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Ecological Simulation (EcoSim) 2.0 Technical Description

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ECOLOGICAL SIMULATION 2.0

The color and clarity of the water column is directly attributable to the depth-dependent distribution of mass and its associated optical properties, i.e., the Inherent Optical Properties (IOPs) of the water column. The mass in the water column can be broken down into constituent parts of living organic (viruses, bacterioplankton, phytoplankton, zooplankton, fish, mammals, etc.), non-living organic (Dissolved Organic Matter-DOM, detritus, marine snow, etc.), non-living inorganic (elements and salts, e.g., gold and nitrate, sediments, etc.), and water itself. Of these mass constituents, the sum of bacterioplankton, phytoplankton, DOM, detritus, marine snow, sediments, and water itself compose the greatest impact on water column color and clarity [*Gordon and Morel*, 1983]. Each of these optical constituents has a unique optical signature, define by its IOPs of absorption, scattering, and scattering phase function. It is the uniqueness of these constituent signatures that has given rise to the ability of inverting a color signal, e.g., satellite ocean color remote sensing, into estimates of pigments, i.e., chlorophyll a, as a proxy for phytoplankton biomass.

As the water clarity and color are directly dependent on the IOPs of the water column, the modeling component of these prognostic systems requires a fundamental set of equations that describe the interactions between the production and destruction of the IOPs. As the IOPs of absorption, scattering, and the scattering phase function can be described by a summation of the individual components, the cycle of color can be described by equations representing the individual active color constituents, i.e., phytoplankton, organic detritus, Colored Dissolved Organic Matter (CDOM), sediments, bathymetry, and bottom classification. The numerical description of the cycling of each component allows for feedback effects between the in-water light field and the production and destruction of color [*Bissett et al.*, 2001]. By extension, the accurate numerical extension of the light field and color would suggest some level of veracity in the description of the biogeochemical cycling of elements as well as the ecological dynamics of the water column.

The marine optical and ecological environment may change at on same time scales as weather changes, so any operational prognostic optical system would need to be embedded into a larger system of data collection and numerical modeling. Such a system would use moorings, ships, Autonomous Underwater Vehicles (AUVs), aircraft, satellites, and physical/ecological/optical numerical models to provide integrated data streams to a wide community of users. The systems would need to be able to assimilate data as it became available, and provide forecasts over a wide range of time and space scales. EcoSim 2.0 is an ecological/optical modeling system that has been developed for a number of applications, with the eventual goal of being incorporated into nowcast/forecast systems.

Many of the biochemical transformation equations are based on the original EcoSim 1.0 formulation [*Bissett et al.*, 1999a; *Bissett et al.*, 1999b]. The justifications of these equations are found in that earlier work. The equations below represent a synopsis of the current version of the model, as well as justifications for additions, deletions, and modifications of that earlier effort. These equations should be considered in full 3-dimensional form in order to accurately define all processes operating on carbon, nitrogen, phosphorous, silica, and iron in this model. Equation (1) shows the generic 3-dimensional form for each state equation, with the advection terms given in x, y, z, coordinates. Diffusion is ignored in this description. The Λ term represents the partial differential equation for the biological, chemical, and optical state transitions (sources and sinks) of each mass constituent.

$\frac{\partial M}{\partial t} = u\frac{\partial M}{\partial x} + v\frac{\partial M}{\partial y} + w\frac{\partial M}{\partial z} + \Lambda M$	(1)

Table 1 gives a description of the variables used in the model. A version of EcoSim 2.0 was used in a numerical analysis of phytoplankton and CDOM dynamics on the West Florida Shelf [*Bissett et al.*, 2003]. The parameters values used in that analysis are given in Tables 2-6. In addition, the latest version of the code has been coupled to a fully 3-D physical modeling, the Regional Ocean Modeling System [*Regional Ocean Modeling System (ROMS)*, 2004]. The code is freely available with registration to the ROMS user group.

1.0 Phytoplankton State Equations

The phytoplankton equations establish a community structure that allows for niche separation across a multitude of competitive dimensions, i.e., growth rate, nutrient uptake, light harvesting, etc. In particular, EcoSim allows for phytoplankton to compete by differential resource utilization. EcoSim also allows the phytoplankton functional groups to adapt to current resource conditions, as well as carry their previous resource history forward in time. This is accomplished by allowing the internal pigment concentrations to vary as a function of light and nutrient history, allowing the luxury uptake of resources, and allowing the non-Redfieldian growth of biomass. These adaptive equations do not violate the biological ocean paradigm of the relative growth rate, μ/μ_{max}, approaching 1.0 across many different ecosystems [*Goldman*, 1980]. Instead, they quantitatively allow the phytoplankton assemblage to compete for limiting resources. It is this competition for resources that drives the changes of absolute phytoplankton growth rate, μ, and the resulting shift to a new dominant phytoplankton group, while maintaining the relative rate of μ/μ_{max} near 1.0. The phytoplankton resources of this model are spectral light, nitrogen, phosphorous, silica, and iron.

The partial differential equations with respect to time for phytoplankton are:

$\Lambda PC_i = \left[\min \left(\mu_{Ll\_i}, \mu_{Nl\_i}, \mu_{Pl\_i}, \mu_{Sl\_i}, \mu_{Fl\_i}, \right) \right] PC_i - e_i PC_i - g_i PC_i - w_{s\_i}\frac{\partial PC_i}{\partial z}$	(2)
$\Lambda PN_i = \rho_{NO3\_i} + \rho_{NH4\_i} + \rho_{DON\_i} - g_i PN_i - w_{s\_i}\frac{\partial PN_i}{\partial z}$	(3)
$\Lambda PP_i = \rho_{DIP\_i} + \rho_{DOP\_i} - g_i PP_i - w_{s\_i}\frac{\partial PP_i}{\partial z}$	(4)
$\Lambda PS_i = \rho_{DISi\_i} - g_i PS_i - w_{s\_i}\frac{\partial PS_i}{\partial z}$	(5)
$\Lambda PS_i = \rho_{DIFe\_i} - g_i PF_i - w_{s\_i}\frac{\partial PF_i}{\partial z}$	(6)
$\Lambda P_i Pg_j = \theta_{ij}^{-1}\left(\Lambda PC_i\right) + \mu_{r\_i}\left(\theta_{ij\_opt}^{-1} - \theta_{ij}^{-1}\right)\left(\Lambda PC_i\right) - g_i P_i Pg_j - w_{s\_i}\frac{\partial P_i Pg_j}{\partial z}$	(7)

where *PC* (phytoplankton carbon), *PN* (phytoplankton nitrogen), *PP* (phytoplankton phosphorous), *PS* (phytoplankton silica), *PF* (phytoplankton iron), and *PPg* (phytoplankton pigments) all have *i* subscript to denote the particular Functional Group (FG) being represented.

The *i* subscript has values of 1 through 7 (Table 3). The equation for phytoplankton pigments, equation (7) represents the transport of the photosynthetic and photoprotective pigments of each FG. As each functional group has a different suite of pigments this equation is in generic form. The *j* subscript refers to individual pigment type, which are described in an earlier publication [*Bissett et al.*, 1999b] and summarized below. The realized growth rate, μ_{r_i}, is the value selected from the minimization function in equation (2). The stoichiometric ratios of the phytoplankton carbon to phytoplankton nitrogen, phosphorous, silica, iron, and pigments are allowed to vary, thus independent calculations must be written for each state variable. This approach is different than the traditional ecological modeling approaches to solving these equations and represents a deviation from Redfield-type stoichiometric assumption of carbon, nitrogen, phosphorous, silica, iron, and pigment fixation. The non-Redfield dynamics of this model is a fundamental difference of EcoSim from other ecological or biogeochemical models.

The time-dependent change in carbon resulting from biological processes is represented by equation (2). Since carbon is the organic currency of the model, increases in cellular populations are represented by an increase in the carbon concentration. The conversion between carbon concentration and cell concentration is assumed to be linear. The time-dependent changes of the phytoplankton nitrogen, phosphorous, silica, iron, and pigments are represented by equations (3) through (7).

1.1 Phytoplankton Carbon Growth

The growth of phytoplankton carbon is given by the first term of equation (2) and states that the increase in carbon at time t+1 is a result of the minimum calculated growth rate as described by light and nutrient limitation. The determination of each of the resource limited growth rates at time t depends first on the temperature-dependent relationship [*Eppley*, 1972]:

$$\mu_{mt} = \mu_m \exp^{0.0633 \quad *(T-27)} \tag{8}$$

where μ_m is the absolute maximum phytoplankton growth rate normalized to a 24 hour period at 27˚, and T is the current temperature. The temperature-dependent maximum growth rate, μ_{mt} is then used in all of the remaining resource limited growth rates.

1.2 Light-limited Carbon Growth

The equations for light-limited growth and photosynthetic efficiency were described in *Bissett et al. (1999a, b)* any exceptions to the light limited carbon growth equations are listed below:

$$\mu_{Ll\_i} = \tanh\left[\frac{\alpha_i \quad \left(E_0 - E_{0\_comp\_i}\right)}{\mu_{mt\_i}}\right] \cdot \exp\left[-decay \quad rate_i \cdot \left(E_0 - E_{0\_inhibit\_i}\right)\right] \cdot \mu_{mt\_i} \tag{9}$$

$$decay \quad rate_i = \frac{7.0 - 0.0}{E_{0\_zerogrowth\_i} - E_{0\_inhibit\_i}} \tag{10}$$

Equation (9) states that the light-limited growth rate of phytoplankton functional group *i*, μ_{Ll_i}, is a hyperbolic tangent function [*Jassby and Platt*, 1976] of the photosynthetic efficiency, α_i, divided the maximum temperature-dependent growth rate, μ_{mt_i}, multiplied by a photo-inhibition

term and μ_{mt_i}. E_0 is the scalar irradiance and $E_{0\_comp\_i}$ is the compensation irradiance below which there is no net growth. The decay rate is calculated as a function of the light level where inhibition starts, $E_{0\_inhibit\_i}$, and the light level where growth is completely inhibited, $E_{0\_zerogrowth\_i}$. (Note in *Bissett et al., 1999a* the minus sign was left off of the exponential decay term of equation (10)). The photosynthetic efficiency, α_i, changes as a function of light and nutrient history of the FG, and is seen in the pigment suite and packaging effect of the FG. The time-dependent change in α_i, is fully described in EcoSim 1.0 [*Bissett et al.*, 1999a; *Bissett et al.*, 1999b].

1.3 Nutrient-limited Carbon Growth

The nutrient-limited carbon growth rate terms μ_{nl_i}, μ_{pl_i}, μ_{sl_i}, and μ_{fl_i}, which stand for nitrogen-, phosphorous-, silica-, and iron-limited growth, respectively, all have the same functionality. This functionality is based on a modified series of equations derived from Droop's formulation of nutrient limited growth [*Bissett et al.*, 1999b; *Droop*, 1968]. These equations incorporate the nutritional state of the functional group at each time step into the calculation of the nutrient-limited growth rate. These equations are:

$\mu_{\chi l\_i} = \bar{\mu}_{\chi l\_i} \left[1.0 - \frac{K_{\chi Q\_i}}{Q_{actual\chi\_i}} \right]$	(11)
$\bar{\mu}_{\chi l\_i} = \mu_{mt\_i} \left[1.0 - \frac{K_{\chi Q\_i}}{Q_{optimal\chi\_i}} \right]^{-1}$	(12)
$K_{\chi Q\_i} = \frac{Mol\ \ \chi_{quota}}{Mol\ \ C_{quota}}$	(13)
$Q_{actual\chi\_i} = \frac{Mol\ \ \chi_{actual} + \rho_{\chi\_i}}{Mol\ \ C_{actual}}$	(14)
$Q_{optimal\chi\_i} = \frac{Mol\ \ \chi_{optimal} + \rho_{\chi \max\_i}}{Mol\ \ C_{optimal}}$	(15)

where χ has values of N, P, S, and F standing for nitrogen, phosphorous, silica, and iron calculations. Equation (11) is the functionality reported by *Droop (1968)*. It requires the values for the unattainable growth rate at an infinite nutrient concentration relative to need (infinite value of $Q_{actual\chi\_i}$), $\bar{u}_{\chi l\_i}$ (equation (12)), the minimum cell nutrient quota in which growth can occur, $K_{\chi Q\_i}$ (equation (13)), and the actual nutrient status of the cell, $Q_{actual\chi\_i}$ (equation (14)), and . The nutritional status of the cell is represented by the stoichiometric ratio of nutrient χ to carbon (since carbon is a proxy for phytoplankton cell concentration), so that $K_{\chi Q\_i}$, $Q_{actual\chi\_i}$, and $Q_{optimal\chi\_i}$ terms have units of Mol χ:Mol C. We solve for the unattainable growth rate, $\bar{u}_{\chi l\_i}$, by inverting equation (11) and substituting the optimal nutrient status for growth, $Q_{optimal\chi\_i}$, for $Q_{actual\chi\_i}$, which gives equation (12). The $Q_{optimal\chi\_i}$ value is given by equation (15), where the optimal nutrient quota for carbon-based growth is added to the maximum uptake of nutrient χ for a given time step, $\rho_{\chi max\_i}$ (see below), and divided by the optimal quota for carbon. For example, if we assume a Redfield nitrogen to carbon relationship is the value for optimal growth, then $Q_{optimal\chi\_i} = (1.0 + \rho_{Nmax\_i})/6.625$. $K_{\chi Q\_i}$ is a phytoplankton parameter (given in Table 1). $Q_{actual\chi\_i}$ is calculated by taking the value of $P\chi$ (Mol χ) from the previous time step, adding it to the total

nutrient uptake at the current time step, $\rho_{\chi max\_i}$, and dividing by the value of *PC* (Mol C) from the previous time step.

1.4 Phytoplankton Nutrient Uptake

One major difference between the nutrient uptake equations of EcoSim 1.0 and 2.0 is that acceleration functions for nutrient uptake (Ecosim 1.0 equations A.11 and A.12) have been eliminated. Closer examination of nutrient uptake, ρ, versus carbon growth, μ, suggests that there is not an acceleration of uptake so much as there is a deceleration of carbon growth for larger phytoplankton species under total resource limitation [*Morel*, 1987]. The net result of such an effect would be internal nutrients stocks increasing at a greater rate than carbon stocks, and would appear to be an acceleration of nutrient uptake, hence the earlier equations A.11 and A.12. However, this result is also simulated by allowing the internal stocks of nutrients to increase at a greater rate than carbon based growth, i.e. nutrient uptake rates that are greater than realized assimilation and growth, and the acceleration functions are unnecessary. In addition, phytoplankton carbon to nutrient ratios are allowed to drop below that of optimal growth, reflecting a "luxury" uptake of nutrients [*Wheeler*, 1983]. This luxury uptake provides a tremendous advantage to larger phytoplankton species as it provides them with the internal nutrient stocks to "bloom" rapidly upon the reduction of the limitation cause by some other limiting resource. This represents a competitive advantage for larger species that partially offsets the diffusive uptake advantages that smaller species have.

Besides the addition of three new limiting nutrients, another major difference in the nutrient dynamics of EcoSim 2.0 is the ability of phytoplankton to take up organic forms of nitrogen and phosphorous. We make the assumption that phytoplankton are strictly autotrophic, and that the DOC associated with these nutrient pools is immediately released back to the water column. We also assume that the ability to take up organic nutrients only occurs after the phytoplankton reach a critical carbon to nitrogen and carbon to phosphorous ratio (K_{sDON} *C:N* and K_{sDOP} *C:P*, Table 1 and 4).

The functionality of uptake is the same by Michaelis-Menten function for all nutrients (as shown in equation (16) ammonium).

$$\rho_{NH_4\_i} = \mu_{mt\_i} \left[\frac{NH_4}{K_{sNH_4\_i} + NH_4} \right] \cdot PN_i \qquad (16)$$

There are similar equations for *DIP*, *DISi*, *DIFe*, *DON*, and *DOP*. The exception to this general equation is the uptake of NO_3, and is represented by (17):

$$\rho_{NO_3\_i} = \mu_{mt\_i} \left[\frac{NO_3}{K_{sNO_3\_i} + NO_3} \; e^{-\psi_{\_i} \cdot NH_4} \right] \cdot PN_i \qquad (17)$$

The ρ_{NO3} term is modified by a nitrate repression term as a function of ammonium concentrations [*Wroblewski*, 1977]. It allows for the preferential uptake of ammonium. Care must be used in the selection of the nitrate uptake repression exponent, Ψ_i, such that "super" uptake does not occur. This happens when the sum of the nitrate and ammonium Michaelis-Menten functions exceed 1.0. The uptake of nutrients is set to zero when the carbon to χ ratio drops below the minimum allowed carbon:χ parameter (Table 1 and 4). In the presence of large quantities of total nitrogen

and phosphorous stocks, nutrient uptake will greatly exceed the carbon growth rate, as the carbon growth rate is also limited by μ_{mt_i}. In these cases, excess nutrients are either immediately released, in the case of small phytoplankton that do not have luxury uptake capabilities, or accumulate until the maximum quota is achieved and then released (Note: a FG with the maximum quota of nutrients, χ, will have its minimum allowable C:χ ratio).

A note on this WFS set of simulation analyses. The iron dynamics have been effectively shut off for phytoplankton, and competition for iron stocks is set to zero. This stems mainly from the lack of initialization and boundary condition data available at the time of this work. Future 4-D simulations will include competition within the iron niche space, so it is incorporated for completeness in these equations.

1.5 Phytoplankton Carbon and Nutrient Loss Terms

The next two terms in equation (2) are the reduction of phytoplankton carbon biomass resulting from excretion (e_i) and grazing and lytic losses (g_i). Excretion is a linear rate of biomass, limited to 0.5% per day [Table 4 *Bjørnsen et al.*, 1988], this is an order of magnitude less than EcoSim 1.0 and results from a re-evaluation of the work of *Bjørnsen (1988)*. Grazing and lytic loss account for the majority of the biomass sink in this model, and is considered the closure term of the phytoplankton equations [*Steele and Henderson*, 1992]. It is modeled as function of a minimum mortality term multiplied by the logarithm of the total functional group mass divided by the refuge population:

$$g_i = mortality_i \cdot \log\left(\frac{PC_i}{refuge_i}\right) \qquad (18)$$

A modification of this equation occurs when the level of PC_i drops below 0.02 Mol C; below this level g_i is set to zero. This establishes a refuge population of FG_i below which there is no grazing or lysis. This function is a significant change from the original coding, and assumes that the magnitude of the carbon concentration is the best indicator of loss due to stress and grazing. This function is the same for carbon and nutrient equations and does not change the stoichiometric ratio of the phytoplankton, i.e., phytoplankton are grazed and lysed at the current C:χ ratio.

1.6 Phytoplankton Vertical Migration and Sinking

The last term of equations (2) through (7) reflects the vertical migration and sinking of phytoplankton. It is assumed to be a linear function, w_{s_i}, of the change in phytoplankton concentration with depth, since the change in concentration at a point in time and depth is a function of the divergence/convergence of the flux [*Bissett et al.*, 1999b].

1.7 Intra-cellular Pigment Changes

Phytoplankton pigment changes (equation (7)) are modeled as a function of the optimal phytoplankton carbon to pigment ratio (θ_{ij_opt}), the current carbon to pigment ratio (θ_{ij}), and the realized growth rate [(r_i *Bissett et al.*, 1999b; *Falkowski and Wirick*, 1981], which is equal to the minimization function in equation (2). The optimal accessory pigment concentrations for each functional group are linear functions of their carbon to chlorophyll a ratio (Table 4). Equation (7) can thus be solved just once for each functional group for its optimal carbon to chlorophyll a ratio (θ_{i_opt}, where the *j* subscript is replaced by 1 representing chlorophyll a and

the other pigments linearly derived from the chlorophyll a to carbon ratio. The calculation of the optimal carbon to chlorophyll a ratio is:

$\theta_{i1\_opt} = \max\left(\theta_{opt\_ll\_i1}, \theta_{opt\_nl\_i1}\right)$	(19)
$\theta_{opt\_ll\_i1} = \theta_{0\_ll\_i1} + slope_{\theta\_ll\_i1} \cdot E_0(z)$	(20)
$\theta_{opt\_nl\_i1} = \theta_{0\_nl\_i1} + slope_{\theta\_nl\_i1} \cdot C_i : N_i$	(21)
$\zeta_{ij} = \zeta_{0\_ij} + slope_{\vartheta\_ij} \cdot \left(\theta_{t\_i} - \theta_{0\_ll\_i1}\right)$	(22)

where θ_{i1_opt} is equal to the maximum carbon to chlorophyll a ratio calculated by light-, nitrogen-limit equations, $\theta_{opt\_ll\_i1}$ and $\theta_{opt\_nl\_i1}$ respectively. $E_0(z)$ is the scalar irradiance at depth z, and $C_i:N_i$ is the current carbon to nitrogen ratio. The total pigment complement of each functional group impacts the growth calculation of each functional group at the next time step via equation (9) and equations A.5 through A.8 of *Bissett et al., (1999b)* by altering the photosynthetic efficiency term, α_i. Equation (7) does not have the g_i function in it because the pigment concentrations are tracked through the carbon to pigment ratios. As carbon is adjusted, so are the pigment concentrations. The accessory pigments are altered each time step that the carbon to chlorophyll a ratio is altered by equation (22), where ζ_{ij} is the pigment to chlorophyll a ratios, and ζ_{0_ij} is the accessory pigment to concentration when the carbon to chlorophyll a ratio at time t equals the minimum light-limited carbon to chlorophyll a ratio.

The changes in intra-cellular pigment concentrations are calculated differently than the nutrient pools. There is conservation of pigment mass in this model during physical advection and mixing, but the time-dependent biochemical change results in the creation and destruction of pigments without tracking the pigment protein sources or the production of pigment by-products. This is different than carbon, nitrogen, phosphorous, silica, and iron stocks, where every mole of each constituent is tracked through the processes of inorganic/organic/inorganic conversions.

2.0 Bacterioplankton State Equations

The terms ΛBC and $\Lambda B\chi$, where χ has terms of N, P, and F in equations (23) and (24) represent the biological sources and sinks of phytoplankton carbon, nitrogen, phosphorous, and iron.

$\Lambda BC = \min\left[\rho_{bc\_el}, \rho_{bc\_nl}, \rho_{bc\_pl}, \rho_{bc\_fl}\right] + \frac{A\,to\,N}{7.0} - g_B BC - w_{sb}\frac{\partial BC}{\partial z}$	(23)
$\Lambda Bx = \min\left[\rho_{bc\_el}, \rho_{bc\_nl}, \rho_{bc\_pl}, \rho_{bc\_fl}\right] \left(\frac{x_b}{C_b}\right) + \frac{A\,to\,N}{7.0}\left(\frac{x_b}{C_b}\right) - g_B Bx - w_{sb}\frac{\partial Bx}{\partial z}$	(24)

The gains in bacteria carbon, nitrogen, phosphorous, and iron are the result of two processes. The first term in equations (23) and (24) represents the growth of carbon biomass resulting from most limiting resource available to the heterotrophic bacterial community. The limiting resources to heterotrophic bacteria are energy in the form of labile DOC, nitrogen in the forms of DON and NH_4, phosphorous in the forms of DOP and DIP, and iron in the form of DIFe. Thus, the growth of heterotrophic bacteria mass is calculated as the smallest of the individual resource limited growth rates. In addition to the growth of heterotrophic bacteria mass, there is additional bacterial biomass increase resulting from the utilization of ammonium

as an electron source for carbon fixation. This is represented by the second term in equations (23) and (24). As uptake and assimilation of carbon, nitrogen, phosphorous, and iron is assumed to be in a fixed stoichiometric ratio for chemolithic activities, this term is carried through the remainder of the $\Lambda B\chi$ equations with a stoichiometric conversion factor. The third term in these equations represents the loss of mass resulting from grazing pressures on the total bacteria community. The last term is the change in biomass resulting from vertical movement.

2.1 Bacterioplankton Carbon and Nutrient Stocks

The structure of the bacterial equations has been altered from the original EcoSim 1.0 coding. This occurred for two reasons. The first is that the simulated bacteria were found to never be limited by NH_4, rendering the equations used from the *Fasham et al., (1990)* model redundant. Thus, equations A.22 through A.27 of EcoSim 1.0 have been eliminated. These equations would have been useful for fixed stoichiometric conversion amongst the organic and inorganic components of the model [*Fasham et al.*, 1990]. However, when the carbon and nitrogen stocks were allowed to vary amongst all of the constituents, i.e., phytoplankton, DOM, fecal material, etc., and gross growth efficiencies of dissolved organic carbon and nitrogen use were allowed to vary, it was found that bacteria were always energy limited and that there were sufficient nitrogen stocks in the DOM pool to satisfy the bacterial nitrogen requirements [*Bissett et al.*, 1999b]. The second reason for the major change of the bacterial equations was that the *Fasham et al., (1990)* equations were built around a single limiting nutrient (nitrogen) with multiple components (DON and NH_4). EcoSim 2.0 constrains bacterial growth by energy (DOC_1) and three limiting nutrients (nitrogen, phosphorous, and iron) in 5 forms (DON, NH_4, DOP, DIP, DIFe). These two issues required deriving a different methodology to simulate bacterial growth and nutrient regeneration.

2.2 Temperature-dependent Growth

The temperature-dependent maximum bacterial, μ_{mt_b}, growth rate was previously defined in Bissett et al., (1999b) and the same equation is utilized in this version of the model.

2.3 Energy-limited Carbon Uptake

Energy resources were the limiting factor for bacterial growth in EcoSim 1.0. The equations to calculated energy uptake are basically the same in EcoSim 2.0, with the exception that colored dissolved organic carbon is not removed from the model as a result of heterotrophic uptake of CDOC, and equation A.32 from *Bissett et al. (1999b)* has been eliminated (see below). This slightly reduces the total available labile pool of DOC for heterotrophic activities. The carbon uptake and assimilation term for bacteria, ρ_{bc_el}, is define as:

$$\rho_{bc\_el} = U_{BDOC1} \cdot \left(1.0 - e_{bc}\right) \cdot GGE_c \tag{25}$$

$$U_{BDOC1} = \mu_{mt\_b} \cdot \left(\frac{DOC_1}{K_{s\_BDOC1} + DOC_1} \right) \cdot BC \cdot \left(GGE_c\right)^{-1} \tag{26}$$

where U_{BDOC1} is the gross uptake of labile DOC by bacteria, GGE_c is the gross growth efficiency of bacteria for carbon. While the equation for ρ_{bc_el} could be simplified by the cancellation of the GGE_c term from the equations, U_{BDOC1} and $e_{bc}U_{BDOC1}$ are used in other locations of the model, so their explicit calculation is required. As in EcoSim 1.0, excretion is removed after the calculation

of total uptake of labile DOC, such that realized the realized gross growth efficiency is slightly less than the GGE_c used.

2.4 Nutrient-limited Carbon Uptake

The nutrient-limited carbon uptake assumes 100% conversion efficiencies for the limiting nutrients of nitrogen, phosphorous, and iron. The bacterial carbon to χ ratio (Table 5) is used to convert total nutrient uptake and assimilation to total carbon assimilation. Uptake of each of the limiting forms of the resources is described by Michaelis-Menten functions.

$\rho_{bc\_nl} = \left[U_{BDON1}\left(1.0 - e_{bn}\right) + U_{BNH4}\right] \cdot \left(\frac{C_b}{N_b}\right)$	(27)
$U_{BDON1} = U_{BDOC1} \cdot \left(\frac{DON_1}{DOC_1}\right)$	(28)
$U_{BNH4} = \mu_{mt\_b} \cdot \left(\frac{NH_4}{K_{s\_BNH4} + NH_4}\right)$	(29)
$\rho_{bc\_pl} = \left(U_{BDOP1} + U_{BDIP}\right) \cdot \left(\frac{C_b}{P_b}\right)$	(30)
$U_{BDOP1} = U_{BDOC1} \cdot \left(\frac{DOP_1}{DOC_1}\right)$	(31)
$U_{BDIP} = \mu_{mt\_b} \cdot \left(\frac{DIP}{K_{s\_BDIP} + DIP}\right)$	(32)
$\rho_{bc\_fl} = U_{BDIFe}$	(33)
$U_{BDIFe} = \mu_{mt\_b} \cdot \left(\frac{DIFe}{K_{s\_BDIFe} + DIFe}\right)$	(34)

ρ_{bc_nl}, ρ_{bc_pl}, and ρ_{bc_fl}, representing nitrogen-, phosphorous-, and iron-limitation, respectively, define the bacterial carbon uptake and assimilation resulting from nutrient-limitation. The gross uptake of labile DON and DOP, U_{BDON1} and U_{BDOP1}, respectively, are functions of the uptake of DOC calculated above in equation 26 and the ratio of DOχ to DOC at the grid cell. The excretion of recalcitrant dissolved organic nitrogen, DON_2, is calculated by $e_{bn}U_{BDON1}$. Like the uptake and assimilation of DOC in equation (25), only the resultant uptake $(1.0 - e_{bn})U_{BDON1}$ is used for uptake and assimilation of total nitrogen calculation. U_{NH4}, U_{DIP}, and U_{DIFe} describe the gross uptakes of inorganic nitrogen, phosphorous, and iron, respectively. Bacteria are not assumed to have luxury storage capabilities. This assumption is based on the ability of bacteria to process DOM via exo-enzymatic reactions, and is different from the above assumptions for phytoplankton that rely on nutrients being passed through the cell wall before processing. After the calculation of the MIN function in equations (23) and (24), all of the excess nutrients are released in the form there were acquired.

As an aside, here are a couple of comments on the bacterial growth equations. As long as the stoichiometric ratio of carbon to χ in dissolved organic matter is less than the defined $C_b{:}\chi_b$ divided by GGE_c, these bacterial equations will always yield an energy limitation versus nitrogen

and phosphorous supplies. In other words, using strictly Redfield growth for phytoplankton and converting this material into DOM will always yield energy limited populations of bacteria. However, these equations become important when there are supplies of DON and DOP are not in phytoplankton Redfield balance, e.g. river runoff, or when phytoplankton compete for DON and DOP resources. Also, the numerical implementation of these equations is difficult. After the MIN function of equations (23) and (24) are calculated, the release of which forms of the material needs to be calculated, in order to maintain mass balance, as well as stoichiometric balance of the other constituents.

2.5 Chemolithic Bacterial Growth

The second term of equations (23) and (24) describes the accumulation of carbon biomass resulting from the chemolithic conversion of ammonium to nitrate, i.e., nitrification. Nitrification is assumed to occur rapidly in the dark in a single step from ammonium to nitrate. This ignores the accumulation of nitrite and the difference between the bacterial communities responsible for the each step. The equation for *AtoN* is described by a Michaelis-Menten function:

$$AtoN = MaxNit \left(\frac{NH_4}{K_{sNit} + NH_4} \right) \quad (35)$$

where *MaxNit* is the maximum nitrification rate in the dark. This estimate of net carbon fixation resulting from the energy acquired from oxidation of NH_4 is assumed to occur at the molar ratio of 1 to 7 [*Ward*, 1982], thus *AtoN* is divided by 7.0 to simulate net bacterial carbon accumulation. The molar ratio of bacterial carbon to χ is used to convert this term in equation (23) to the second term in each of the other bacterial stock equation (24).

2.6 Bacterial Grazing Losses, Lytic Losses, and Vertical Migration

The variance of total bacterial stocks is far less than that of phytoplankton in the open ocean [*Carlson et al.*, 1996], so we assume that the grazing and lytic losses are a one to one function of the bacterial growth. Thus, g_bBC and $g_bB\chi$ of equation (23) and (24) are:

$$g_BBC = \min\left[\rho_{bc\_el}, \rho_{bc\_nl}, \rho_{bc\_pl}, \rho_{bc\_fl} \right] + \frac{AtoN}{7.0} \quad (36)$$

$$g_BB\chi = \min\left[\rho_{bc\_el}, \rho_{bc\_nl}, \rho_{bc\_pl}, \rho_{bc\_fl} \right] \left(\frac{\chi_b}{C_b} \right) + \frac{AtoN}{7.0} \left(\frac{\chi_b}{C_b} \right) \quad (37)$$

and bacterial concentrations do not vary with time. The bacterial equations describe the mechanisms for biochemical transformation of organic and inorganic materials and set rate limiting processes on the regeneration of nutrients in the water column. In coastal communities, the assumption of limited variance of the bacterial community may be challenged. Future work will address this issue. Bacteria are also not assumed to vertically migrate, or sink. Thus, w_{sb} is set to 0.0 m d^{-1}.

3.0 Dissolved Organic Matter State Equations

The biochemical transformation equations of DOM are approximately the same as in EcoSim 1.0. The exception is that nitrogen fixation by *Trichodesmium* spp. is not included [equation A.36 *Bissett et al.*, 1999b] in this model. Dissolved Organic Matter (DOM) refers to the total of mass of carbon, nitrogen, and phosphorous in these forms. Dissolved organic silica and iron organic forms are ignored, and the total stocks of these elements are incorporated in their inorganic equations (58) and (59). While there is evidence that silica and iron exist in chelated organic forms [*Hutchins et al.*, 1999; *Sunda and Huntsman*, 1997], there is little validation data to resolve the separate dissolved inorganic and organic forms. The time-dependent changes in Dissolved Organic Carbon (DOC), Nitrogen (DON), and Phosphorus (DOP) resulting from biological and chemical processes are:

$\Lambda DOC_1 = \sum_{i=1}^{7}\left\{e_i PC_i + FecDOC_i \cdot \left(1.0 - colorFR_1\right) \cdot g_i PC_i\right\} + BacDOC \cdot \left(1.0 - colorFR_1\right) \cdot g_b BC - U_{BDOC_1} + UVDOC_1 + UVDOC_2$	(38)
$\Lambda DOC_2 = \left(1.0 - colorFR_2\right) \cdot e_{bc} U_{BDOC_1}$	(39)
$\Lambda DON_1 = \sum_{i=1}^{7}\left\{FecDOC_i \cdot g_i PN_i\right\} + BacDOC \cdot g_b BN - U_{BDON1} - U_{PDON1}$	(40)
$\Lambda DON_2 = e_{bn} U_{BDON_2}$	(41)
$\Lambda DOP_1 = \sum_{i=1}^{7}\left\{FecDOC_i \cdot g_i PP_i\right\} + BacDOC \cdot g_b BP - U_{BDOP_1} - U_{PDOP_1}$	(42)

The *i* subscript denotes the class of DOM, and has values of 1 for labile DOM, and 2 for recalcitrant DOM.

3.1 Dissolved Organic Carbon

The first term of labile DOC equation (38) is the summation of all of the additions to the DOC_1 pool by phytoplankton processes. The first component of this summation is the excretion by phytoplankton described above in equation (2). The next component is the uncolored fraction of labile DOC released by sloppy grazing and lytic processes. This release of labile DOC is assumed to be a constant fraction of the total g_iPC_i term ($FecDOC_i$; Table 1 and 5), dependent on the trophic dynamics the particular functional group [*Bissett et al.*, 1999b]. The colored/uncolored fraction of this material is also assumed to be a constant fraction of the released material ($colorFR_1$; Table 1 and 5). The second term of equation (38) represents the release of labile DOC from the loss processes operating on the bacterial community. The total release is also a linear function of the total loss (*BacDOC*) and is also separated into colored/uncolored components. The third term of the equation represents the loss of DOC_1 stocks from bacterial uptake (U_{BDOC1}; equation (26)). The last two terms are the release of uncolored labile DOC from the photolysis of colored labile DOC ($UVDOC_1$) and recalcitrant DOC ($UVDOC_2$). These terms are described in detail in *Bissett et al. (1999a)* and summarized in the colored dissolved organic carbon section below.

The other form of DOC in the model is considered recalcitrant over an annual time scale (equation (39)). This form of DOC (DOC_2) is thus only impacted by the excretion of this

material, $e_{bc}U_{BDOC1}$, during the uptake and use of labile DOC (DOC_1) by bacteria. This excretion of recalcitrant DOC also has colored and uncolored components ($colorFR_2$; Table 1 and 5).

3.2 Dissolved Organic Nitrogen

Dissolved organic nitrogen also has two forms, labile DON_1 and recalcitrant DON_2. These are described by equations (40) and (41). Like the equation for DOC_1, the first term of equation (40) is the summation of the impacts of the phytoplankton equations on the stock of DON_1, g_iPN_i. Unlike DOC_1, there is no direct excretion of DON_1 from phytoplankton. The $FecDOC_i$ term is the same used in the DOC_1 equation. The second term of equation (40) describes the increase in DON_1 resulting from bacteria grazing and lysis, multiplied by the same *BacDOC* term found in equation (38). The next term, U_{BDON1}, is net uptake of DON_1 by bacteria described by equation (28). The last term, U_{PDON1}, describes the total uptake of DON by phytoplankton, and is calculated by:

$$U_{PDON1} = \sum_{i=1}^{7} \rho_{DON1\_i} \qquad (43)$$

The recalcitrant form of dissolved organic nitrogen, DON_2, is only impacted by the excretive release of DON by bacteria, $e_{bn}U_{DON1}$, during the uptake and assimilation step in equation 28.

3.3 Dissolved Organic Phosphorous

There is only one form of dissolved organic phosphorous carried in this simulation. This form is labile, since it is assumed that all of the DOP is recycled during the course of an annual time period. The equation for labile DOP, (42), has the same type of terms found in the DON_1 equation. The first term is the summation of the phytoplankton grazing and lytic releases, the second term is the release from bacterial grazing and lysis, the third term is the uptake of DOP_1 by bacteria, and the fourth term is the summation of the phytoplankton uptake. The last term has the form of:

$$U_{PDOP1} = \sum_{i=1}^{7} \rho_{DOP1\_i} \qquad (44)$$

4.0 Colored Dissolved Organic Carbon State Equations

The partial differential equation for colored dissolved organic carbon ($CDOC_i$) is the same as the 3-D advection equation (1). The *i* subscript denotes the class of CDOC, and has a value of 1 for labile CDOC, and 2 for recalcitrant CDOC. In this formulation all of the Colored Degradational Matter [CDM *Siegel et al.*, 1995] color is associated with the CDOC pool and its cycling. While there are color bonds associated with other organic matter [DON *Bushaw et al.*, 1996], we assume that all of the CDM color may be incorporated in a CDOC term. The time-dependent changes in CDOC resulting from biological and chemical processes are:

$\Lambda CDOC_1 = \sum_{i=1}^{7}\{FecDOC_i \cdot colorFR_1 \cdot g_i PC_i\} + BacDOC \cdot colorFR_1 \cdot g_b BC - UVDOC_1 - UVDIC_1$	(45)
$\Lambda CDOC_2 = colorFR_2 \cdot e_{bc} U_{DOC1} - UVDOC_2 - UVDIC_2$	(46)

The cycling of dissolved color is codified in this model by tracking the carbon associated with this specific pool of DOM. While there is still much work to be accomplished on the chemical nature of DOM and CDOM, we have made a reasonable approximation of the cycling of color that allows us to track the impacts of autochthonous and allochthonous sources of color in this simulation. The major difference between EcoSim 1.0 CDOM cycling and EcoSim 2.0 CDOM cycling is that in 2.0 we assume that bacteria do not use material associated with the colored bonds as an energy source. This greatly reduces the total demand on $CDOC_1$ stocks, and allows the stocks of color to accumulate to levels seen in the validation data. In addition, the specific absorptions of $CDOC_1$ and $CDOC_2$ were modified to reflect recent research in ocean color and microbial ecology. In particular, the research of Vodacek et al., [1997] and Moran et al. [2000] suggests that bacteria do not appear to use CDOM for energy or nutrients, thus the specific absorption of $CDOC_1$ was chosen to equal that of $CDOC_2$ in the assumption that color is strictly concentrated from its initial production to its final state. This version of EcoSim also uses new values for pure water absorption [*Pope*, 1993; *Pope and Fry*, 1997]. The assumption of no net bacterial use of color combined with the new water absorption values requires the recalculation of $colorFR_1$ to 3.23% from 1.6% in EcoSim 1.0.

4.1 Labile Colored Dissolved Organic Carbon

The first term of equation (45) is similar to the first term of the DOC_1 (equation (38)). This is a summation term of all of the release of colored labile DOC from grazing and lysis of phytoplankton. There is no release of $CDOC_1$ by phytoplankton excretion, as this excreted material is assumed to be simple carbohydrates. The $FecDOC_i$ and $colorFR_1$ terms are the same as in equation (38). The next term is the release of $CDOC_1$ from the grazing and lysis of bacteria. Again, *BacDOC* and $colorFR_1$ are the same as in equation (38). The last two terms of this equation are $UVDOC_1$ and $UVDIC_1$. These terms represent the loss of $CDOC_1$ from photo-chemical processes, and provide the quantity of carbon transformed into labile, uncolored DOC (DOC_1) and dissolved inorganic carbon (DIC).

4.2 Recalcitrant Colored Dissolved Organic Carbon

The equation for recalcitrant CDOC ($CDOC_2$) is similar to that of recalcitrant DOC. The first term is the color produced from bacterial excretion of $CDOC_2$ during the heterotrophic use of labile DOC_1, $e_{bc}U_{BDOC1}$. This excretion is multiplied by the recalcitrant colored fraction, $colorFR_2$, to yield the biochemical source of $CDOC_2$. The last two terms, $UVDOC_2$ and $UVDIC_2$, represent the loss of carbon (and color) resulting from photochemical destruction of the absorbing material in the $CDOC_2$ pool.

4.3 Photo-Chemical Alteration of Colored Dissolved Organic Carbon

The following equations define the $UVDOC_i$ and $UVDIC_i$ terms.

$UVDOC_i = a_{CDOCi}(410) \cdot RtUVDOC \cdot \frac{E_d(0^-)}{1500.0} \cdot \exp\left[\int_{0^-}^{z} K_d(300,z)\ dz\right]$	(47)
$UVDIC_i = a_{CDOCi}(410) \cdot RtUVDIC \cdot \frac{E_d(0^-)}{1500.0} \cdot \exp\left[\int_{0^-}^{z} K_d(300,z)\ dz\right]$	(48)
$a_{CDOCi}(410) = a^*_{CDOCi}(410) \cdot CDOC_i$	(49)
$K_d(300,z) = \left[a_{CDOC2}(410) + a_{CDOC1}(410)\right]\exp\left[S_{UV}(300.0-410.0)\right] + K_{d\_w}(300.0)$	(50)

$a_{CDOCi}(410)$ refers to the absorption of $CDOC_i$ at 410 nm in wavelength. This term is calculated by the multiplication of the carbon specific absorption, $a^*_{CDOCi}(410)$ and the concentration of $CDOC_i$. *RtUVDOC* and *RtUVDIC* are the absorption specific rates of conversion of $CDOC_i$ to labile DOC and DIC. These equations contain a slight modification of the original EcoSim 1.0 formulation in that the diffuse attenuation of downwelling irradiance at 300 nm, $K_d(300)$, is used as the exponential decay term. The photolysis of CDOM is calculated at 300 nm, because this wavelength represents the peak in photochemical action spectrum for photo-chemical reactions (Bissett et al., 1999a and references therein). In EcoSim 1.0, we used just the $K_w(300)$ value to attenuate photolysis [*Bissett et al.*, 1999a]. The current formulation is a more accurate representation of the attenuation of Ultra-Violet (UV) irradiance in the water column, and allows for feedbacks between $CDOC_i$ concentrations and the attenuation of photolysis. S_{UV} in equation (50) is given a value of 0.0145.

A closer examination of the *RtUVDIC* and *RtUVDOC* terms in EcoSim 1.0 revealed some significant problems in the original calculations. In the original calculation, we selected the greatest rates of loss from the Miller and Zepp (1995) work from their short term incubations, where the time-dependent change was calculated in a linear fashion. However, we applied these over long time periods, at effectively exponential rates since we were summing the results of these calculations over very short time steps. In addition, the more recent work of Moran et al., 2000 suggested these rates were much slower than those that we had calculated. Recalculation of these rates suggests they are much smaller, and that the dominant fraction of carbon lost from photo-chemcial reductions of CDOM is transferred to the inorganic carbon pool. These new rates are 0.0193 and 0.0034 μmol m l^{-1} hr^{-1} at 410 nm (from 0.62 and 0.57 in EcoSim 1.0), for *RtUVDIC* and *RtUVDOC*, respectively. Lastly, rates used in the experiments listed above typically used constant irradiance sources for their determination of photo-chemical loss rates. These irradiances sources were at or greater than full solar irradiance. Therefore, to accurately account for the changing solar irradiance over the course of the day and year, the 1500.0 μmol quanta m^{-2} s^{-1} factor in the equation normalizes irradiance to the approximate maximum for solar irradiance in sub-tropical environments.

5.0 Fecal Organic Matter State Equations

The fecal matter equations ((51) though (53)) represent the time dependent sources and sinks of the particulate matter produced from the loss terms on phytoplankton and bacteria. The *j* subscript denotes the particular class of fecal material being represented and has a value of 1 for slowing sinking fecal material and 2 for rapidly sinking fecal material. The term $\Lambda F\chi_j$ in equation (52) represents the biological sources and sinks of fecal carbon, nitrogen, phosphorous,

and iron. There is no silica incorporation in bacteria biomass, so fecal silica equation (53) does not contain the $BacPEL_j$ term.

$$\Lambda FC_j = \sum_{i=1}^{7}\left\{FecPEL_{ji}\cdot g_i PC_i\right\} + BacPEL_j \cdot g_B BC - regenC_j(z)\cdot FC_j - w_{sF\_j}\frac{\partial FC_j}{\partial z} \quad (51)$$

$$\Lambda F\chi_j = \sum_{i=1}^{7}\left\{FecPEL_{ji}\cdot g_i P\chi_i\right\} + BacPEL_j \cdot g_B B\chi - regen\chi_j(z)\cdot F\chi_j - w_{s\chi\_i}\frac{\partial F\chi_i}{\partial z} \quad (52)$$

$$\Lambda FS_j = \sum_{i=1}^{7}\left\{FecPEL_{ji}\cdot g_i PS_i\right\} - regenS_j(z)\cdot FS_j - w_{sF\_i}\frac{\partial FS_i}{\partial z} \quad (53)$$

The first terms of these equations are a summation of the g_iPC and $g_iP\chi$ terms found in equations (2) through (6), multiplied by the fraction of the material that passes into the particulate pool, $FecPEL_j$. This fraction is determined from an approximation of the length of the food web and assimilation efficiencies of the grazers [*Bissett et al.*, 1999b]. The next term in equation (52) is the addition to the fecal stocks from losses on the bacterial stocks. Again the g_BBC and $g_BB\chi$ terms are multiplied by an estimate of the fraction of material ($BacPEL_j$) that passes from the microbial food web into the sinking particulate flux.

The second to last term in these equations is the regeneration term. The calculation of the regeneration term is significantly altered from the EcoSim 1.0 formulation. In EcoSim 1.0, the simulated water depth was >1000 m. It was required that the non-stoichiometric alteration of the descending particles be addressed. In this simulation, the maximum depth is 40 m at the offshore boundary, thus the flux calculations are not required. In addition, there are two classes of fecal material in this simulation. The first is a non-sinking class that is subjected to regeneration processes. The second is a rapidly sinking class that is assumed to make it to the sediments where it is lost to the model and is therefore not subjected to regeneration pressures. This is affected by setting the regeneration term to zero for the rapidly sinking class, j=2.

$$regenC_1(z) = regenC_1 \exp^{0.092(T-30)} \quad (54)$$

The regeneration equation for fecal nitrogen, phosphorous, silica, and iron is identical to carbon. $Regen\chi_1$ is set to 10% d^{-1} [*Moore et al.*, 2001] with the exception of $RegenS_1$ which is set to 13% d^{-1} [*Bidle and Azam*, 1999], multiplied by the temperature-dependent function (where the base number decreases from a temperature of 30° C). This exponential function is the same function used to modify bacteria maximum growth.

6.0 Inorganic Nutrient State Equations

The time dependent changes in the inorganic nutrients resulting from biochemical transformations are described by:

$$\Lambda NO_3 = -\sum_{i=1}^{7}\rho_{NO_3\_i} + AtoN \quad (55)$$

$$\Lambda NH_4 = \sum_{i=1}^{7}\left\{-\rho_{NH_4\_i} + FecCYC_i \cdot g_i PN_i\right\} + BacCYC \cdot g_B BN - AtoN \cdot \left[1.0 + \frac{1}{7} \cdot \left(\frac{N_b}{C_b}\right)\right] - U_{NH4} + \sum_{j=1}^{2}\left\{regenN(z) \cdot FN_j\right\}$$	(56)
$$\Lambda DIP = \sum_{i=1}^{7}\left\{-\rho_{DIP\_i} + FecCYC_i \cdot g_i PP_i\right\} + BacCYC \cdot g_B BP - \frac{AtoN}{7.0} \cdot \left(\frac{P_b}{C_b}\right) - U_{DIP} + \sum_{j=1}^{2}\left\{regenP(z) \cdot FP_j\right\}$$	(57)
$$\Lambda DISi = \sum_{i=1}^{7}\left\{-\rho_{DISi\_i}\right\} + \sum_{j=1}^{2}\left\{regenS(z) \cdot FS_j\right\}$$	(58)
$$\Lambda DIFe = \sum_{i=1}^{7}\left\{-\rho_{DIFe\_i} + FecCYC_i \cdot g_i PF_i\right\} + BacCYC \cdot g_B BF - \frac{AtoN}{7.0} \cdot \left(\frac{F_b}{C_b}\right) - U_{DIFe} + \sum_{j=1}^{2}\left\{regenF(z) \cdot FF_j\right\}$$	(59)

In this model, the sum of ammonium and nitrate represent total dissolved inorganic nitrogen. Nitrite is assumed to be a constituent of the ammonium pool [*Bissett et al.*, 1999b]. Alkalinity affects on the predominate form of phosphorous, silica, and iron are ignored, hence the description of these terms as total inorganic phosphorous, silica, and iron. The time dependent change in nitrate, ΛNO_3, is driven by losses from uptake by phytoplankton and gains from the nitrification of ammonium. The change in ammonium, ΛNH_4, results from losses from phytoplankton, heterotrophic bacteria, and nitrifying bacterial uptake, and gains from phytoplankton and bacteria grazing and lysis, as well as regeneration of nitrogen from fecal nitrogen. The change in total inorganic phosphorous from biochemical sources and sinks, ΛDIP, is a function of losses resulting from phytoplankton, heterotrophic bacteria, and nitrifying uptake, and gains from phytoplankton and bacteria grazing and lysis, as well as regeneration from fecal phosphorous. The change in dissolved inorganic silica, $\Lambda DISi$, results from phytoplankton uptake and fecal silica regeneration. Lastly, the changes in dissolved inorganic iron, $\Lambda DIFe$, result from losses by phytoplankton, heterotrophic bacteria, and nitrifying bacterial uptake, and gains from the lysis and grazing on bacteria and phytoplankton, as well as regeneration from fecal iron.

Most of the terms in the equations ((55) through (59)) representing the biochemical changes in nutrient stocks have been previously described. The terms $FecDOC_i$ (in the DOM equations), $FecPEL_i$ (in the fecal matter equations), and $FecCYC_i$ sum to 1.0, and thus reflect the different pools in which all of the grazed and lyzed material calculated by the g_iPC_i and $g_iP\chi_i$ terms are placed. The same is true for the *BacDOC*, *BacPEL*, and *BacCYC* (they sum to 1.0) and the bacterial loss terms, g_BBC and $g_BB\chi$.

The *AtoN* term in equation (55) represents the material converted to nitrate. This term is multiplied by the factor of (1.0/7.0 times the N_B to C_B ratio) in the ammonium equation, which represents the additional ammonium-based nitrogen that is fixed into bacterial biomass from this chemolithic oxidation process. The *AtoN* terms in the phosphorous and iron equations are just multiplied by the stoichiometric ratio of bacterial assimilation, χ_B to C_B (there is no *AtoN* term in the silica equation because bacteria do not assimilate silica). The next-to-last terms in the ΛNH_4,

ΛDIP, and $\Lambda DIFe$ equations represent the uptake by heterotrophic bacteria. The last term in these equations (and the $\Lambda DISi$ equation) is the regeneration of fecal matter.

7.0 Dissolved Inorganic Carbon State Equation

The time dependent changes in the inorganic nutrients resulting from biochemical transformations are described by:

$$\Lambda DIC = \sum_{i=1}^{7}\left\{-\left[\min\left(\mu_{ll\_i}, \mu_{nl\_i}, \mu_{pl\_i}, \mu_{sl\_i}, \mu_{fl\_i}\right)\right] PC_i + FecCYC_i \cdot g_i PC_i\right\} + U_{BDOC} \cdot \left(1.0 - GGE_c\right) + BacCYC \cdot g_B BC - \frac{AtoN}{7.0} + regenC\left(z\right) \cdot FC_i + UVDIC_1 + UVDIC_2 \quad (60)$$

where the biochemical change in the stocks of dissolved inorganic carbon, ΛDIC, results from losses by phytoplankton and nitrifying bacteria uptake, and gains from heterotrophic conversion of grazed phytoplankton and bacteria, heterotrophic use of DOC, regeneration of fecal carbon, and photolysis of labile and recalcitrant CDOC. All of the terms have been described previously. The first term is the summation of the net phytoplankton impacts on the DIC pool (-growth, +higher trophic respiration). The next term is the bacterial respiration of DOC used for energy, represented by the uptake of labile DOC, U_{BDOC}, multiplied by the $(1.0 - GGE_c)$. The third term is the release of DIC from higher tropic respiration on the grazed bacterial production. The fourth term is the reduction in DIC by the fixation of inorganic carbon by nitrifying bacteria. The fifth term is the DIC released from the regeneration of fecal carbon. The last two terms represent the release of DIC from photolytic oxidation of $CDOC_1$ and $CDOC_2$, respectively.

8.0 Notes on the Optical Model

Equation 17 of *Bissett et al., (1999a)* was altered to reflect recent work by the original authors [*Morel and Maritorena*, 2001].

$$\tilde{b}_{bp}\, b_b(\lambda, z) = 0.30\left[Chla(z)\right]^{0.62} \cdot \left[0.002 + 0.01\left(0.5 - 0.25\log\left[Chla(z)\right]\right) \cdot \left(\frac{550}{\lambda}\right)\right] \quad (61)$$

This equation calculates backscatter as a function of total chlorophyll a concentration at level z, *Chla(z)*, at a wavelength of 550 nm. It is given spectral dependency by the wavelength parameter, λ. Total chlorophyll a concentration is equal to the sum of all chlorophyll a across all FGs at each level in the model.

9.0 Parameter Definitions

Table 1 – Definitions of variables and parameters

Phytoplankton	**Symbol**	**Units**
Variables		
Maximum 24 hr, temperature-dependent carbon specific growth rate	μ_{mt}	d^{-1}
Light-limited carbon specific growth rate	μ_{ll}	d^{-1}
Optimal Carbon to Chlorophyll a ratio under light-limitation	θ_{l_opt}	mg C (mg Chl a)$^{-1}$
Optimal Carbon to Chlorophyll a ratio under nutrient-limitation	θ_{n_opt}	mg C (mg Chl a)$^{-1}$

Photosynthetic efficiency	α	$(\mu mol\ quanta\ m^{-2})^{-1}$
Scalar Irradiance at depth z	$E_0(z)$	$\mu mol\ quanta\ m^{-2}s^{-1}$
Exponential decay of light-limited growth rate from light inhibition	decay rate	$(\mu mol\ quanta)^{-1}$
Nutrient-limited carbon specific growth rate	$\mu_{\chi l}$	d^{-1}
Unattainable growth rate for infinite nutrient concentration	$\bar{u}_{\chi l\_i}$	d^{-1}
Minimum nutritional status of functional group	$K_{\chi Q}$	$\mu mol\ \chi\ (\mu mol\ C)^{-1}$
Maximum nutritional status during balanced growth	$Q_{optimal\chi}$	$\mu mol\ \chi\ (\mu mol\ C)^{-1}$
Actual nutritional status	$Q_{actual\chi}$	$\mu mol\ \chi\ (\mu mol\ C)^{-1}$
Nutrient χ cellular transport flux	ρ_χ	$\mu mol\ \chi\ liter^{-1}d^{-1}$
Phytoplankton carbon specific grazing rate	g	d^{-1}
Parameters		
Maximum 24 hr, 27° carbon specific growth rate	μ_m	d^{-1}
Half-saturation constant for nutrient χ uptake	K_{s_i}	$\mu mol\ \chi\ liter^{-1}$
Nitrate uptake repression exponent	ψ	$(\mu mol\ NH_4\ liter^{-1})^{-1}$
Minimum Carbon to Nutrient χ ratio	Min C:χ	$\mu mol\ C : \mu mol\ \chi$
Maximum Carbon to Nutrient χ ratio	Max C:χ	$\mu mol\ C : \mu mol\ \chi$
Carbon to Nitrogen ratio where DON uptake begins	K_{sDON} C:N	$\mu mol\ C : \mu mol\ N$
Carbon to Phosphorus ratio where DOP uptake begins	K_{sDOP} C:P	$\mu mol\ C : \mu mol\ P$
Compensation irradiance	E_{0_comp}	$\mu mol\ quanta\ m^{-2}s^{-1}$
Scalar irradiance at which inhibition starts	$E_{0\_inhibit}$	$\mu mol\ quanta\ m^{-2}s^{-1}$
Scalar irradiance at which growth is equal to zero	$E_{0\_zerogrow}$	$\mu mol\ quanta\ m^{-2}s^{-1}$
Nutrient-replete maximum Carbon to Chlorophyll a ratio	θ_{n_max}	$mg\ C\ (mg\ Chl\ a)^{-1}$
Accessory Pigment to Chlorophyll a ratio	ζ	$mg\ acc.\ pig.\ (mg\ Chl\ a)^{-1}$
Maximum phytoplankton carbon specific excretion rate	*e*	d^{-1}
Sinking rate	w_s	$meters\ d^{-1}$
Minimum mortality rate	mortality	d^{-1}
Refuge population below which no grazing or lysis occurs	refuge	$\mu mol\ C\ liter^{-1}$
Bacterial		
Variables		
Maximum 24 hr, temperature-dependent specific growth rate	μ_{mt_b}	d^{-1}
Quantity of ammonium converted to nitrate via nitrification	*AtoN*	$\mu mol\ N\ liter^{-1}\ d^{-1}$
Bacterial carbon specific grazing rate	g_b	d^{-1}
Uptake of DOC	U_{BDOC1}	$\mu mol\ DOC\ liter^{-1}\ d^{-1}$
Uptake of NH_4	U_{BNH4}	$\mu mol\ NH_4\ liter^{-1}\ d^{-1}$
Uptake of DON	U_{BDON1}	$\mu mol\ DON\ liter^{-1}\ d^{-1}$
Uptake of DIP	U_{BDIP1}	$\mu mol\ DIP\ liter^{-1}\ d^{-1}$
Uptake of DOP	U_{BDOP1}	$\mu mol\ DOP\ liter^{-1}\ d^{-1}$
Uptake of DIFe	U_{BDIFe}	$\mu mol\ DIFe\ liter^{-1}\ d^{-1}$
Parameters		
Maximum 24 hr, 30° carbon specific growth rate	μ_{m_b}	d^{-1}
Bacteria C:χ	Bac C:χ	$\mu mol\ C : \mu mol\ \chi$
Half-saturation constant for energy-limited growth	K_{sBDOC1}	$\mu mol\ DOC\ liter^{-1}$
Gross growth efficiency for carbon substrate	GGE_c	*unitless*

Gross growth efficiency for substrate χ	GGE_{χ}	*unitless*
Half-saturation constant for nutrient χ growth	$K_{s\_B\chi}$	µmol χ liter^{-1}
Maximum 24 hr nitrification rate	MaxNit	d^{-1}
Half-saturation constant for nitrification	K_{sNit}	µmol N liter^{-1}
Excretion of relict DOC during bacterial uptake of labile DOC	e_{bc}	*unitless*
Excretion of relict DON during bacterial uptake of labile DON	e_{bn}	*unitless*
Sinking rate	w_{sb}	meters d^{-1}
Dissolved Organic Matter		
Variables		
Total absorption of CDOC at 410 nm	$a_{CDOC}(410)$	m^{-1}
Total attenuation at 300 nm	$K_d(300)$	m^{-1}
Amount of labile CDOC photolyzed to DIC	$UVDIC_1$	µmol C liter^{-1} d^{-1}
Amount of relict CDOC photolyzed to DIC	$UVDIC_2$	µmol C liter^{-1} d^{-1}
Amount of labile CDOC photolyzed to colorless labile DOC	$UVDOC_1$	µmol C liter^{-1} d^{-1}
Amount of relict CDOC photolyzed to colorless labile DOC	$UVDOC_2$	µmol C liter^{-1} d^{-1}
Parameters		
Fraction of phytoplankton grazing released to labile DOC	FecDOC	*unitless*
Fraction of bacterial grazing released to labile DOC	BacDOC	*unitless*
Fraction of newly released labile DOC that is colored (CDOC)	$colorFR_1$	*unitless*
Fraction of newly released relict DOC that is colored (CDOC)	$colorFR_2$	*unitless*
Absolute specific rates of conversion of CDOC to labile DOC	RtUVDOC	µmol m l^{-1} hr^{-1} at 410 nm
Absolute specific rates of conversion of CDOC to DIC	RtUVDIC	µmol m l^{-1} hr^{-1} at 410 nm
Specific absorption of CDOC at 410 nm	$a^*_{CDOC}(410)$	m^2 g^{-1} CDOC
Fecal Matter		
Variables		
Regeneration of fecal carbon to DIC	RegenC	d^{-1}
Regeneration of fecal matter to inorganic nutrient χ	Regenχ	d^{-1}
Parameters		
Fraction of phytoplankton grazing released as fecal pellets	FecPEL	*unitless*
Fraction of bacterial grazing released as fecal pellets	BacPEL	*unitless*
Sinking rate	w_{sF}	meters d^{-1}
Dissolved Inorganic Matter		
Parameters		
Fraction of phytoplankton grazing that is metabolized	FecCYC	*unitless*
Fraction of bacterial grazing that is metabolized	BacCYC	*unitless*
General		
Variable		
Temperature	t	°C

10.0 Initial Conditions And Ecological Parameters For Ecosim 2.0 On The West Florida Shelf

The ecological model was initialized with constant concentrations over the domain (Table 2). The total phytoplankton concentration was equally divided amongst the 7 functional groups (Table 3) and their C:χ ratios used to establish the other elemental state variables were given by the minimum levels for each functional group found in the functional group parameters table (Table 4), where χ represents nitrogen, silica (where applicable), phosphorus, and iron. The initial C:χ ratios for bacteria were 5:60:1000 for nitrogen, phosphorus, and iron, respectively. The initial C:χ ratios for fecal matter were 8:8:128:1000 for nitrogen, silica, phosphorus, and iron, respectively. The initial C:χ ratios for DOC_1 were 6.625:106 for nitrogen and phosphorus, respectively. The initial C:χ ratios for DOC_2 were 15:106 for nitrogen and phosphorus, respectively. The shoreward boundary conditions used on DOY 267 and 309 are in Table 6. Parameters described in Table 1, but not listed in the following Tables are given in *Bissett et al., 1999a and b*.

Table 2 - Initial Conditions

State Variable	Concentration (µmol liter^{-1})
Total Phytoplankton Carbon	0.84
Total Bacterial Carbon	0.85
Fecal Carbon 1	0.002
Fecal Carbon 1	0.002
Dissolved Organic Carbon 1	2.75
Dissolved Organic Carbon 2	55.0
Colored Dissolved Organic Carbon 1	0.636
Colored Dissolved Organic Carbon 2	0.057
Nitrate	0.25
Ammonia	0.025
Silicate	0.25
Phosphate	0.0172
Iron	0.001

Table 3 – Phytoplankton Functional Groups

Group Number	Species Type	References
FG 1	Prochlorococcus (high chl b)	[*Moore et al.*, 1995; *Partensky et al.*, 1993]
FG 2	Prochlorococcus (low chl b)	[*Moore et al.*, 1995; *Partensky et al.*, 1993]
FG 3	Synechococcus	[*Barlow and Alberte*, 1985; *Glibert and Ray*, 1990; *Kana et al.*, 1992; *Kana and Glibert*, 1987; *Moore et al.*, 1995]
FG 4	Generic Large Diatom	[*Cleveland and Perry*, 1987; *Geider and Osborne*, 1987; *Geider and Platt*, 1986; *Haxo*, 1985; *Hoepffner and Sathyendranath*, 1992; *Jeffrey*, 1976; *Laws and Bannister*, 1980; *Perry et al.*, 1981; *Schofield et al.*, 1990]
FG 5	Generic Small Diatom (< 5µm diameter)	[*Geider et al.*, 1985; *Reynolds et al.*, 1997]
FG 6	Toxic Dinoflagellate	[*Johnsen and Sakshaug*, 1993; *Shanley and Vargo*, 1993]

	(*cum Karenia brevis*)
FG 7	Generic Non-toxic Dinoflagellate

Table 4 – Phytoplankton Parameter Values

	FG 1	FG 2	FG 3	FG 4	FG 5	FG 6	FG 7
μ_m	1.28	1.45	2.00	3.70	3.70	1.00	2.00
K_{sNO3}	0.100	0.100	0.167	0.824	0.412	0.824	0.824
K_{sNH4}	0.050	0.050	0.083	0.414	0.208	0.414	0.414
K_{sSiO}	N/A	N/A	N/A	1.824	1.412	N/A	N/A
K_{sPO4}	0.00625	0.00625	0.01044	0.05150	0.02575	0.05150	0.05150
K_{sFe}	N/A	N/A	N/A	N/A	N/A	N/A	N/A
K_{sDON}	N/A	N/A	N/A	N/A	N/A	2.0	2.0
K_{sDOP}	N/A	N/A	N/A	N/A	N/A	2.0	2.0
ψ	12.00	12.00	6.50	1.28	2.60	1.28	1.28
Max C:N	6.625	6.625	6.625	14.000	17.750	17.000	17.000
Min C:N	6.625	6.625	6.625	6.625	6.625	6.625	6.625
Max C:Si	N/A	N/A	N/A	5.521	5.521	N/A	N/A
Min C:Si	N/A	N/A	N/A	5.521	5.521	N/A	N/A
Max C:P	106.0	106.0	106.0	106.0	106.0	130.0	130.0
Min C:P	106.0	106.0	106.0	106.0	106.0	106.0	106.0
Max C:Fe	N/A	N/A	N/A	N/A	N/A	N/A	N/A
Min C:Fe	N/A	N/A	N/A	N/A	N/A	N/A	N/A
K_{sDON} C:N	N/A	N/A	N/A	N/A	N/A	14.0	14.0
K_{sDOP} C:P	N/A	N/A	N/A	N/A	N/A	110.0	110.0
ϕ_m	0.0833	0.0833	0.0833	0.0833	0.0833	0.0833	0.0833
E_{0_comp}	1.0	6.0	6.0	10.0	10.0	10.0	10.0
$E_{0\_inhibit}$	40.0	105.0	10000.0	10000.0	10000.0	10000.0	10000.0
decay rate	0.100	0.001	0.000	0.000	0.000	0.000	0.000
θ_{n_max}	100.0	150.0	160.0	60.0	42.0	124.0	124.0
$slope_{\theta ll}$	0.8000	0.3000	0.1000	0.1200	0.1144	0.4779	0.4779
θ_{0ll}	20.00	15.00	30.00	25.00	14.80	47.53	47.53
$slope_{\theta nl}$	N/A	N/A	N/A	12.20	6.832	10.35	10.35
θ_{0nl}	N/A	N/A	N/A	60.0	42.0	124.0	124.0
$slope_{PacEff}$	N/A	N/A	N/A	0.01429	0.01838	N/A	N/A
Max_{PacEff}	N/A	N/A	N/A	0.50000	0.50000	N/A	N/A
$slope_{\zeta ChlB}$	-0.02	-0.00100	N/A	N/A	N/A	N/A	N/A
ζ_{ChlB}	2.4	0.2	N/A	N/A	N/A	N/A	N/A
$slope_{\zeta ChlC}$	N/A	N/A	N/A	-0.00136	-0.00120	0.00000	0.00000
ζ_{ChlC}	N/A	N/A	N/A	0.340	0.340	0.056	0.056
$slope_{\zeta PSC}$	N/A	N/A	N/A	-0.012	-0.0104	0.0000	0.000
ζ_{PSC}	N/A	N/A	N/A	2.000	2.000	1.106	1.106
$slope_{\zeta PPC}$	0.0138	0.0162	0.0090	0.0000	0.0000	0.0018	0.0018
ζ_{PPC}	0.3000	0.3000	0.3000	0.1000	0.1000	0.1600	0.1600
$slope_{\zeta LPUb}$	N/A	N/A	N/A	N/A	N/A	N/A	N/A
ζ_{LPUb}	N/A	N/A	N/A	N/A	N/A	N/A	N/A
$slope_{\zeta HPUb}$	N/A	N/A	-0.1300	N/A	N/A	N/A	N/A

ζ_{HPUb}	N/A	N/A	20.000	N/A	N/A	N/A	N/A
FecDOC	0.41670	0.41670	0.41670	0.33330	0.33330	0.33330	0.33330
FecPEL(1)	0.08335	0.08335	0.08335	0.16670	0.16670	0.16670	0.16670
FecPEL(2)	0.08335	0.08335	0.08335	0.16670	0.16670	0.16670	0.16670
FecCYC	0.41660	0.41660	0.41660	0.33330	0.33330	0.33330	0.33330
e	0.005	0.005	0.005	0.005	0.005	0.005	0.005
w_S	0.0	0.0	0.0	0.0	0.0	0.0	0.0
mortality	0.01	0.01	0.01	0.01	0.01	0.01	0.01
refuge	0.02	0.02	0.02	0.02	0.02	0.02	0.02

Table 5 – Other state variable parameter values

State Variable	Value
Bacterial	
μ_{m_b}	2.0
Bac C:N	5:1
Bac C:P	12:1
Bac C:Fe	1000:1
K_{s_BDOC1}	130.0
K_{s_BNH4}	26.0
K_{s_BDIP}	10.833
K_{s_BDIFe}	2.6
GGE_c	0.300
GGE_χ	1.000
e_{bc}	0.040
e_{bn}	0.005
Maximum 24 hour AtoN	0.040
K_{sNit}	0.100
w_{sb}	0.000
*Bac*DOC	0.4583
*Bac*PEL(1)	0.0834
*Bac*PEL(2)	0.0000
*Bac*CYC	0.4583
Fecal	
w_{sF1}	0.00
w_{sF2}	Infinite
Dissolved Organic Matter	
colorFR_1	0.0323
colorFR_2	0.0930
*Rt*UVDOC	0.0034
*Rt*UVDIC	0.0193
a^*_{CDOC1}	5.080
a^*_{CDOC2}	5.080
S_{UV}	0.0145

Table 6 – Inshore boundary conditions for pulse case. Concentrations were added to state variables on DOY 267 and 309.

State Variable	Concentration (µmol liter^{-1})
Dissolved Organic Carbon 1	397.263
Dissolved Organic Nitrogen 1	20.054
Dissolved Organic Phosphorus 1	1.3
Colored Dissolved Organic Carbon 1	0.82
Colored Dissolved Organic Carbon 2	8.2

Nitrate	0.947
Ammonia	1.309
Silicate	9.46
Phosphate	0.867
Iron	0.003

11.0 References

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