIGURE 8.3

are sequentially “moved” to conveyors (Figures 8.5 and 8.6). For this model, the lifetime of a cell is 4 days. A minimum population of 50 cells/m³ is maintained for each group.

8.2.4. Nutrient Concentrations and Nutrient Requirements

Nutrient concentrations for both Si and N are expressed as the number of moles in the cubic-meter parcel of water. The loss of nutrients over time is a function of the uptake rate per phytoplankton cell and the total number

FIGURE 8.4

FIGURE 8.5

FIGURE 8.6

$$Uptake\ Nutrient = V_{max} \text{ Nutrient} * ([Nutrient]/([Nutrient] + Ks\ Nutrient)), \quad (1)$$
[illegible]

FIGURE 8.7

8.3. Model Results

The results discussed in this section have been derived under a set of simplifying assumptions. Specifically, the present model examines dynamics with two phytoplankton groups. As with any marine environment, there are more than two phytoplankton groups, and within groups, phytoplankton species have significantly different responses to both light and nutrients. Phytoplankton in the natural environment are always subject to grazing pressure from zooplankton. Inclusion of grazing in this model would add another dynamic variable affecting the number of phytoplankton cells and increasing the regeneration time of N. The addition of more than two nutrients would add further realism to the model.

8.3.1. Physical Dynamics

In order to illustrate the physical dynamics in the model, let us follow total diatoms and dinoflagellate populations over the course of two years. In this case, the effects of light and nutrients are equal for both phytoplankton groups. To generate equal nutrient requirements for both groups, the K_s value for Si is set to 0 so that N is the only nutrient being equally utilized by both groups. The dynamics shown in Figure 8.9 are a function of variable mixing depth, period of rotation of the parcel of water and the annual change in the incident solar radiation. Differences between years illustrate the variable use of the N pool over the year and the feedback of increasing cell numbers, increased attenuation and decreasing light available for growth.

FIGURE 8.9

8.3.2. Light and Growth

In configuring the model to a constant mixing depth (20 meters), and no mixing over the solar cycle each year, the model runs illustrate the impact of light and nutrients on the two phytoplankton populations. In general, diatoms in the coastal oceans show higher maximum growth rates than other phytoplankton groups. If the maximum growth rate in the model is increased from 1.0 to 1.2 (maximum dinoflagellate growth rate is set to 1.0), the model output shows significantly higher diatom populations over time (Figure 8.10). Although the dinoflagellates show a rapid increase at the beginning of each year, about one month into each year numbers decrease because of the lack of light from the high attenuation of the large diatom population.

With the growth rates of both phytoplankton groups equal, the ability of the cells to compete for light can be examined. I_k is the minimum light level at which maximum photosynthesis (and growth) can be achieved. The lower the value for I_k , the lower the light needed to saturate maximum growth. Species in both phytoplankton groups have been shown to have low I_k values. For example, ice algae (both diatoms and dinoflagellates) are embedded in surface ice over the winter and are exposed to extremely low incident light. Figure 8.11 shows the case in which the diatom I_k is set to 3.2 moles photons/m²/d and dinoflagellates have lower I_k (2.5 moles photons/m²/d). In this case, dinoflagellates easily dominate over diatoms, with similar light limitation dynamics as in Figure 8.10.

By altering both the maximum growth rates and the I_k values simultaneously in the model, the interactions between the variables can be elucidated.

FIGURE 8.10

FIGURE 8.11

For example, set I_k values to those in Figure 8.11, the maximum growth rate for diatoms to 1.26 and leave the maximum dinoflagellate growth at 1.0. Run the model for four years to see both inter- and intra-annual dynamics (Figure 8.12). Despite a higher growth rate, diatom abundance is now not so high as that for dinoflagellates. The ability of dinoflagellate cells to better compete for light allows them to peak earlier than diatom cells. The higher

FIGURE 8.12

growth rate for diatoms, however, prevents the light limited decline shown in Figures 8.10 and 8.11. Dinoflagellates increase with each successive season because of a higher initial seed population at the beginning of each year, while diatoms show the opposite trend. Interestingly, if the light level is decreased under these conditions (mixing depth increased), the intensity of the interannual trend decreases.

8.3.3. Nutrient Dynamics

Let us next examine the impact of nutrients on phytoplankton communities. To do so, we assume there are no mixing dynamics and that growth and responses to light are equal for diatoms and dinoflagellates. We also assume that both phytoplankton groups are equally dependent on the availability of N. With these assumptions, the response of the diatom population to two initial N concentrations can be seen. Over the two years, the first condition (N at 0.003 moles/m³) shows the population simply responding to changes in the incident solar irradiance over the year (Figure 8.13). The second run assumes a starting value of N = 0.0004 moles/m³ and shows temporary increases in population which are followed by declines. The dynamics in the second condition are in response to limiting N concentrations. When N is limiting, cell numbers decrease and it is only when the N pool is recycled (set at 14 days) that it is again available for phytoplankton growth. Notice at the beginning of each year the N pool has ample time to accumulate during the winter months, resulting in a delay in the severest nutrient limitation.

FIGURE 8.13

In addition to the N concentration affecting variability in the phytoplankton populations, changes the half-saturation constant (K_s) regulate the ability of cells to take up nutrients. Higher K_s values require higher ambient nutrient concentrations to maintain maximum nutrient uptake rates. With N concentrations replete (0.003 moles/m³), the K_s value of diatoms is increased. Figure 8.14 shows the ratio of diatoms to dinoflagellates equals 1 over the year when the K_s values are identical (0.0005 moles/m³) for both groups. As the K_s for diatoms is increased incrementally to 0.001 moles/m³ (run 4), the ability of dinoflagellates to utilize N is higher than that of the diatoms and the dinoflagellate population dramatically increases relative to diatoms.

Until now, we have not considered the influence of a second nutrient on the two populations. If the K_s for Si uptake is set to 0.00005 moles/m³, diatom abundance is dependant on two nutrients, and dinoflagellate populations increase over time relative to diatoms (Figure 8.15). Unless both N and Si are replete in the environment, the maximum growth rate for the diatoms cannot be realized. For diatoms, either N or Si will limit growth, depending on the physiological demand and the population size in the parcel of water. This demonstrates **Liebig's "Law of the Minimum"**—at any given time, if one nutrient is below the minimum requirement, the maximum growth potential of phytoplankton cannot be reached.

The model can be used to test responses in phytoplankton growth to varying Si to N ratios. As a consequence, we can explore different scenarios, ranging from replete to limiting concentrations for both nutrients. Such exploration is particularly useful, for example, to illuminate implications of nutrient loading in a coastal ocean. Figure 8.16 shows the results of three

FIGURE 8.14

FIGURE 8.15

sets of sensitivity runs for three N concentrations spanning three orders of magnitude (0.0003, 0.003 and 0.030 moles/m³). For each run, the Si concentration is varied (0.001, 0.003, 0.008 moles/m³), producing a range of Si : N ratios from 0.033 to 26.67. All nine runs are shown in Figure 8.16. The first set of runs (Graphs 1 through 3 in Figure 8.16), with 0.001 moles/m³ of Si, shows the ratio of diatoms to dinoflagellates as being below 1. With

FIGURE 8.16

higher concentrations of N, the population of dinoflagellates increases. This is despite setting the growth rate higher for diatoms (1.05). This result is essentially being found in the Baltic Sea and coastal regions (Elmgren 1989). Si concentrations have been shown to either remain the same, or to decrease, with the amount of N loading increasing, thereby changing the ratio of nutrients and selecting against siliceous phytoplankton such as diatoms. With Si concentrations higher (0.003 or 0.008 moles/m³), there is ample Si to maintain maximal growth of diatoms and dominate over the year.

8.4. Conclusions

This model illustrates the use of STELLA in describing a competitive biological interaction between two phytoplankton species. Although simple in its approach, the model incorporates some of the complexities inherent to the processes resulting in phytoplankton growth, such as physical mixing and the responses to in water light fields. As with any modeling exercise, it was important in this model to begin the model formulation with a simple and basic interaction, then build in the complexity. The center of the model is the response of growth to nutrients and the differential response of the individual groups to the two nutrients. Light is added and used to regulate the nutrient requirement for each species and light, in turn, is driven by the mixing dynamics.

The response of the model is similar to the competitive interactions in the marine environment, with one phytoplankton group dominating when the nutrient required for growth is present. Although diatoms in this case have ample supplies of nitrate, if the nutrient concentration for silicate is not adequate for maximal growth, this model shows that dinoflagellates will always dominate. The increased occurrence and frequency of non-siliceous phytoplankton blooms, often dinoflagellates, have become a concern because they are often toxic and can increase mortality in fish, shellfish, birds, and marine mammals. Changes in phytoplankton communities in the coastal ocean will directly impact both the local coastal food webs and pelagic species that depend on coastal habitats for reproduction and/or seasonal feeding. From a larger ecological perspective, these model results, and the real changes that are occurring in coastal phytoplankton assemblages, illustrate the significance and far-reaching effects of nutrient runoff and coastal eutrophication.

8.5. Questions and Tasks

1. For the physical mixing part of the model, alter the parameters for mixing depth and period of mixing with time and look at the changing light dynamics. What is the mixing depth at which the populations are light-limited for growth during mid-July on Julian day 197?

2. Use the built-in PULSE function to examine the effects of pulsed nutrients, rather than changing the nutrient ratios as discussed earlier in the chapter.
3. The model follows the dynamics in a 1 m^3 parcel of water (i.e. one depth at a time). How would you change the model to provide the depth-integrated response (i.e. the entire water column at a given time) of these phytoplankton communities to different nutrients?
4. The present model includes two phytoplankton species—diatoms and dinoflagellates—and two nutrients. Add either a third competitor or a third nutrient to the model. How do the resulting dynamics change?
5. Explore ways to add phytoplankton grazers (zooplankton) to the model, where, for example, the grazer's feeding efficiency is based on the number of phytoplankton cells, the size and/or type of phytoplankton. How do the effects of changes in nutrient and light regimes now affect phytoplankton dynamics?

PHYTOPLANKTON COMMUNITIES MODEL

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DIA_GROWTH = DIA_Growth_Si * ((EXP(Iz/DIA_Ik) - EXP(-
Iz/DIA_Ik)) / (EXP(Iz/DIA_Ik) + EXP(-Iz/DIA_Ik)))
DIA_Ik = 3.2
DIA_Kq_Si = 40e-12
DIA_Umax_Si = 1
DINO_GROWTH = DINO_Growth_N * ((EXP(Iz/DINO_Ik) - EXP(-
Iz/DINO_Ik)) / (EXP(Iz/DINO_Ik) + EXP(-Iz/DINO_Ik)))
DINO_Ik = 3.2
DINO_Kq_N = 40e-12
DINO_Umax_N = 1
Iz = Io * EXP(-1 * ATT * Z)
ATT = .03 + ((TOTAL_DIATOMS + TOTAL_DINOFLLAGELLATES) * 10E-8)
Imax = 20
Imin = 1.5
Io = (Imax * SIN(PI * Julian_Day / 365) ^ 3) + Imin
PERCENT_LIGHT = Iz / Io
NITROGEN(t) = NITROGEN(t-dt) + (REGEN_N3 - N_LOSS) * dt

INIT NITROGEN = 3e-3
REGEN_N3 = CONVEYOR OUTFLOW
N_LOSS =
(DIA_UPTAKE_N * (TOTAL_DIATOMS)) + (DINO_UPTAKE_N * (TOTAL_DI
NOFLAGELLATES))
REGEN_N(t) = REGEN_N(t-dt) + (N_LOSS - REGEN_N1) * dt

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INIT REGEN_N = 0
    TRANSIT TIME = 4
    INFLOW LIMIT = INF
    CAPACITY = INF
N_LOSS =
    (DIA_UPTAKE_N*(TOTAL_DIATOMS))+(DINO_UPTAKE_N*(TOTAL_DI
NOFLAGELLATES))
REGEN_N1 = CONVEYOR OUTFLOW
REGEN_N2(t) = REGEN_N2(t-dt) + (REGEN_N1-REGEN_N3) * dt

INIT REGEN_N2 = 0
    TRANSIT TIME = 10
    INFLOW LIMIT = INF
    CAPACITY = INF
REGEN_N1 = CONVEYOR OUTFLOW
REGEN_N3 = CONVEYOR OUTFLOW
DIA_UPTAKE_N =
    CN*DIA_Vmax_N*(NITROGEN/(NITROGEN+DIA_Ks_N))
DIA_Ks_N = .5e-3
DIA_Vmax_N = 0.4e-9
DINO_Ks_N = .5e-3
DINO_Vmax_N = 0.4e-9
CN = GRAPH(PERCENT_LIGHT)
    (0.00, 0.00), (0.1, 0.5), (0.2, 1.00), (0.3, 1.00),
    (0.4, 1.00), (0.5, 1.00), (0.6, 1.00), (0.7, 1.00),
    (0.8, 1.00), (0.9, 1.00), (1, 1.00)
REGEN_Si(t) = REGEN_Si(t-dt) + (Si_LOSS-REGEN_Si1) * dt

INIT REGEN_Si = 0
    TRANSIT TIME = 4
    INFLOW LIMIT = INF
    CAPACITY = INF
Si_LOSS = CHECK*(TOTAL_DIATOMS)
REGEN_Si1 = CONVEYOR OUTFLOW
REGEN_Si2(t) = REGEN_Si2(t-dt) + (REGEN_Si1-REGEN_Si3)
* dt

INIT REGEN_Si2 = 0
    TRANSIT TIME = 30
    INFLOW LIMIT = INF
    CAPACITY = INF
REGEN_Si1 = CONVEYOR OUTFLOW

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REGEN_Si3 = CONVEYOR OUTFLOW
SILICATE(t) = SILICATE(t-dt) + (REGEN_Si3-Si_LOSS) * dt

INIT SILICATE = 6e-3
REGEN_Si3 = CONVEYOR OUTFLOW
Si_LOSS = CHECK*(TOTAL_DIATOMS)
DIA_UPTAKE_Si = Vmax_Si*(SILICATE/(SILICATE+Ks_Si))
CHECK = if DIA_UPTAKE_Si/Vmax_Si >= .99 then Vmax_Si
else DIA_UPTAKE_Si
Ks_Si = 0
Vmax_Si = DIA_UPTAKE_N*1.0
Z = if Length_of_Rotation_Period = 0 then
Mixed_Layer_Depth else
(Mixed_Layer_Depth/2*(1+SIN(2*PI*TIME/Length_of_Rotatio
n_Period)))
Julian_Day = IF TIME<= 365 THEN TIME ELSE (TIME-
365*(INT(TIME/365)))
Length_of_Rotation_Period = GRAPH(Julian_Day)
(0.00, 0.00), (36.5, 0.00), (73.0, 0.00), (110, 0.00),
(146, 0.00), (183, 0.00), (219, 0.00), (256, 0.00),
(292, 0.00), (329, 0.00), (365, 0.00)
Mixed_Layer_Depth = GRAPH(Julian_Day)
(0.00, 20.0), (36.5, 20.0), (73.0, 20.0), (110, 20.0),
(146, 20.0), (183, 20.0), (219, 20.0), (256, 20.0),
(292, 20.0), (329, 20.0), (365, 20.0)
DIATOMS(t) = DIATOMS(t-dt) + (DIATOM_DB-DIA_HOLD1) * dt

INIT DIATOMS = 50
DIATOM_DB = DIA_GROWTH*(DIATOMS+DIA_HOLD2)
DIA_HOLD1 = DIATOMS-50
DIA_HOLD2(t) = DIA_HOLD2(t-dt) + (DIA_HOLD1-DIA_HOLD3)
* dt

INIT DIA_HOLD2 = 0
TRANSIT TIME = 4
INFLOW LIMIT = INF
CAPACITY = INF
DIA_HOLD1 = DIATOMS-50
DIA_HOLD3 = CONVEYOR OUTFLOW
DIA_HOLD4(t) = DIA_HOLD4(t-dt) + (DIA_HOLD3-DIA_HOLD5)
* dt

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INIT DIA_HOLD4 = 0
  TRANSIT TIME = 30
  INFLOW LIMIT = INF
  CAPACITY = INF
DIA_HOLD3 = CONVEYOR OUTFLOW
DIA_HOLD5 = CONVEYOR OUTFLOW
DIA_HOLD6(t) = DIA_HOLD6(t-dt) + (DIA_HOLD5-DIA_HOLD7)
* dt

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INIT DIA_HOLD6 = 0
DIA_HOLD5 = CONVEYOR OUTFLOW
DIA_HOLD7 = DIA_HOLD6
RATIO = TOTAL_DIATOMS/TOTAL_DINOFLAGELLATES
TOTAL_DIATOMS = DIATOMS+DIA_HOLD2
DINOFLAGELLATES(t) = DINOFLAGELLATES(t-dt) +
(DINOFLAGELLATE_DB-DINO_HOLD1) * dt

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INIT DINOFLAGELLATES = 50
DINOFLAGELLATE_DB =
DINO_GROWTH*(DINOFLAGELLATES+DINO_HOLD2)
DINO_HOLD1 = DINOFLAGELLATES-50
DINO_HOLD2(t) = DINO_HOLD2(t-dt) + (DINO_HOLD1-
DINO_HOLD3) * dt

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INIT DINO_HOLD2 = 0
  TRANSIT TIME = 4
  INFLOW LIMIT = INF
  CAPACITY = INF
DINO_HOLD1 = DINOFLAGELLATES-50
DINO_HOLD3 = CONVEYOR OUTFLOW
DINO_HOLD4(t) = DINO_HOLD4(t-dt) + (DINO_HOLD3-
DINO_HOLD5) * dt

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INIT DINO_HOLD4 = 0
  TRANSIT TIME = 30
  INFLOW LIMIT = INF
  CAPACITY = INF
DINO_HOLD3 = CONVEYOR OUTFLOW
DINO_HOLD5 = CONVEYOR OUTFLOW
DINO_HOLD6(t) = DINO_HOLD6(t-dt) + (DINO_HOLD5-
DINO_HOLD7) * dt

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INIT DINO_HOLD6 = 0
DINO_HOLD5 = CONVEYOR OUTFLOW
DINO_HOLD7 = DINO_HOLD6
TOTAL_DINOFLAGELLATES = DINOFLAGELLATES+DINO_HOLD2
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