

Connecting metabolic rate and temperature to population growth rates in marine autotrophs

Andrea Belgrano^{*}, Peter Steadman^{*}, and Damian Gessler^{**†}

^{*}National Center for Genome Resources
2935 Rodeo Park Drive East, Santa Fe, New Mexico 87505

A Milestone Report for Aim 4, Subproject 4, of the

Department of Energy Genomes to Life project:
Carbon Sequestration in *Synechococcus sp.*: From Molecular Machines to Hierarchical Modeling

Synopsis An overarching challenge for science today is to discover how to integrate data and theory applicable at the molecular level to processes operational at the ecosystem level. A specific challenge for this project is to integrate the biotic molecular mechanism of carbon sequestration in the marine cyanobacterium *Synechococcus* to the abiotic process of carbon cycling and ecosystem dynamics.

The scientific model This report presents results of the first prototype of the scientific modeling of this process. We deploy a major advance in ecology developed over the last six years in the papers of West *et al.* (1997, 2001), Gillooly *et al.* (2001), Belgrano *et al.* (2002), Belgrano and Brown (2002), Li (2002), Gillooly *et al.* (2002), Enquist *et al.* (2003), and Savage *et al.* (2004). These publications (seven of nine published in either *Science* or *Nature*) show a stunning agreement of data and theory relating body mass and temperature to development time, ontogenetic growth, metabolic rate, population growth rates and density, and macroecological patterns. The implications for this project are immediate, since the rate of carbon fixation—*i.e.*, the rate of resource acquisition and the removal of CO₂ from the water column—is tightly linked to cellular division rates; these in turn drive population growth, which influences community composition and the biotic influence on the carbon cycle.

[†] To whom correspondence should be addressed: Damian Gessler, National Center for Genome Resources, 2935 Rodeo Park Drive East, Santa Fe, New Mexico 87505; phone: (505) 995-4403, fax: (505) 995-4432, email: ddg@ncgr.org,

Metabolic rate (measured in Watts) can be seen as the power stored in a population or trophic level. This power is related to cellular processes via the equation:

$$B(M, T) = B_0 e^{-E/kT} M^{3/4}$$

where $B(M, T)$ is the average metabolic rate of an individual, M is the average mass of an individual, T is the temperature, E is the average activation energy of metabolism (~ 0.6 eV), k is Boltzmann's constant (8.62×10^{-5} eV K $^{-1}$), and B_0 is a taxon-specific normalization constant (Gillooly *et al.* [2001] using the notation of Savage *et al.* 2004). The use of a theory capturing the dependency of temperature and the activation energy of metabolism is important for our model, since we are interested in how changes in oceanic temperature—for example, as driven by changes in atmospheric temperature due to rising CO $_2$ levels—affect the biotic components of oceans as sources or sinks for carbon. This effect will occur via changes in population growth rates and carrying capacities, and this needs to be linked to data on the rate of carbon fixation for *Synechococcus*.

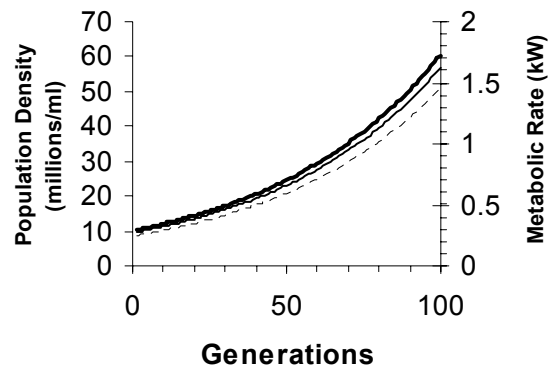
The Computational model To model the dynamics, we use a model of hierarchically linked levels that encompass processes spanning disparate time scales. Disparate time-scale modeling is a challenge. How does one, for example, integrate simulations of molecular processes—which may take hours of compute time to simulate a process that takes nanoseconds in simulation time (such as protein folding)—with ecosystem processes that may take milliseconds of compute time to simulate a process that take months or years in simulation time (such as a simple seasonal temperature oscillator)? Simply time-slicing on the smallest time unit is both unfeasible and, as we show, unnecessary. Additionally, technically integrating over disparate time-scale processes from the molecular to the ecosystem level requires intellectually integrating disparate disciplines and expertise, such as a molecular biology and ecology. Thus a technical modeling solution has to work in an environment of disparate expertise.

We solve the first problem by connecting processes at different levels to (possibly different) clocks. All processing is done via an event-driven model. The clocks orchestrate time-stamped events, making sure that all processing is done in temporal order and only at those time coordinates where computations must be performed. Thus

the simulation proceeds via a series of time-stamped *moments*, always advancing by the next pending event, without time-slicing between events. Clocks can be defined in arbitrary units, such as seconds/minutes/hours or “next generation” counters.

We solve the second problem by encapsulating dependencies via posting and consuming parameters. Levels are composed of software agents called *nodes*; a given level of expertise communicates with other levels by its nodes advertising that they supply parameters, such as the ambient oceanic temperature in degrees Kelvin, or the metabolic rate of the population in Watts, and/or that they require parameters. Because information is communicated via parameters, instead of being tightly coupled to implementations, expertise is encapsulated in levels and linked via the natural scientific language of rates, concentrations, amounts, and so forth.

Integrated Results The figure below shows the exponential growth rate of a population of picoplankton (*e.g.*, average length less than 2 μm , which include bacteria such as *Synechococcus* and *Prochlorococcus*) parameterized for the North Atlantic.



The simulations generating the figure are based on published data as cited later in this report. The figure shows the two fundamentals of the rise in average population metabolic rate—*i.e.*, a demand on the carbon resource of the environment—with population size and temperature. The bold line is population density; the upper solid line is total population metabolic rate at 15°C, the lower dashed line is total population metabolic rate at 14°C. The total power of the population—a measure proportional to the total amount of carbon fixed in the population—increases with population density.

Additionally, for a given density, populations at a higher temperature have a higher total metabolic rate. Not evident from the figure is that populations with a higher metabolic rate will grow faster, yet have a lower carrying capacity (Savage *et al.* 2004). This acts to conserve the total metabolic rate of the trophic level (the so-called “energetic equivalence rule” [EER]: Gillooly *et al.* 2001; Li 2003; Enquist *et al.* 2003 and references therein). This means the mean body mass will decrease, changing the community composition including predation pressures on picoplankton.

Justification and Rationale for the Scientific Approach

Climate, CO₂, and Ecology Individuals and populations undoubtedly experience climate locally, through temperature, wind, currents, rain and snow. Nevertheless, such meteorological and oceanographic features are often governed by phenomena extending over much larger areas. Interaction between the ocean and atmosphere may form dynamical systems, exhibiting complex patterns of variation, which may profoundly influence ecological processes in a number of ways (Belgrano *et al.* 2002). The most well-known example of a large-scale coupled ocean-atmosphere system is the El Niño-Southern Oscillation (ENSO). It originates in the tropical Pacific and generates impacts in both marine and terrestrial environments over a large part of the globe. In the North Atlantic there exists a somewhat similar ocean-climate system with comparably extensive effects, namely the North Atlantic Oscillation (NAO). The effect of the NAO on surface air temperature has been recognized since at least 1770 and scientists have been studying it since the 1880’s. Only fairly recently, however, has the NAO been shown to be a major driving force of the climatic systems of the Northern Hemisphere (Belgrano *et al.* 2000). Almost all of the early work on the NAO dealt solely with physical aspects. Since the mid-1990’s an increasing number of investigations have focused on the relationships between the temporal patterns seen in the North Atlantic Oscillation and the variability observed in biological populations. While statistical links between regional climate indices and ocean ecology have been made, the underlying mechanistic connections are not yet fully understood (Belgrano *et al.* 2000).

These climatic oscillations are linked to the sink of CO₂ in the ocean and to the interannual variability in ocean uptake (Bates *et al.* 2002). Therefore the supply,

sequestration, and transfer of CO₂ are a suite of complex mechanisms of biological and physical processes.

It is of paramount importance to understand the complexities that are at the base of the biotic-abiotic and abiotic-abiotic relationships among organisms. This will allow us to predict the emergent properties of a system and derive some simple general laws that will apply across ecosystems at both temporal and spatial scales. Ecological complexities need to be explained by simple rules and we need to develop a new theoretical framework for this purpose, which is one of the goals of this DOE-funded GTL project.

The complex dynamics of ecological communities and population dynamics and the resulting patterns of temporal and spatial variation are not well understood (Solé *et al.* 2002; Ottersen *et al.* 2001). To predict changes in the abundance and distribution of organisms due to large-scale abiotic fluctuations will require appropriate community theories. Assessing the relative contribution of extrinsic abiotic environmental variability and intrinsic biological processes on the performance of individuals and dynamics of populations requires knowledge on how the biotic interactions are altered the external driving forces. It is tempting to assume a simple linear relationship between environmental noise and the biological processes influenced by them. However, it is more likely that biological components respond nonlinearly to abiotic signals. Because of non-linear dynamics and stochasticity, responses to climate variation and CO₂ dynamics will likely be far less straightforward than expected. Also, our possibilities of signal detection may be limited because of community embedding (Stenseth *et al.* 2002). Responses to abiotic environmental change may be: 1) masked; or 2) difficult to interpret because of uncertainty of what ecological models are the best representations of the system (Stenseth *et al.* 2002).

A critical task for understanding how climate/CO₂ variability affects natural systems is consequently the formulation of relevant population and community models. One of the problems is that only rarely is the effect on a population directly. The response may be mediated through other trophic levels (*e.g.*, the climatic influences first plants then herbivores) or a direct influence (*e.g.*, on reproduction) may be modified by other interactions (*e.g.*, increased mortality due to predation). Further, different species, even ecologically similar ones, may respond to the same abiotic environmental fluctuations in

different ways. For example, time lags may be an important source of nonlinearities, and otherwise similar species of different body size may respond differently due to different time lags as a consequence of allometric scaling of resource requirements and life history characteristics. Climate/CO₂ changes may affect the distribution and abundance of organisms by evolutionary as well as ecological responses. Selection for life-history traits can be strong and responses fast.

New statistical challenges arise firstly; there is often no substantive knowledge on the form of the parameter functions. Non-parametric (or semi-parametric) modeling may then be helpful for exploring the shape of the parameter functions. Secondly, it is essential to identify a small set of pertinent biological response parameters to be functions of climate/CO₂, and/or other abiotic conditions, for model interpretation and model identification purposes.

We need to understand further self-organization properties in ecosystems as a collective outcome or “emergent property” of the aggregate of the independent dynamical responses of populations and communities to external environmental conditions (Reynolds 2001). Changing environments may result in changing “filters” which lead towards alternative outcomes, when the identities of the best-fit of the species available may also be varying (Harris 1986). The question that remains to be answered is: How such small-scale responses and interactions of individuals become aggregated and assembled into recurrent, emergent, high-order structures. This particular point reflect the interest of this DOE/GTL project in understanding the molecular machines and their regulatory networks in *Synechococcus* sp.

The Scientific Model

A phenomenological approach Only recently have biological oceanographic studies that reflect the coupling of physical-climatic fluctuations tried to integrate ecological processes at realistically large spatial and temporal scales in the oceans (Li 2002; Belgrano & Brown 2002).

Macroecology can be regarded as a new research agenda for biological oceanography, aiming to develop new ecological models, which can explain the emergent structure and dynamics of complex ecological systems in terms of basic physical and

biological principle (Brown & West 2000). Macroecological patterns of marine phytoplankton abundance from very small cells termed picophytoplankton (<2 μm), to increasing size, small nanoplankton cells (2-10 μm), and to larger nanoplankton cells (10-20 μm) as described by Li (2002), clearly show the importance of studying emerging large-scale aggregation of biological units in a new allometric perspective for “scaling up the oceans”.

Recent work has shown that unicellular algae, and vascular seed plants all fall on the same general allometric scaling function describing rates of biomass production (Niklas & Enquist 2001), and that plant abundance is similarly energetically constrained in terrestrial and aquatic systems by energy inputs as described by the “energetic equivalence rule” (Damuth 1981; Enquist *et al.* 1998; Belgrano *et al.* 2002). The energetic equivalence rule predicts that the metabolic rate of a population, $B_T \propto N \cdot B_i$, where N is the population density or the number of individuals and $B_i = B(M,T)$ is the metabolic rate of individuals. Because $N \propto M^{-3/4}$ and $B_i \propto M^{3/4}$, $B_T \propto M^{-3/4} \cdot M^{3/4} \propto M^0$, is invariant with respect to body size as described by Damuth (1981) and supported recently by Savage *et al.* (2004). Therefore empirically the population-level energy use can be written as $E = NB \propto M^{-3/4} \cdot M^{3/4} \propto M^0$ as reported by Ernest *et al.* (2003). This is also based on the fact that mass and temperature dependence for the metabolic rate of an organism scale as $B(m,T) = B_0 e^{-E/kT} m^{3/4}$, where m is an individual body mass, vs. M for the mean individual body mass (West *et al.* 1997; Gillooly *et al.* 2001). More precisely allometric scaling for phytoplankton abundance (cell density, N) and cell volume (body mass, M) scale as $N \propto M^{-3/4}$ therefore given the rate of energy use by whole organisms (metabolism, Q) that scale with body size as $Q \propto M^{3/4}$, the energy used by all the phytoplankton cells, independently of species composition that make up a size class is the same as that used by all the phytoplankton making up other size classes as: $NQ \propto M^{-3/4} \cdot M^{3/4} \propto M^0$ (Belgrano & Brown 2002; Li 2002; Belgrano *et al.* 2002). If we now consider for pelagic systems different trophic levels, the total energy flux of a trophic level, Q_{tot} , should be invariant with respect to body size and equal to the rate of limiting resource supply, R , from the environment ($R = Q_{tot} = NQ \propto M^{-3/4} \cdot M^{3/4} \propto M^0$) (Enquist *et al.* 1998; Enquist *et al.* 2003).

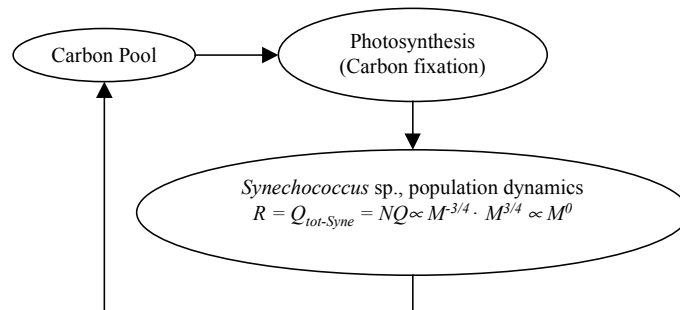
These scaling relationships are at the base of our understanding of energy use in a system such as the ocean. Therefore we can consider a carbon pool as a source of energy available to *Synechococcus* sp., and component processes can be regarded as the agents carrying the “decoding and coding” necessary for the organism to carry out specific processes and mechanisms such as adaptive behavior to environmental changes. At the population level our departure point will be to model different populations of *Synechococcus* sp., and other phytoplankton and zooplankton groups of different size classes using the logistic equation growth model in the form of:

$$N_t = N_0 e^{rt}$$

where the growth rate, r , the Malthusian parameter of the population (Turchin 2001) is equal to:

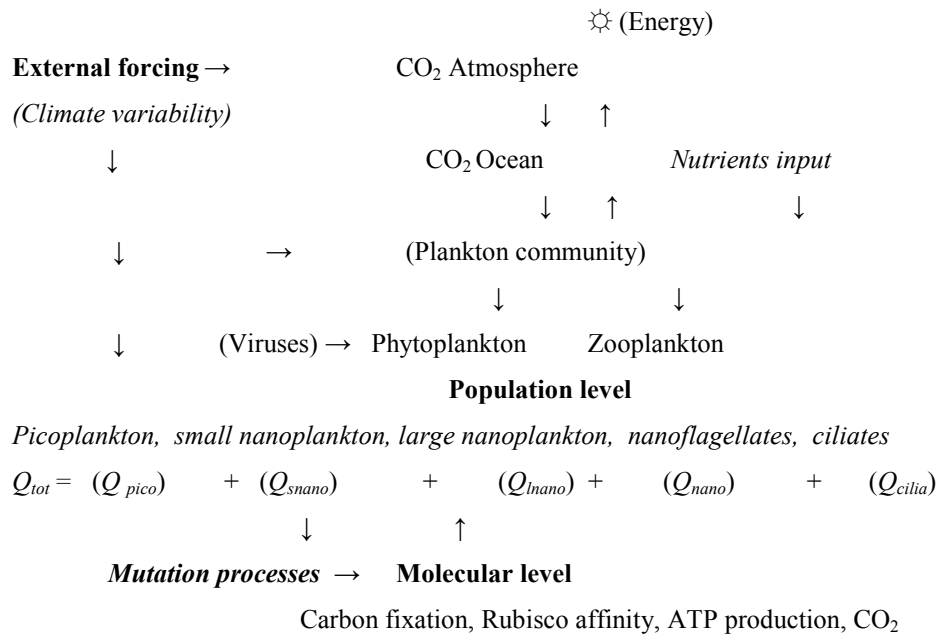
$$r = b - d_s - d_v - d_p$$

where b = birth rate; d_s = death due to starvation (resource limitation); d_v = death due to viruses (infection); and d_p = death due to predation, *i.e.* bottom-up and top-down pressures from the environment and other trophic levels. As Savage *et al.* (2004) showed, the intrinsic rate of the population growth, r_{max} , and the carrying capacity, K , depend on the both the individual metabolic rate and the resources supply rate. Thus we seek to link the logistic equation to the *Synechococcus* sp., population model using as a starting point the very basic cycle of:



This will show if the limiting resource supply, R , from the environment in *Synechococcus* sp., will reflect the allometric scaling ($R = Q_{tot} = NQ \propto M^{3/4} \cdot M^{3/4} \propto M^0$), proposed by Enquist *et al.* (1998; 2003).

At a second phase the model will be linked to the ocean exchange of CO₂ between the ocean and the atmosphere and two different ecological trophic levels in a hierarchical fashion as depicted below:



In this general scheme we hope to have a better understanding of the underlying mechanisms linking size, temperature, and metabolic rate for *Synechococcus* sp., in relation to carbon fixation, carbon sequestration and global carbon cycling in a changing environment. As suggested by Ernest *et al.* (2003) at the population level the use of energy is influenced by metabolism and thermodynamic constraints at different trophic levels, thus metabolism can be regarded as a fundamental trait linking individual and ecosystem processes.

One way to link the carbon cycle to ecosystem processes using the ideas described so far is to use ecosystem respiration as a way to quantify the fluxes of CO₂ and energy at the ecosystem level. As described by (Rivkin & Legendre 2001) the net flux of CO₂ between the atmosphere and the ocean is partly controlled by processes at the pelagic food web level, such as carbon uptake by phytoplankton via photosynthesis,

remineralization back to CO₂ , heterotrophic community respiration, and via the export of dissolved and particular biogenic carbon in the ocean deep layers.

In terrestrial ecosystems Enquist *et al.* (2003) showed that the fluxes of CO₂ and energy are invariant of ecosystem biomass, but are strongly influenced by temperature, variation in cellular metabolism, and by the rate of supply of limiting resources. Their finding is based on the recent work of Gillooly *et al.* (2001), showing that the metabolic rates of individuals, $B(M,T)$, can be accounted by the effects of body size, M , and absolute temperature, T , in a general model of the form:

$$B(M,T) = b_0 e^{-E/kT} M^{3/4}.$$

From this model, Enquist *et al.* (2003) derived a general expression, based on the fact that the respiration rate of an ecosystem, B_e , is equal to the sum of individual metabolic rates, $B(M,T)$, for all organisms in the system, thus:

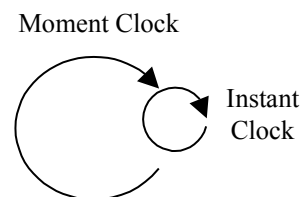
$$\ln(R) \propto \ln(Q_{tot}) \propto \ln(B_e) = -E k / T + \ln(B_0 C)$$

where C is a measure of the size abundance distribution of organisms. This equation describes the ecosystem respiration dependence on temperature, thus reflects the role of metabolism in constraining respiration at the ecosystem level.

The Computational Model

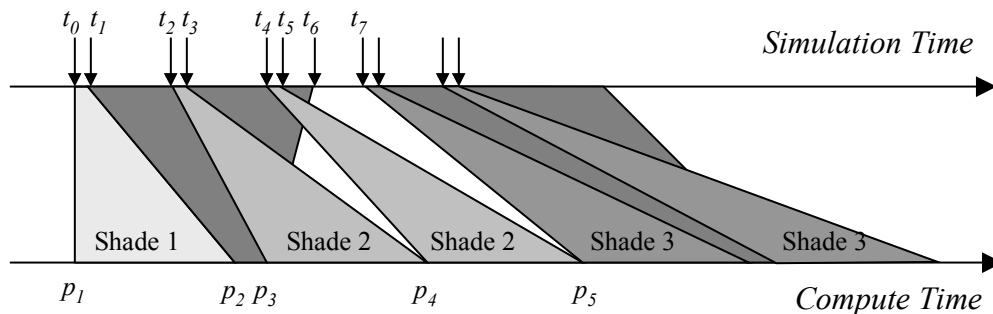
The Simulation Engine Our modeling approach is to use a disparate time simulation engine. Disparate time scheduling and synchronization is done by scheduling events with user-defined clocks. Events are call-backs on nodes that signal the current state of a node. Nodes register themselves with clocks to schedule their events. In this manner, a *moment*, *i.e.*, a point in time, is visited if and only if there is processing to be done at that point. Since any arbitrary amount of time can pass between moments, the simulation can combine processes taking nanoseconds with those taking gigaseconds without time-slicing at every nanosecond.

Because nodes must request and supply parameter values based on their state, each moment is decomposed into an arbitrary number of *instants*. An instant is a compute cycle that allows the updating and delivery of parameters for a



“frozen” moment in time. For events that are a-temporal, for example, the notification of state change (vs. the actual simulation of a natural process), nodes can schedule events with the Instant Clock for instantaneous delivery of that event. Only nodes that are receivers for events for that moment or are delivering parameters for those receivers are included in the moment’s compute cycle. Thus the simulation proceeds moment by moment, visiting only those nodes with scheduled processing relevant for that moment.

A schematic demonstration of an example of this scheduling is as below:



In this model, the node at p_1 takes some large amount of compute time to advance the simulation the small time step from t_0 to t_1 . Its state is indicated by the light gray area called “Shade 1,” and it changes its state on each occurrence of a second node, indicated by the dark gray region. For example, a node modeling the quantity of DOC (Dissolved Organic Carbon) available in the ocean would adjust its quantity of carbon as a function of the demand on this resource by changing population sizes of autotrophs. In the diagram above, the node is self-regulating and schedules an event to send to itself at time t_2 . Computing resources then go to the second node (the dark gray shading at p_2) that takes a small amount of computational time to advance the simulation to time t_6 . Thus at compute time p_3 , the simulation engine thus has requests for new processing at simulation time t_2 and t_6 . Because the next simulation moment is $t_2 < t_6$, the scheduler “skips” all simulation time between time t_1 and t_2 —where there are no pending events and thus no processing to be done—and advances the simulation to time t_2 , holding delivery of the event due at t_6 . The simulation engine continues in this manner, orchestrating the delivery of events so that regardless of when they are scheduled, they are always delivered in monotonically increasing time. In the language of time simulations, we would say that nodes are allowed be arbitrarily optimistic (scheduling events in the

future), but the platform is strictly conservative (no node ever receives an event in its past). The actual delivery of events is done via a call-back on a data structure of events saved with each node, so nodes may cancel the sending of events if a change in state so warrants so long as their clock time is less than the event's scheduled delivery time.

The simulation handles parameters by automatically scheduling parameter request calls before passing control to a node's event handler. Thus from the perspective of a modeler modeling at a level of expertise, all parameters are automatically up-to-date upon entry to the event handler. Thus modelers using the platform simply fire events and respond to events; all the scheduling and delivery mechanisms are handled automatically for them, and all events are always received in monotonically increasing temporal order, regardless of the amount of time it took to compute the current state.

Methods We deployed the above in a first-run prototype linking temperature and metabolic rate to picoplankton growth rates. The hierarchical model starts with an Ecosystem node that supplies the parameter of temperature appropriate for the North Atlantic Ocean ($273.15 + 15 = 288.15$ °K). The Ecosystem encompasses a trophic level node of Autotrophs, which supply parameters of the total trophic level metabolic rate and the population density. Starting density is set at $1 \times 10^7 l^{-1}$ (Glover *et al.* 1986). Picoplankton body mass is approximately $1 \times 10^{-9} g$, based in part on West *et al.*'s (2001) citing of a value of $3 \times 10^{-9} g$ as the body mass of a mammalian cell. In these simulations we use a constant instantaneous growth rate of $r = b - d$, where the birth rate is based on an average doubling time of $t_d = 0.69$ per day ($b = \ln(2)/t_d$) (Vaulot 1995). A mortality rate ($d = 0.46$) is based on estimates of viral lysis (Suttle & Chen 1992) and predation. An important maturation of this model is to replace the constant growth rates used here with a feedback from actual population sizes. This will require a new Heterotroph node to exert the top-down pressure of predation and a Carbon Pool node for resource acquisition.

Autotrophic mean population metabolic rate is based on a decomposition of the metabolic rate into maintenance, replacement, and population growth components following Savage *et al.* (2004):

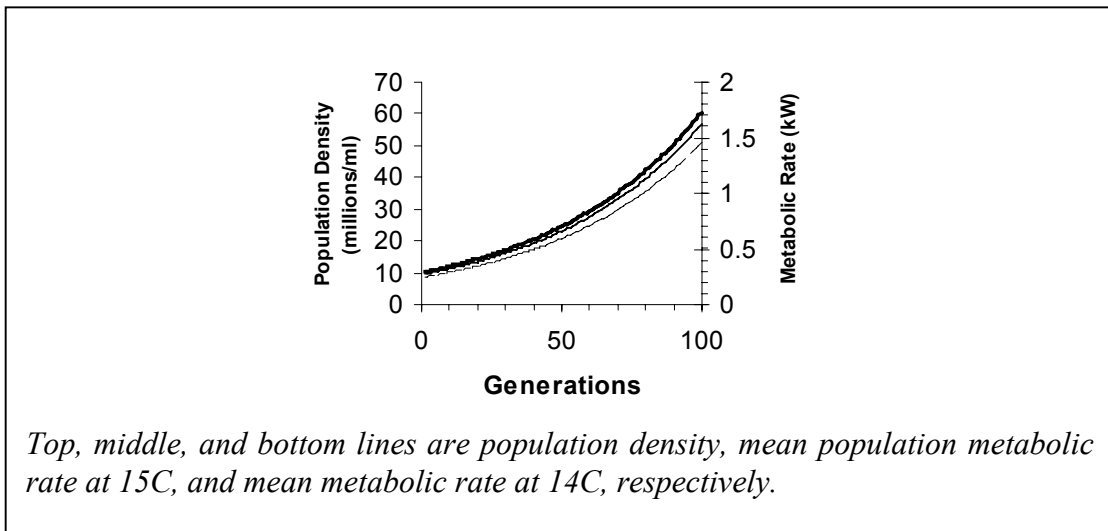
$$B_{POP}(M, T, t) = N(M, T, t) \left[B(M, T) + \frac{E(M)}{S(M, T)} \right] + E(M) \frac{dN(M, T, t)}{dt}$$

where $N(M, T, t)$ is the population size (density), $B(M, T)$ is the mean individual metabolic rate, $E(M)$ is the amount of energy required to make an individual, $S(M, T)$ is the average life span, and $r = \frac{1}{N} \frac{dN}{dt}$. These components are computed each generation from a Picoplankton node, which is a sub-level to Autotroph.

The Picoplankton node uses data from Gillooly *et al.* (2001) for the mean individual metabolic rate and life span for unicellulars and invertebrates as a function of temperature. We then use an estimate of $E(M) = E_c \times M$ for $E_c = 2.1 \times 10^{-5}$ J from West *et al.* (2001) for the average energy required to make a cell.

Thus the flow of control is that the Picoplankton generates estimates for the maintenance, replacement, and growth components of the metabolic rate based on the Ecosystem temperature and the Picoplankton body mass. These are passed as parameters up to the Autotroph level which calculates population metabolic rate and density. We ran simulations for temperatures of 14°C and 15°C.

Results The simulations show the expected increase in mean population metabolic rate as correlated with increasing population size. They also show a rise in the metabolic rate with a rise in temperature. Population densities are in accord with those reported in the literature.



Discussion The results show a linking of individual metabolic rate with population growth, which is a necessary basis of the entire modeling approach. Sub-levels to individual metabolic rate link to carbon fixation; super-levels to population density link to ecosystem dynamics. There are two important directions in which to mature the model. The first is to introduce an explicit Carbon Pool and Heterotrophic level so that growth rates and a carrying capacity are implicitly regulated by body mass, temperature, resource acquisition, starvation, infection, and predation. Body mass, temperature, infection, and predation can be parameterized from the literature. Resource acquisition, and its effect on starvation (nutrient limitation), is the key link between this Aim and the rest of the GTL Project. The molecular processes of carbon fixation map the rate of carbon sequestration with the rate of ATP production. This will vary as a function of temperature. The hierarchical modeling approach allows us to “black box” this transformation, and then expose it in increasing detail as supplied by the other Aims of the Project.

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