

A white paper on relevant aspects of  
Population Dynamics, Marine Community Ecology, and Oceanography  
of Marine Microbes

for the Department of Energy Genomes to Life project:

CARBON SEQUESTRATION IN *SYNECHOCOCCUS SP.*:  
FROM MOLECULAR MACHINES TO HIERARCHICAL MODELING

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**Preamble** The purpose of this document is to collect in a single place an introductory exposition of theory and data relevant to the simulation and modeling of marine microbes in their natural environment. This report is by no means exhaustive, nor even representative, of the vast knowledge already published in this area. It is to be used as a starting place or preliminary reference guide for more detailed studies. Content is based heavily on the references cited in the footnotes. The organization begins with: *i*) an introduction to the basic theoretical models of population growth and how they are linked to concepts of fitness; *ii*) the ecology of marine microbes, *i.e.*, how the *ex situ* models of population growth may be embedded in ecological systems; and *iii*) how relevant aspects of oceanography—essentially carbon and nitrogen cycles—interact with the community ecology. The completed exposition should outline a framework for modeling population growth within ecological trophic levels, which in turn exist in an ocean environment. Two additional white papers address the molecular ecology of marine microbes (*i.e.*, how sub-cellular processes affect growth rates and fitness), and simulation techniques and software engineering patterns respectively.

**Introductory Population dynamics**<sup>1</sup> In population dynamics we are interested in identifying and understanding those forces that affect population growth rates: how quickly populations grow or decline, if they are able to attain and maintain an equilibrium size, and how stable the populations are to perturbations around the equilibrium. We also recognize that populations are not homogeneous entities, but are a collection of individuals at different life stages. Consideration of this allows a classic and elegant mapping of growth parameters to “reproductive value” or fitness.

*Logistic Equation* Classical modeling *does* consider a population as a single, homogeneous entity. Consider a bacterial population that reproduces via binary fission in a nutrient-rich, benign environment. The former condition (binary fission) states that each individual is replaced by two individuals after a reproduction; the latter condition allows us to invoke the approximation that all cells reproduce (*i.e.*, none die before reproduction, or the proportion of those that die versus those that reproduce is vanishingly small). This means that:

$$N_n = 2^n N_0 \quad (1)$$

where  $N_0$  is the starting population size and  $n$  is some number of generations. This equation shows the population doubling every generation, without limit. As such, it may be appropriate during the early stages of population growth but fails to account for factors that will eventually limit growth, such as competition or predation.

We can map some arbitrary time  $t$  to the number of generations  $n$  by the simple relationship:

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<sup>1</sup> Content and equation notation is from, or based heavily on, Valiela 1995 Chptrs 3 and 4.

$$N_n = 2^{(t/t_d)} N_0$$

$$\ln(N_t) = \ln(N_0) + t \ln(2)/t_d \quad (2)$$

where  $t_d$  is the population doubling time: *viz.*  $t = t_d$  when  $N_t = 2N_0$ . The log relationship between  $N_t$  and  $t$  means that the slope of  $\ln(N_t)$  vs.  $t$  (the change in the log of the population size over time) is linear, or constant. This slope is equivalent to the growth rate of the population, or in other words:

$$r = \frac{\ln(2)}{t_d} = \frac{\ln(N_t) - \ln(N_0)}{t} \quad (3)$$

Let us relax the binary fission assumption and address any form of reproduction by extending the above model from the discrete case of “doubling each generation” to the continuous case of “instantaneous growth” with some instantaneous birth rate  $b$  and some mortality  $d$ . Thus from (3):

$$N_t = N_0 e^{rt} \quad (4)$$

where  $r = b - d$ . Equation (4) implies that  $\lim_{t \rightarrow 0} \frac{\Delta N}{\Delta t} \cdot \frac{1}{N} = \frac{dN}{dt} \cdot \frac{1}{N} = b - d = r$ ; *i.e.*, the instantaneous growth rate is the rate of change in population size per individual. This growth rate  $r$  is sometimes also called the *Malthusian parameter* of the population.

Equation (4) exhibits exponential growth without limit. Classical modeling techniques impose a limit by declaring some constant population size  $K$  to be the *carrying capacity* of the population. By doing so, they make no claim as to what limits population growth (be it competition for space or nutrients, disease, predation, etc.), they merely observe that all populations are limited eventually, and so this is incorporated into the model by a gradual decrease in the population growth rate as the population size  $N$  approaches  $K$ . At  $N = K$ ,  $r = 0$ . Mathematically this is expressed in the *logistic equation* as:

$$\frac{dN}{dt} = rN \frac{(K - N)}{K}$$

$$N_t = \frac{K}{1 + ae^{-rt}} \quad (5)$$

for some constant  $a$ . We can solve for  $a = K/N_0 - 1$  given the boundary condition  $N_t = N_0$  at  $t = 0$ . The negative exponential in the denominator means that  $N_t \rightarrow K$  as  $t \rightarrow \infty$ ; *i.e.*, the population’s time-invariant state is at its carrying capacity.

Parenthetically, there is an interesting way to re-write the logistic equation as:

$$x_{n+1} = rx_n(1 - x_n) \quad (6)$$

for a redefined  $r$ . This simple equation has been used as a model for studies in chaotic systems. For  $r < 1$ ,  $x_n \rightarrow 0$ ; *i.e.*, the population goes extinct. For  $1 \leq r < 3$ , the population goes to some time-invariant value called a fixed point. It reaches this value independent of the starting value  $x_0$ . For  $3 \leq r \leq 3.57$ , the population oscillates over time amongst a set of values, a property called periodicity. For  $3.57 < r$ , the system is chaotic: small differences in  $x_0$  or  $r$  produce sequences of  $x_n$  that increasingly differ from each other; these sequences never settle down to a time-invariant value. A key property of interest is that equ. (6) is completely deterministic, yet one loses the ability to predict values of  $x_n$  for large  $n$  to the degree that there is some uncertainty in  $x_0$  (the initial condition) or  $r$  (the parameter). Natural populations rarely if ever satisfy a parameterization equivalent to  $3.57 < r$ .

*Survival Life Tables* An additional assumption we would like to relax is the assumption that populations are homogeneous entities. In reality, populations are a collection of individuals. Individuals may be grouped in life stages, such as larvae, juveniles, and adults. Each life stage may have a different mortality rate, probability of surviving to the next stage, probability of reproduction, etc. These life stages are often organized into *survivorship tables* such as the one below<sup>2</sup>:

Age class ( <i>e.g.</i> , in years)	Population size	Proportion surviving (survivorship)	Number dying in this age class	Mortality rate	Average number alive in this age class	Mean life expectancy at age class
$x$	$n_x$	$l_x = \frac{n_x}{n_0}$	$d_x = n_x - n_{x+1}$	$q_x = \frac{d_x}{n_x}$	$L_x = \frac{1}{2}(n_x + n_{x+1})$	$e_x = \frac{1}{n_x} \sum_x^\infty L_x$
0	142	1.000	80	0.563	102	1.58
1	62	0.437	28	0.453	48	1.97
2	34	0.239	14	0.412	27	2.18
3	20	0.141	4.5 <sup>a</sup>	0.225	17.75	2.35
4	15.5 <sup>a</sup>	0.109	4.5 <sup>a</sup>	0.290	13.25	1.89
5	11	0.077	4.5 <sup>a</sup>	0.409	8.75	1.45
6	6.5 <sup>a</sup>	0.046	4.5 <sup>a</sup>	0.692	4.25	1.12
7	2	0.014	0	0.000	2	1.50
8	2	0.014	2	1.000	1	0.50
9	0	-	-	-	-	-

<sup>2</sup> Table structure and data are from Table 3.1 of Valiela (1995). <sup>a</sup> Estimated.

Notice in the above table that the average life expectancy for individuals in class  $x$  ( $e_x$ ) is approximate constant at 2; this reflects the fact that each year the population size is approximately cut in half (notice the trend in  $L_x$ ). A constant decay rate with a mean life span independent of time is indicative of an exponential decay process. Not all species display an exponential decay in individual survivorship—indeed survivorship curves may display rapid decay initially followed by long tails, constant decay, or an almost constant survivorship initially followed by a decline.

Survivorship tables are linked to population growth and fitness via *fecundity tables*

Age class (in years)	Population size	Proportion surviving (survivorship)	Age-specific fecundity: Number of female offspring per female of age $x$ (reproductive output)	Age-specific reproductive rate
$x$	$n_x$	$l_x = \frac{n_x}{n_0}$	$m_x$	$R_x = l_x m_x$
...				

An important statistic from fecundity tables is the *net reproductive rate*,  $R_0 = \sum_0^\infty l_x m_x$ . The net reproductive rate is the average number of female offspring produced in a female's lifetime. If there are not separate sexes, then the reproductive rate is measured over all individuals. The net reproductive rate is directly relevant to the growth rate of the population via:

$$R_0 = e^{rT} \tag{7}$$

for generation length  $T$  (e.g., time in years). Thus if a population is size  $N_T$  at time  $T$ , then  $R_0 = e^{rT} = N_T/N$ . For non-overlapping generations, it is sometimes preferable to estimate  $r$  from the equation:

$$\sum_{x=0}^{\infty} e^{-rx} l_x m_x = 1 \text{ or in continuous form } \int_0^{\infty} e^{-rx} l_x m_x dx = 1. \tag{8}$$

In the 1920s, the great biologist J. B. S. Haldane showed that for  $T =$  average generation time, the difference between (7) and (8) in terms of estimating  $r$  is minimal.

Lastly, we can relate  $l_x$  (survivorship or probability of surviving to age  $x$ ) and  $m_x$  (the number of females born to a female of age  $x$ ) to the concept of *reproductive value*.

Reproductive value is the present value of future offspring—analogueous to the time value of money. Mathematically it may be expressed as<sup>3</sup>:

$$V_x = \frac{e^{rx+1}}{l_x} \sum_{i=x}^{\infty} e^{-ri} l_x m_x . \quad (9)$$

Reproductive value is this the average number of female offspring that a female is expected to leave after age  $x$  relative to the number of females at that age. In other words, the reproductive value is the relative contribution of each age class to the population's time-average growth rate. Reproductive value curves are usually uni-modal: they are not zero at  $x = 0$  (because newborns have some probability of surviving and thus will at a later point contribute to the population's growth); they peak at some intermediate age; and they then decline to 0 as age increases and it becomes increasingly unlikely that any individuals survive.

The Malthusian parameter  $r$  can be seen as the rate of spread of an allele within a population. It is related to the classical concepts of (absolute) *Wrightian fitness* and selection coefficients via  $W = 1 \pm S = e^{rT}$  or  $\ln(W) = rT$  when  $T = 1$  (*i.e.*, the discrete case where  $T$  corresponds to one generation). Capital letters refer to absolute fitness, and are related to relative Wrightian fitness via  $w = W/\bar{W} = 1 \pm s$ . We may finally relate these to the net reproductive rate via:

$$\begin{aligned} \frac{\Delta N}{N} &= \bar{S} = \bar{W} - 1 \\ \bar{W} &= \frac{\Delta N}{N} + 1 \\ &= \frac{\Delta N + N}{N} \\ &= \frac{N_a}{N} \\ &= R_0 = \sum_{x=0}^{\infty} l_x m_x \end{aligned}$$

where  $N_a$  is the number of individuals after selection (sometimes referred to as the number in the filial generation).

*Coupling cell growth to population growth*<sup>4</sup> It may be relevant for our studies to link the prokaryotic cell cycle to growth rates in a manner more detailed than that of simple binary fission. This can present a mechanistic way in which to link external factors such as temperature and light to population growth rates.

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<sup>3</sup> See Goodman (1982) for the use of  $e^{rx+1}$  vs. the traditional Fisherian term  $e^{rx}$ .

<sup>4</sup> Content and equation notation is from, or based heavily on, Vaulot (1995).

Photosynthetic prokaryotes have discrete times of DNA synthesis that roughly correspond to the eukaryotic cell cycle phases of G<sub>1</sub>, S, and G<sub>2</sub>. Yet some bacteria can begin a second round of chromosomal replication before the first round—and binary fission—have completed. This tends to destroy the notion of separate G<sub>1</sub>, S, and G<sub>2</sub> phases. Valout (1995) reports that some *Synechococcus* and *Prochlorococcus* strains may have more than two copies of their genome per cell—sometimes as many as five. “The interpretation of these observations is that initiation of new replication origins is not synchronous and that the DNA replication cycle and the division cycle are loosely coupled in these genera (Binder and Chisholm 1995).” (Vaulot 1995).

A straight-forward method to determine the effect of external factors on the cell cycle is to apply a factor and to note if or when the cells are arrested. A limitation of this method is that the cells must be culturable. Still, such methods have broadly determined that decreases in temperature tend to slow the cycle by slowing progression through every stage. Thus population growth rates are expected to decrease with water temperature.

Light deprivation is known to affect photosynthetic bacteria like *Synechococcus*. “In *Synechococcus*, darkness blocks cell division and prevents the initiation of new replication forks (Mann and Carr 1974; Binder and Chisholm 1990). In *Prochlorococcus*, ... light limitation only affects G<sub>1</sub> but darkness blocks cells in all cell cycle phases including S (Vaulot, unpublished data).” (Vaulot 1995). Light may affect cells by either moderating their cell cycle, thus causing a synchronicity between cellular division and light and dark cycles, or by influencing an endogenous circadian clock. There is evidence for circadian clocks in *Synechococcus* (Vaulot and Chisholm 1987).

For *Synechococcus*, *Prochlorococcus*, and all species reported by Vaulot (1995), nitrogen is only required in G<sub>1</sub>: nitrogen starvation in other phases does affect not the cell cycle, but under starvation conditions cells will accumulate in G<sub>1</sub>. Winter samples of *Prochlorococcus* from the Mediterranean Sea showed very few in either S or G<sub>2</sub>. Cells entered S and G<sub>2</sub> within 24 hrs of the addition of nitrogen. Summer samples of *Synechococcus* from the same sea showed no response to additional nitrogen, though Vaulot (1995) does not report the distribution of cell cycle stages.

Phosphorus starvation arrests *Prochlorococcus* in all stages. Cultured cells arrested in G<sub>1</sub> or G<sub>2</sub> could resume their cycle upon the addition of phosphorous, but cells arrested in S could not resume the cycle. In the Summer samples of *Synechococcus* reported above, the addition of phosphorus did not cause the cells to “respond.”

Vaulot (1995) discusses methods to use data on the cell cycle to estimate population growth rates. He explores and then dismisses the *mitotic index method*, a method that is based on counting the occurrence of an identifiable event in the cell cycle (e.g., cells with two nuclei just prior to cytokinesis). The method is strongly dependent on the accurate estimation of the duration of the event ( $t_d$ ), and this parameter cannot be accurately extrapolated from cultured to natural conditions. A second method is discussed called the *cell cycle method*. This method estimates  $t_d$  from field data as well as the duration of other stages, and is thus considerably more accurate (see references in

Vaulot 1995). Based on flow cytometry estimates of cell cycle data, Vaulot (1995) reports that *Prochlorococcus* and *Synechococcus* are "... highly synchronized to the daily light cycle with division rates of the order of 1 doubling per day (0.69 day<sup>-1</sup>)."

**Introductory Marine Community Ecology**<sup>5</sup> The last 10-15 yrs has seen a small revolution in marine community ecology. There has been an increased recognition of the importance of microbes in planktonic food webs—microbes now believed to account for as much as 50% of the total marine biomass. Concomitantly, these organisms are now believed to play an increasingly important role, with "bacterial respiration consuming much of primary production." Primary production is that initial direct generation of biomass from autotrophic carbon fixation, such as via photosynthesis or chemosynthesis. Organic matter for bacterial respiration comes from partly from dissolved organic matter (DOM), but also from other bacteria, phytoplankton, and animals, thereby implicating bacteria as an important *microbial loop* in the planktonic food web. Recent estimates of bacterial numbers are higher than previously thought (see below), but tend to exhibit a relatively small variance, suggesting that bacterial populations are under strong, stabilizing dynamic forces. This view—not entirely accepted by all—tends to base the entire marine community on a viral/prokaryotic foundation. Marine predation is strongly dependent on size, with larger plankton being predominantly generalists on the next smaller class<sup>6</sup>.

picoplankton	< 2 μm	viruses and bacteria
nanoplankton	2 – 20 μm	
microplankton	20 – 200 μm	large phytoplankton small zooplankton
macroplankton	200 – 2,000 μm	large zooplankton
megaplankton	> 2 mm	

*Viruses* Viruses are approximately 0.02 μm in diameter, with densities of 10<sup>6</sup> – 10<sup>7</sup>/ml in ocean surface waters and perhaps an order of magnitude higher in coastal waters. Viruses can have a heavy toll on bacteria: 2-16% of marine bacteria may be infected, possibly causing lytic rates 2-24%/hr. Lysis is one mechanism that increases dissolved organic carbon (DOC), thereby producing a carbon source for photosynthetic plankton. Suttle and Chen (1992) estimate 8-26% of bacterial mortality is caused by viruses. Viruses, of course, affect eukaryotes also, and there is evidence on increased algal mortality due to viruses as a correlated response to increased phosphate levels.

<sup>5</sup> Content and direct quotations are from, or based heavily on, Valiela 1995 Chptrs 4 and 9 unless otherwise noted.

<sup>6</sup> There are exceptions: for example, bivalve larvae consume *Synechococcus* (0.5 μm). Also, there are many known preferences of grazing preferences for or against certain taxa of phytoplankton, e.g., zooplankton do not consume blue-green bacteria.

*Bacteria* Bacteria are approximately 1-2  $\mu\text{m}$  in size, with densities of  $10^5 - 10^8/\text{ml}$ . According to Kjelleberg *et al.* (1993) “The oceans contain  $10^{22}$  liters of water, and as there are  $10^7$  to  $10^9$  bacteria per liter [ $10^4 - 10^6/\text{ml}$ ], a significant portion of the world’s bacteria ( $10^{30}$ ) live in the water column of the oceans.” Bacteria acquire carbon by ingesting DOM directly, releasing exoenzymes to break down particulate matter into DOM, or by predation on other plankton. The latter source is probably not a significant component for most bacteria, though the former two may be of equivalent quantitative importance in providing the bacteria’s total organic intake. Bacteria may account for half of the total carbon fixation in marine environments. This is positively correlated with phytoplanktonic production, nutrient enrichment (*e.g.*, eutrophication), and temperature. Despite an increase in production in nutrient-rich waters, the relative contributory production of bacteria decreases: in nutrient-poor waters, bacteria may be five times more productive than phytoplankton, but this decreases to 1:1 levels in nutrient-rich waters. Production is measured as total biomass; productivity: the rate of change in biomass.

Most ocean waters are oligotrophic, that is they are essentially deserts<sup>7</sup>. Water masses in the deep ocean may have residence times of 1000 yrs, compared to 2-10 yrs for the Antarctica intermediate waters (Marshall 1979). This means that bacteria deep in the water column are likely to experience a prolonged, stable nutrient-poor environment. Laboratory experiments have maintained stable marine bacterial populations [presumably in a starved or semi-starved state] for 5-7 yrs (Hood *et al.* 1986; Nissen 1987). Bacteria have distinct morphological, physiological, and genetic programs in both response and recovery from starvation conditions. Kjelleberg *et al.* (1993) conclude that “... starved, nongrowing cells are metabolically active ... [and] participate in carbon cycling in the ocean, *i.e.*, they are not dormant and the nongrowing state is a regular state of the natural life-cycle of bacteria.”

In pelagic environments, nutrient levels and grazing have a strong affect on controlling bacterial densities. “In the oligotrophic Sargasso Sea, bacterial productivity ranged from 0.8 to 6  $\text{mg C l}^{-1} \text{d}^{-1}$ , whereas in summer in Chesapeake Bay, it ranged from about 8 to 70 and over tropical seagrass beds from 20 in winter to 200 in summer.” (Kjelleberg *et al.* 1993; see citation for original sources). Bacterial production shows a dependency on temperature (seasons, latitude, depth), and a complicated correlation with primary production, presumably because of factors affecting the availability of carbon<sup>8</sup>. The correlation is complicated, because factors such as the weather affect ocean currents, which in turn create non-trivial horizontal mixing of organic matter amongst surface waters that later settle in geographically disparate locations. In summary, bacterial activity is strongly affected by the availability of nutrients and organics, the latter being tightly correlated with phytoplanktonic distributions.

*Heterotrophic nanoflagellates and nano- and microplanktonic protozoans*  
Nanoflagellates are major consumers of bacteria and viruses. They occur in densities of  $10 - 10^5/\text{ml}$ , and with approximately 1:1000 nanoflagellates:bacteria when found

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<sup>7</sup> This text is a summary of Kjelleberg *et al.* 1993, which was also the source for the included citations.

<sup>8</sup> *e.g.*, “Interestingly, it has been shown that marine bacteria in the subarctic Pacific are carbon and/or energy deprived rather than limited by nitrogen or phosphorus (Kirchman 1990).” Kjelleberg *et al.* 1993.

together. “In one study, viruses provided up to 9% of the carbon, 14% of the nitrogen, and 28% of the phosphorus consumed by nanoflagellates in cultures where there were  $10^6$  bacteria  $\text{ml}^{-1}$  and  $10^7$  to  $10^8$  viruses  $\text{ml}^{-1}$  (Gonzalez and Suttle 1993)” (Valiela 1995). Nanoflagellate consumption of bacteria is high enough to suggest, though not prove, that bacteria may be controlled by this “top-down” pressure.

Marine systems exhibit properties of cascading controls, for example there is evidence that releasing nanoflagellate predation pressure can result in an increase in bacterial abundance, though nanoflagellate control of bacterial abundance tends to weaken when nanoflagellates themselves are under top-down predation. Currently, it is premature to conclude that predation is the *primary* pressure controlling bacterial dynamics: indeed, the above section summarized evidence that nutrient and organic availability are likely to have a major “bottom-up” effects. Protozoans also consume bacteria, though top down control by the largest protozoans is primarily through intermediate nano- and microplanktonic groups.

*Top-down and bottom-up controls* Studies tend to support strong top-down controls in freshwater systems, but marine systems are more complicated. For example, there is strong evidence of bottom-up  $\uparrow$ nutrient  $\rightarrow$   $\uparrow$ ocean productivity  $\rightarrow$   $\uparrow$ fish population effects in marine systems, but these implicitly produce concurrent top-down effects ( $\uparrow$ fish densities  $\rightarrow$   $\downarrow$ dominant zooplankton). Fish cause size-specific predation, as larval and adult predation pressures differ. Larvae may be under intense density-dependent competition, while it is believed that adult populations rarely over-exploit their prey, thereby decoupling a strong regulatory effect between those levels. The generalist nature of zooplankton predation means virtually no species is without predators, and thus pelagic food webs tend to be “unstructured” (Issacs 1973), versus the tighter top-down control often seen in freshwater systems. This is likely due to a number of factors, one of which may simply be that marine fish are  $10 - 10^4$  less densely distributed than freshwater fish, and thus density-independent controls may interfere with a tight cascading effect between trophic levels. In general, trophic levels in marine systems are more loosely coupled, and it is more difficult to combine top-down and bottom-up pressures in a single, unified model.

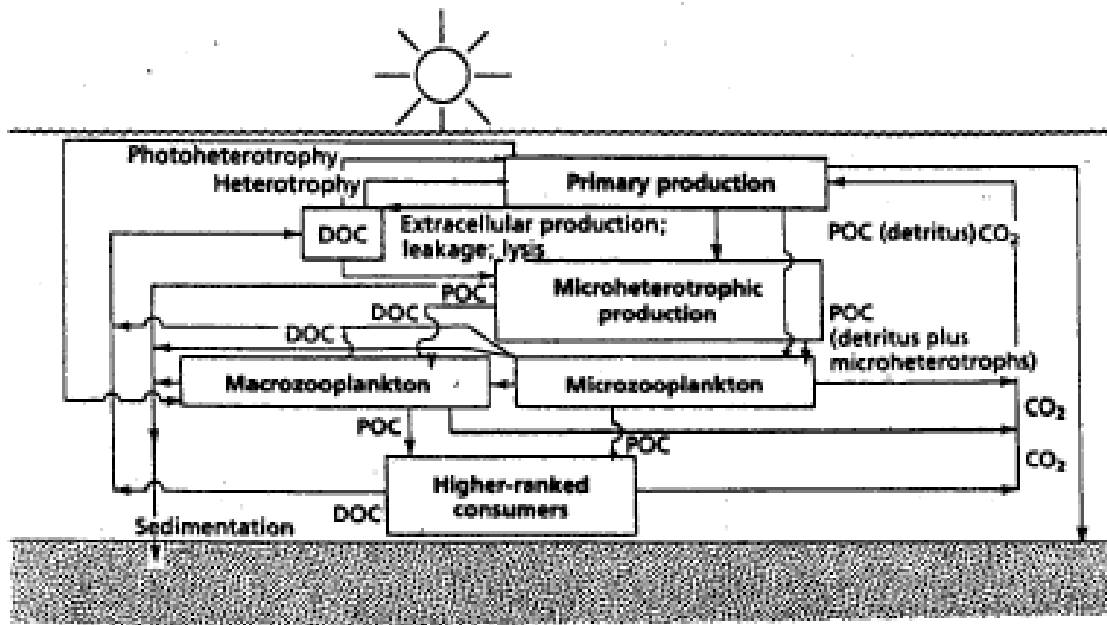
These generalization do not apply to marine mammals. Marine mammal population dynamics are tightly linked to food availability. It is not clear, though, how or if these pressures cascade through the food web. For example, whale harvesting has reduced the annual consumption of krill by whales from  $1.9 \times 10^8$  tons/yr in 1900 to 40 tons/yr in 1984. Yet total oceanic annual consumption of krill has remained constant at  $4.7 \times 10^8$  tons/yr. The difference of  $2.8 \times 10^8$  tons/yr of has been made up by increased consumption by seals, birds, fish, and squid (data from Table 9-2 of Valiela 1995, Chptr 9 summarizing Laws 1985). This example highlights the difficulty of constructing reliable trophic models when the full set of interactions is unknown.

Top-down and bottom-up controls can be seen partially in terms of the classic tension between competition and predation, and the relative effects of density-dependent and independent forces. But these factors are not orthogonal, because, for example, food availability may be a dominant, density-independent factor up to a certain level, but then

may invoke increasingly stronger scramble competition and density-dependent effects as abundance increases further still. Thus, just as there is no general consensus on the relative contributions of competition and predation (nor necessarily need there be), there is no broadly applicable law as to when population abundance is density dependent or independent. This should temper any naive application of the logistic model described earlier.

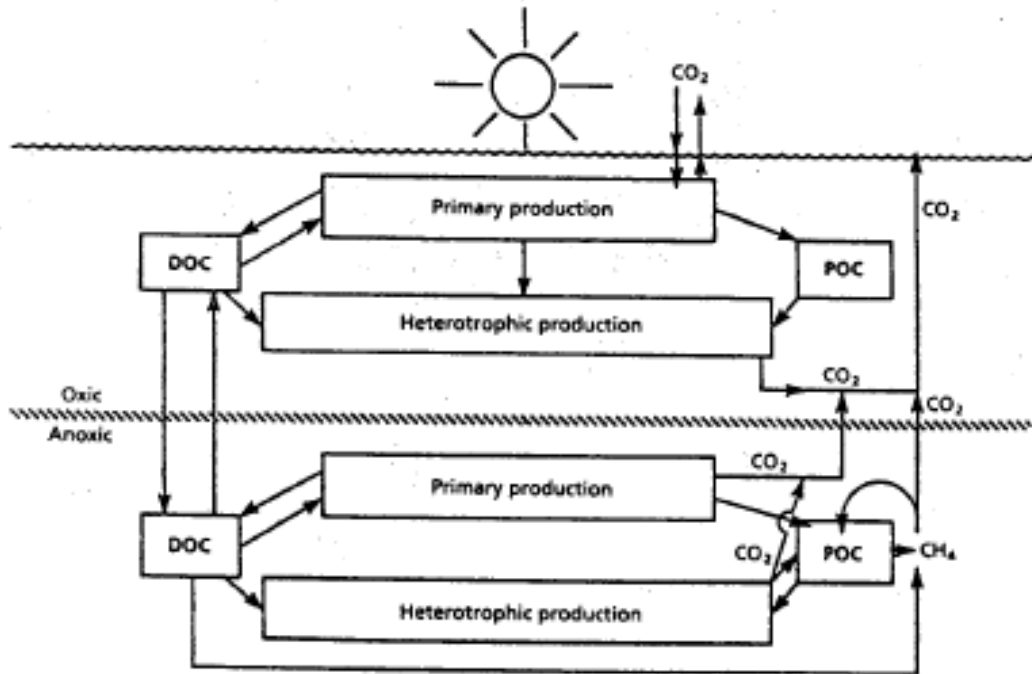
**Introductory Oceanography**<sup>9</sup> A good introduction to oceanography would cover physical chemistry, geology, geography, metrology, hydrology, and of course marine biology in an exposition of the role of the world’s oceans in our planet’s history. This “Introduction” does not do that. It does, though summarize a paper quite relevant to this carbon sequestration project entitled “Interaction of nitrogen and carbon cycles in the marine environment” (Paerl 1993). In doing so, it highlights the role of biogeochemistry in oceanography.

*Carbon and Nitrogen Cycles* It is well known that nitrogen can be a limiting factor in marine primary and secondary production. In nutrient-poor environments, nitrogen and carbon create tightly linked interactions, for example, the fixed nitrogen supply can tightly regulate photosynthetic carbon fixation rates, which in turn affect organic carbon availability for nitrogen fixers. This tight linking tends not to be observed in the other nutrient cycles (P, S, Si), though Fe may be an exception. Figures 1 and 2 summarize carbon cycling through trophic levels. Microbial groups that may have similar carbon roles may have very different nitrogen roles, as, for example, nitrogen fixing (nitrogen



**Figure 1** [Figure 14.9 of Paerl 1993: “Planktonic trophic interactions between microbial primary producers, heterotrophs, and higher-ranked consumers. Resultant carbon fluxes under aerobic conditions are illustrated. Elements of the microbial organic and inorganic recycling component (microbial loop) of the microbial food web are also incorporated into this schematic diagram.”]

<sup>9</sup> Content and direct quotations are from, or based heavily on, Paerl 1993 otherwise noted.



**Figure 2** [Figure 14.10 from Paerl 1993: “Carbon flux interactions between primary producers and microheterotrophs in representative oxic and anoxic waters. Soluble organic and inorganic carbon fluxes across the oxic-anoxic interface are also included.”]

[N<sub>2</sub>] → ammonia [NH<sub>3</sub>] and denitrifying (nitrate [NO<sub>3</sub>]<sup>-</sup> → nitrogen [N<sub>2</sub>]) microflora both rely on similar carbon as an energy source.

Major revisions to nitrogen and carbon cycles have occurred in the last 20 yrs in large part as a recognition of the increasingly large role played by pico- and nanoplankton. This has tended to soften the standing model that most oceanic primary production is due to micro- or “net” plankton. This means that much, possibly the majority, of carbon and nitrogen cycles occur via primary production of viruses, bacteria, and small protists. Of noted importance is the cyanobacterial picoplankton *Synechococcus* spp. and *Synechocystis* spp. (Waterbury *et al.* 1979; Iturriaga and Mitchell 1986; Olson *et al.* 1990). The difficulty in detecting nutrient utilization, but the recognized importance of the roles of picoplankton leads Paerl (1993) to state that “Trophic roles of and interactions between photosynthetic pico- and nanoplankton, heterotrophic bacteria, and microzooplankton are far more complex than previously recognized. These complexities have a significant impact on the routes and amounts of oceanic carbon and nitrogen flux.” (see Paerl 1993 for sources).

The role of pico- and nanoplankton in nitrogen and carbon cycles has a further effect of challenging conclusions based on macroscale measurements. Significant flux may occur at spatial and temporal scales that are unaccounted for by traditional techniques. Thus logical sequences of events such as the nitrogen loading of nitrogen-depleted coastal waters increasing carbon fixation, which in turn reduces atmospheric CO<sub>2</sub>, need to be carefully examined with due attention paid to the role of pico- and

nanoplankton. “If off-shelf transport of POC [particulate organic carbon] and PON [particulate organic nitrogen] is a significant component of carbon flux, then coastal interception of carbon dioxide may significantly mediate the air-sea carbon dioxide balance. (Walsh *et al.* 1981, 1985).”

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