Nitrate supply and demand in the mixed layer of the ocean

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ABSTRACT: We define a new dimensionless number, S, to be the ratio of nitrogen supply to nitrogen demand of new primary production in the pelagic ecosystem. When $S > 1$, we expect high-nutrient, low-chlorophyll (HNLC) conditions. Using the results of a new model of nitrogen input and consumption for the mixed layer of the ocean, we calculate S for selected oceanic regimes. Those generally accepted to be HNLC are characterised by $S > 1$. The bio-optical terms in this model (specific absorption of pigments, parameters of the light-saturation curve) are known to respond to addition of iron. Using these known responses, we recalculated the expected value of S under hypothetical enrichments of the selected regimes with iron. In each case, the magnitude of S was reduced, but not always below unity. The maximum value of chlorophyll biomass that can be sustained in a given mixed layer may be calculated from consideration of either the bio-optics or the nitrogen supply. The maximum realised biomass will be the smaller of these 2 estimates.

KEY WORDS: High-nutrient low-chlorophyll · HNLC · Iron fertilisation · Plankton models · IronEx

INTRODUCTION

Among the issues that have captured the interest of ocean biogeochemists during the past decade, the significance of areas with high residual nutrients (in particular nitrate) and low chlorophyll concentration (the so-called HNLC regime) is prominent (Chisholm & Morel 1991). It has been inferred that such systems are, in some way, biologically limited (Martin et al. 1990b): otherwise, the nutrients would be consumed, with a concomitant increase in phytoplankton biomass (as indexed by chlorophyll concentration). Iron, an essential element for autotrophic physiology, has been identified as a potentially limiting resource (Martin & Fitzwater 1988), with the corollary that addition of iron to the ocean would enhance photosynthesis by phytoplankton (Martin et al. 1990a, Coale et al. 1996), leading to complete utilisation of the ambient nitrate. Here, we show that HNLC regimes need not be considered as anomalous marine ecosystems; rather, they should be seen as elements of a continuum in which the biological dynamics are controlled by the ratio of nutrient supply to the nutrient demand of the local primary production, which is determined by the bio-optical characteristics of the pelagic ecosystem. We introduce a new dimensionless number, S, that captures the dynamics and diagnoses whether a given region will be HNLC, either in its pristine condition or after treatment with iron.

That the nitrate is not exhausted (by definition) in HNLC regions is an indication that it is resupplied, if not continuously then at least fast enough (on the average) to exceed the demands of new production (Dugdale 1967, Platt et al. 1989). An important mechanism for nutrient resupply to the upper mixed layer is entrainment through deepening of the layer (Gardner et al. 1993), for example following passage of a storm system (or a mesoscale eddy). Against this background, we constructed and examined (Platt et al. 2003) a simple, analytic model (Fig. 1) of phytoplankton and nutrients in a mixed layer whose depth is modulated intermittently.

MODEL DESCRIPTION

The model is an idealised representation of dynamics in the pelagic ecosystem. Below the mixed layer, nitrate concentration (N_d) is fixed, and the biomass of phytoplankton is zero. When the mixed layer deepens, the entrained water replenishes some or all of the nitrate consumed by growth and dilutes the biomass, increasing the optical transparency. When the mixed layer shallows, nitrate and biomass are lost from it: biomass thus lost cannot re-enter the mixed layer. The intrinsic time step of the model is 1 d. In the mixed layer, the concentrations of chlorophyll and nitrate are $B(t)$ and $N(t)$, respectively, evaluated at the start of Day t. The mixed-layer depth $Z_m(t)$ is perturbed intermittently (not every day) by step changes of common amplitude (a) around a mean depth (Z_m^0), with such changes occurring at the end of the day.

The increase in mixed-layer chlorophyll through photosynthesis on a given day is:

$$\frac{P(t)}{\chi Z_m(t)} = \frac{P_m^B B(t) D}{\chi \theta(t)} \left[f(I_*^m) - f(I_*^m e^{-\theta(t)}) \right] \qquad (1)$$

where we have the primary production $P(t)$ within the mixed layer, the daylength D, a known function (Platt & Sathyendranath 1993) $f(\cdot)$ of the normalised noon irradiance I_*^m (the noon irradiance I_0^m scaled by the ratio of the photosynthesis parameters α^B/P_m^B, where α^B is the initial slope of the photosynthesis-irradiance curve and P_m^B is the specific production at saturating light), the ratio of carbon to chlorophyll χ, and the optical thickness of the mixed layer $\theta(t) = Z_m(t)K(t)$, where $K(t) = K_w + k_c B(t)$ is the diffuse vertical attenuation coefficient, with K_w the attenuation due to water and k_c the specific attenuation coefficient of chlorophyll.

In the simplest case, the loss term for phytoplankton biomass can be taken as a constant fraction (λ) of the biomass. We have solved this system, and full details
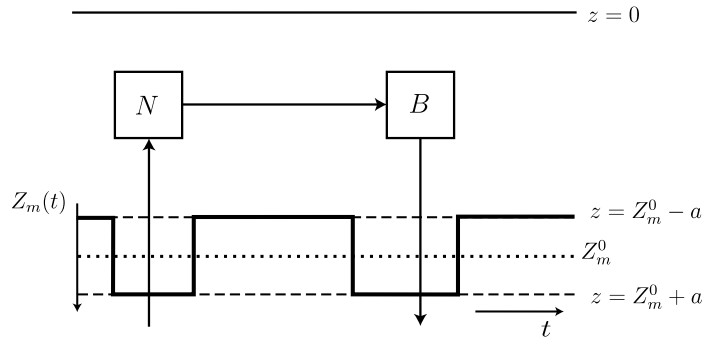
$$B(t+1) = \left[(1-\lambda)B(t) + \frac{P(t)}{\chi Z_m(t)} \right] (1 - \Delta(t)),$$

$$N(t+1) = N(t) - \left(\frac{\nu P(t)}{\chi Z_m(t)} \right) (1 - \Delta(t)) + (N_d - N(t))\Delta(t),$$

where

$$\Delta(t) = \begin{cases} \dfrac{Z_m(t+1) - Z_m(t)}{Z_m(t+1)}, & \text{if } Z_m(t) < Z_m(t+1); \\ 0, & \text{if } Z_m(t) \geq Z_m(t+1). \end{cases}$$

Fig. 1. Schematic of basic model, with governing equations. Nitrate, N, is supplied from the reservoir (concentration N_d) below the mixed layer and converted to biomass, B, of phytoplankton. Depth z is positive downwards. Mixed-layer depth, $Z_m(t)$, is modulated intermittently about Z_m^0 in a series of steps of common amplitude $2a$ but variable timestep. Time t increases in steps of 1 d. The daily primary production in the mixed layer is $P(t)$. A fraction (λ) of the biomass is lost each day from the layer. The stoichiometric equivalents of nitrogen and carbon, relative to chlorophyll, are ν and χ respectively. The quantity $\Delta(t)$, which is zero except when the mixed layer deepens, accounts for the redistribution of material by vertical mixing

are presented elsewhere (Platt et al. 2003). The solutions lead to explicit expressions for the bounds on residual nitrate and biomass. The biomass will converge to a stable, globally attracting value set by the mixed-layer depth, the loss term and the bio-optical properties of phytoplankton (i.e. for a given parameter set and constant mixed-layer depth, all biomass simulations will converge to the same biomass value, regardless of the initial biomass value used). The maximum attainable biomass (B_u) will be the value to which it converges at the shallow mixed-layer depth (see Appendix 1). This maximum will be attained provided that nitrogen supply is sufficient; beyond that, increased nitrogen supply will have no effect on the upper bound for biomass, but will lead to residual nitrate in the mixed layer. The lower bound for the residual nitrate concentration (N_r) will be higher for higher nitrate concentration below the mixed layer (N_d), smaller maximum biomass, and shorter intervals between storms (see Appendix 1).
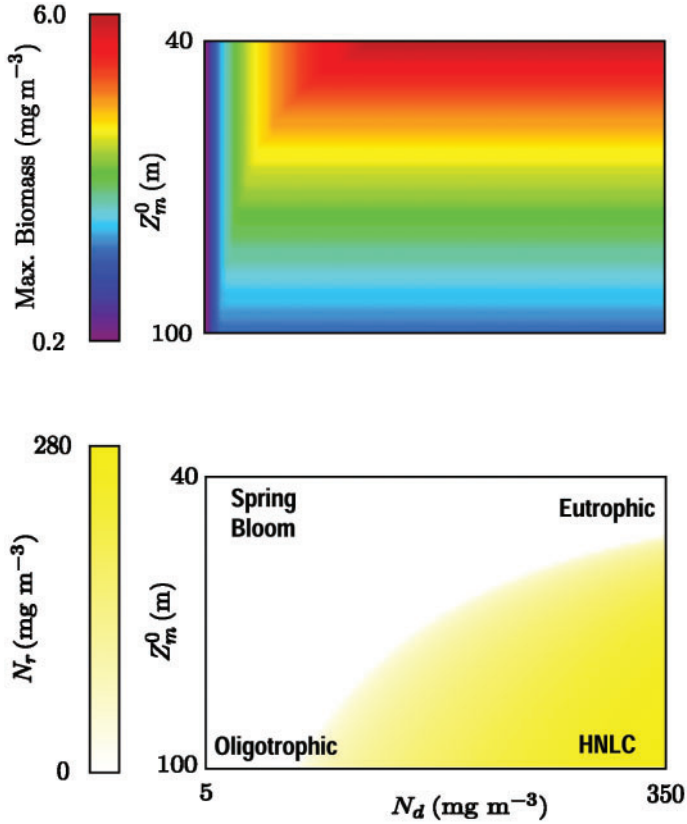
Fig. 2. Computed maximum biomass (B_u or B_{sp}) and minimum residual nitrate (N_r) computed using the model, for a range of Z_m^0 and N_d values. Parameters were fixed at the following realistic values: $\chi = 90$ mg C (mg chl)$^{-1}$; $\lambda = 0.6$ (dimensionless); $\nu = 8.8$ mg N (mg chl)$^{-1}$; $a = 25$ m; $D = 13$ h; $I_*^m = 10$ (dimensionless); $k_c = 0.05$ m^2 (mg chl)$^{-1}$; $k_w = 0.043$ m^{-1}; $P_m^B = 10$ mg C (mg chl)$^{-1}$ h^{-1}; and $T = 7$ d. Various environments, such as oligotrophic, eutrophic, or high-nutrient, low-chlorophyll regions, and phenomena such as the spring bloom, can result from differences in forcing (mixed-layer depth and concentration of nitrogen below mixed layer) for phytoplankton populations with identical properties. (See 'Model description' for definition of parameters)

Thus, the residual nitrate in the ocean is set by the balance between supply and demand for this nutrient: both of these terms are under the influence of physical forcing. The nitrate-chlorophyll plane may be seen as a bidirectional continuum in which the HNLC regimes occupy, at most, 1 quadrant (Fig. 2). They will occur in the appropriate region of parameter space, even when no essential growth factor is lacking. Of course, unavailability of a substrate critical for growth may constitute a condition favouring high levels of unconsumed nitrate (through suppression of nitrate demand), but such unavailability does not appear to be a necessary condition for HNLC.

RESULTS

A new dimensionless number

Generally, HNLC conditions should occur whenever and wherever nitrate is resupplied at a rate exceeding the demands of local new production. We can express this condition in the form of a dimensionless number, S, calculated (conservatively) as $S =$ (minimum nitrate nitrogen supply rate)/(maximum nitrate equivalent of new production), where both quantities are expressed per unit volume in the mixed layer. If T is the maximum interval between deepening events and $2a$ is the typical excursion of the mixed-layer depth following passage of a storm system, the numerator will be $2aN_d/[(Z_m^0 + a)T]$, the entrained nitrogen $2aN_d$ being distributed after deepening over a layer of thickness $(Z_m^0 + a)$ every T days. The denominator $P\nu/[(Z_m^0 - a)\chi]$ is the primary production P, calculated from Eq. (1) for the case where biomass is equal to the upper bound B_u (which occurs when the mixed layer depth is $Z_m^0 - a$), and converted to nitrogen units by the factor ν/χ, where ν is the ratio of nitrogen to chlorophyll in phytoplankton tissue. Then,

$$S = \left(\frac{2aN_d}{PT}\right)\left(\frac{Z_m^0 - a}{Z_m^0 + a}\right)\frac{\chi}{\nu} \qquad (2)$$

If $S > 1$, we may anticipate HNLC conditions. This will tend to be the case for large excursions of the mixed-layer depth, low mixed-layer production, high nitrate concentrations at depth, and shorter intervals between storms. Generally, we anticipate that if T is large, the biomass will tend to be limited by nutrient exhaustion, whereas for small T, biomass will tend to be limited by dilution, leaving residual, unconsumed nutrients.

Application to oceanic regimes

We calculated N_r and S for various oceanic regions (Table 1). To achieve this, we adjusted the value of λ for each region such that the computed value of B_u (see Appendix 1) agreed with the observations. Eq. (1) then gave the primary production P, which was used in Eq. (2) to give S. It is also possible (Platt et al. 2003) to calculate N_r from Eq. (A1) (see Appendix 1). The magnitudes of S are consistent with conventional designation of the regions as HNLC or not, illustrating the utility of the dimensionless index as a diagnostic.

In the case of the Sargasso Sea, the calculated residual nitrate was negative for both spring and summer

conditions. This non-physical result implies that, although the values for B_u are possible from a bio-optical perspective, the supply of nitrate from below may be insufficient to sustain such values. In spring, the observed biomass can be reached temporarily, only because the pre-bloom nitrate concentration in the mixed layer is sufficiently high; the spring maximum B_{sp} (see Appendix 1) is 3.82 mg chl m^{-3}. For the case of summer in the Sargasso Sea, the bio-optical maximum in biomass can be reached only in those years for which the vertical mixing is greater than assumed here. The values of B_u for both spring and summer in the Sargasso Sea are transient maxima and will erode as soon as the initial nitrate stock in the mixed layer becomes exhausted. In Table 1, the values in parentheses correspond to the maximum biomass (B_N in Appendix 1) that could be maintained by the given nitrate supply.

It is now of interest to investigate how S and N_r might change under the addition of iron in those regions characterised as HNLC. In the context of our model (Eq. 1), mixed-layer primary production could be enhanced through modification of the normalised photosynthesis parameters or the specific attenuation coefficient (Platt et al. 2003). From the results of experiments conducted in the equatorial Pacific (Lindley & Barber 1998), we calculated a 40% increase in α^B and a 27% decrease in k_c for the water enriched with iron compared with the values for the control. A corresponding decrease in χ of 53% has been observed (Landry et al. 2000). For the Southern Ocean, using the changes in K and B during the course of the iron-enrichment experiment (Gall et al. 2001), we deduced that k_c decreased by 56% from 0.072 to 0.032 m^2 (mg chl)$^{-1}$ following addition of iron. We used values for the photosynthesis parameters reported for the Southern Ocean (Mitchell et al. 1991). The value of the assimilation number P_m^B following addition of iron was estimated by matching the calculated production to the observations, requiring an increase in P_m^B of 68%.

Using these results as a basis, we can now estimate the magnitudes of S under addition of iron for the field experiments IronEx-I, IronEx-II and the Southern Ocean Iron RElease Experiment (SOIREE) (Martin et al. 1993, Coale et al. 1996, Boyd et al. 2000 respectively). In each case, there is a reduction in S, as expected, but only in the case of IronEx-II does S fall below unity and N_r below zero. However, $B_N > B_u$; therefore, B_u can be attained, but not sustained unless nitrate supply is increased (so that $N_r > 0$). On the other hand, the maximum observed biomass during SOIREE is shown to be sustainable ($S > 1$ and $N_r > 0$), as was observed to be the case because the bloom persisted for many weeks.

One of the uses of this analysis is to deduce λ, which is difficult to measure directly. In the Sargasso Sea and in the equatorial Pacific the values lie in the range from about 30 to 40%. For the Southern Ocean λ is significantly lower, at 15%. Following iron enrichment, inferred values of λ increased in all 3 experiments (Table 1), reflecting an increase in either grazing pressure or sinking rates or both. The retrieved λ is greater for IronEx-I than that for IronEx-II, consistent with observations (Lindley & Barber 1998). Thus, although the model is very simple, it is able to capture the principal features of the major iron-manipulation experiments. Furthermore, the model can be used to analyse changes to the 'top-down' control on the phytoplankton upon addition of iron to the system.

DISCUSSION

Episodic increase in mixed-layer depth in response to changes in wind stress is well known (Sakshaug et al. 1991). It is also known that mixed-layer depths are changing in the world ocean on decadal time scales. In HNLC regimes, high and intermittent wind stress, and a tendency for a net supply of nutrients to the surface ocean, are often salient characteristics of regional meteorological forcing (Mitchell et al. 1991, Sakshaug et al. 1991). To the extent that weather patterns (in particular the distribution of wind-stress curl and the frequency and intensity of storms) may be modified through the suite of processes collectively known as climate change, we could expect the world distribution of HNLC regimes to change accordingly.

We have used a simple representation of hydrodynamics, such that the nitrate supply rate in our S calculation is determined by the extent and frequency of mixed-layer deepening. However, other mechanisms of nitrate supply could be considered, such as a constant supply due to wind-driven upwelling, for which a value of S could again be calculated. In further work (Edwards et al. unpubl. work) we have considered more explicitly the temporal dynamics of the mixed layer. Moreover, because the choice of closure term (loss term of the highest trophic level modelled) has often been found to strongly influence the dynamics of models (Steele & Henderson 1992, Edwards & Yool 2000), we have also investigated the use of a quadratic loss term in place of the linear loss term (Edwards et al. unpubl. work).

Because photosynthesis lowers the partial pressure of carbon dioxide in the surface layers of the ocean, fertilisation of HNLC regions with iron has been advanced as a possible mechanism for mitigation of

Table 1. Input parameters and computed model outputs for selected oceanographic regions and conditions. Z_m^0: mean depth (m) of mixed layer; a: amplitude of oscillation of mixed-layer depth, m; k_c: biomass-specific vertical attenuation coefficient for photosynthetically active radiation, m^2 $(mg\,chl)^{-1}$; α^B: initial slope of the photosynthesis-irradiance curve, $mg\,C$ $(mg\,chl)^{-1}$ h^{-1} $(W\,m^{-2})^{-1}$; P_m^B: specific production at saturating light $(mg\,C\,mg^{-1}\,chl)$ h^{-1}; λ: biomass loss (dimensionless); χ: carbon to chlorophyll ratio, $mg\,C$ $(mg\,chl)^{-1}$; B_u: maximum biomass, $mg\,chl\,m^{-3}$; N_r: residual nitrate, $mg\,N\,m^{-3}$. Quantity S (ratio of N supply to N demand of new primary production) is dimensionless. Published parameter values used whenever available. For SOIREE, photosynthetic parameters were adjusted in primary production model to match observed production per unit biomass. Daylength, D, and noon irradiance, I_0^m, were computed using geographic location and season and a clear-sky model, yielding values of 12.7 h and 324 W m^{-2} for Sargasso Sea spring, 13.2 h and 340 W m^{-2} for Sargasso Sea summer, 12 h and 350 W m^{-2} for the equatorial Pacific, and 16 h and 90 W m^{-2} for the Southern Ocean respectively. Remaining parameters were held constant for all locations: $K_w = 0.042$ m^{-1}, $\nu = 8.8$ mg N $(mg\,chl)^{-1}$ and $T = 7$ d (where K_w = attenuation due to water, ν = ratio of N to chlorophyll in phytoplankton tissue, and T = maximum interval between deepening events). The loss term λ was a free parameter, adjusted so that B_u equalled the maximum reported values of biomass from literature. Values in parentheses correspond to the maximum biomass, B_N (see 'Application to oceanic regimes'). N_r and parameter S were then computed using the input parameters. SOIREE: Southern Ocean Iron RElease Experiment

Region and condition	Input parameters (observed and inferred)								Modelled outputs		
	Z_m^0	a	N_d	k_c	α^B	P_m^B	λ	χ	B_u	N_r	S
Sargasso Sea[a]											
Spring	55	15	56	0.05	0.140	6.2	0.40	50	2.98 (1.64)	−199	0.33
Summer	85	15	4.34	0.05	0.053	2.4	0.31	50	0.25 (0.10)	−17	0.27
Equatorial Pacific[b]											
Typical	50	20	112	0.037	0.060	6	0.29	150	0.24	98	15
IronEx-I[c]	50	20	112	0.027	0.084	6	0.68	70	0.57	41	2.7
IronEx-II[c]	50	20	112	0.027	0.084	6	0.43	70	2.98 (4.15)	−133	0.81
Southern Ocean[d]											
Typical	65	8	350	0.072	0.276	1.1	0.15	90	0.26	335	32
SOIREE[c]	65	8	350	0.032	0.276	1.85	0.29	45	1.82	167	2.4

[a]Platt et al. (1990, 1992), McGillicuddy et al. (1995), McGillicuddy & Robinson (1997)

[b]Martin et al. (1994), Gardner et al. (1995), Lindley et al. (1995), Murray et al. (1995), Chai et al. (1996), Coale et al. (1996), Loukos et al. (1997), Lindley & Barber (1998), Landry et al. (2000)

[c]Field experiments

[d]Mitchell et al. (1991), Boyd et al. (2000), Gall et al. (2001), Lancelot et al. (2000)

the anthropogenically enhanced greenhouse effect caused by increasing concentrations of carbon dioxide in the atmosphere (Martin et al. 1990a). The results presented here provide a framework within which the results of oceanographic expeditions to HNLC regions could be discussed and interpreted, especially with respect to their bearing on the issue of iron fertilisation. Our analysis shows that, although lack of a limiting resource (e.g. iron) may constitute a sufficient condition for occurrence of HNLC regions, it is not a necessary condition for their existence. Even when phytoplankton growth is stimulated by addition of iron, other bio-optical and physical factors may limit the evolution of biomass and nutrients in the mixed layer. Our results show that iron stimulation may be of only transient value, at least in some regions and under some conditions of physical forcing. Furthermore, the observed responses are achieved at the cost of changing the dominant phytoplankton population (as evidenced by the change in k_c), with unknown consequences to the integrity of the pelagic ecosystem if iron enrichment were pursued as a long-term strategy. Needless to say, any large-scale modification of the ocean ecosystem should be undertaken only with extreme caution.

Appendix 1. Calculation of upper and lower bounds on biomass and nitrate respectively

UPPER BOUNDS ON BIOMASS

Bio-optical maximum

From the bio-optical point of view, using Eq. (1) and Fig. 1, the upper bound B_u (Platt et al. 2003) is the solution of the equation

$$B_u = (1-\lambda)B_u$$
$$+\frac{P_m^B D B_u}{\chi(K_w + k_c B_u)(Z_m^0 - a)}\left[f\left(I_*^m\right) - f\left(I_*^m e^{-(K_w + k_c B_u)(Z_m^0 - a)}\right)\right] \quad (A1)$$

This maximum biomass will be attained only if the mixed layer remains shallow for a sufficiently long time (because when the mixed layer deepens the biomass will be diluted). The value of B_u is used to give the production necessary to calculate S, since for S we require the maximum new production, which is the production when $B = B_u$. Eq. (A1) cannot be solved analytically to give B_u explicitly as a function of the parameters (note how B_u appears on the right-hand side), but in Platt et al. (2003) we give some insight into the dependence of B_u on the parameters. This result is independent of nitrogen supply.

Nutrient-limited maximum

Initial supply: When we take the nitrogen supply into account, other limitations apply. The maximum possible biomass will occur when the deep nitrogen concentration N_d is converted completely into chlorophyll. This could arise, for example, following deep winter-mixing when the initial nitrogen concentration in the mixed layer is equal to N_d: it is the stereotypic case for the spring bloom, and we refer to this bound as B_{sp}. It is given by

$$B_{sp} = \frac{N_d}{\nu}(1-\lambda)$$

with the implication that the conversion was made in 1 d (upper limit). If the conversion took, say, n days, the term $(1-\lambda)$ would be replaced by $(1-\lambda)^n$. This bound cannot be sustained without an adequate resupply of nitrogen, failing which the estimate of residual nitrate N_r in the mixed layer will be negative.

Episodic supply: The spring-bloom case is an extreme one, for which the surface and deep nitrate concentrations are the same. More typical is the case where mixed-layer nitrate $N(t) < N_d$ and nitrate is resupplied through entrainment by deepening of the mixed layer. For an excursion of the mixed layer $(2a)$, the entrained nitrate is $2aN_d$ redistributed over a depth interval, $Z_m^0 + a$, to give a final concentration of $2aN_d/(Z_m^0 + a)$. Then, after complete conversion of the nitrate to chlorophyll, we find B_N, the maximum nitrogen-supply-limited biomass, is

$$B_N = \frac{2aN_d}{\nu(Z_m^0 + a)}(1-\lambda)$$

Thus, we find the upper bounds on the biomass by considering either the nitrate supply or the bio-optical properties. The maximum realised biomass will be whichever of the bounds is the smallest, depending on the conditions. The maximum observed biomass would be the lower of the bio-optical or the nitrate-limited maxima.

LOWER BOUND ON NITRATE

The lower bound, N_r, on the nitrate is given by Platt et al. (2003):

$$N_r = N_d - \nu B_u\left[1+\lambda\left(\frac{1}{G(1-G^{1/T})} - 1\right)\right]$$

where $G = (Z_m^0 - a)/(Z_m^0 + a)$.

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