INTRODUCTION

With the discovery of the existence and importance of the picophytoplankton and the microbial loop, a new paradigm of planktonic communities has arisen: the autotrophic picoplankton can generally outcompete the larger phytoplankton for nutrients. The picoplankton, however, are grazed by protists, which have short response time scales—similar to the generation times of the picoplankton. The rapid response of herbivorous protists to changes in picoplankton growth rate limits the net population growth rate of the picoplankton to close to zero. The larger ‘netphytoplankton’ (>10 µm), however, tend to be grazed by metazoan zooplankton, which have relatively long generation times and therefore long response times to changes in phytoplankton growth rate. As a result, the biomass of small phytoplankton and the microbial loop represent a relatively constant background in the ocean, and larger phytoplankton account for variability associated with physical forcing and nutrient inputs.

This paradigm has been articulated in many forms in the literature, perhaps most concisely as the ‘ecumenical iron hypothesis’ (Morel et al., 1991; Cullen, 1995). There is a great deal of evidence supporting the constancy of the picoplankton biomass and the variability of netphytoplankton biomass under fluctuating environmental forcing. A particularly vivid example was given by the IronEx II experiment (Coale et al., 1996), in which iron enrichment of a high-nutrient, low-chlorophyll (HNLC) environment led to about a doubling of the picoplankton biomass, but up to an 85-fold increase in some species of diatom. Chisholm has shown that increases in chlorophyll over the constant picoplankton ‘background’ tend to be confined to increasingly large size classes of phytoplankton, particularly diatoms and dinoflagellates (Chisholm, 1992). Phytoplankton blooms in coastal upwelling regions and fronts tend to be dominated by diatoms and other large phytoplankton (e.g. review in Kiørboe, 1993). Similarly, the spring bloom in temperate waters is largely a product of increases in diatoms rather than picoplankton.

While the data support the tenor of the paradigm presented above, there has been some ambiguity in the use of
the concepts of ‘response time scale’ and ‘grazing’, and their equivalents, in the literature. Response time scale will be defined here as the time scale over which changes in biomass occur. Grazing will be defined as the rate at which phytoplankton biomass is lost to grazers. Both of these will be defined mathematically below. Some authors are quite clear on the specific role of grazing pressure in determining the phytoplankton biomass in the face of a fluctuating environment, while others use the ideas of response time scale and grazing response somewhat interchangeably.

Given the ambiguity in the use of these concepts, it seemed prudent to attempt to clarify the relative importance of response time scales and grazing in determining the magnitude of phytoplankton blooms in a fluctuating environment. To do this, a model was developed which included these two processes (and only these processes) explicitly. The model was used to test the ‘response time scale’ hypothesis:

\[ P_{K} \text{; picoplankton are held to constant levels due to the short response time scale of their grazers, while netphytoplankton fluctuate with environmental forcing due to the long response time scale of their metazoan grazers.} \]

While such a hypothesis may not have appeared in the literature exactly as stated above, it is a useful starting point for addressing the relative contributions of response time scales and grazing in controlling phytoplankton blooms.

**MODEL**

To explore the response time scale hypothesis, it was necessary to develop a model that included the phytoplankton and zooplankton time scales explicitly. The model was based on the equations for a first-order kinetic reaction, and it is worth exploring this equation prior to presenting the full model:

\[ \frac{dP}{dt} = \frac{E_{s} - P}{\tau_{g}} \]  

(1)

Here \( P \) is the phytoplankton concentration, \( K_{P} \) the carrying capacity and \( \tau_{g} \) the phytoplankton response time scale.

As steady state, \( P = K_{P} \), and the phytoplankton concentration does not change. If \( P \neq K_{P} \), then the phytoplankton concentration will increase or decrease until \( P = K_{P} \). The time scale over which \( P \) approaches \( K_{P} \) is controlled by \( \tau_{g} \), the phytoplankton response time scale. For large \( \tau_{g} \), the time over which \( P \) changes is long, and vice versa for small \( \tau_{g} \). The farther \( P \) is from \( K_{P} \), the faster the initial change in \( P \). Solving this equation for step changes in \( K_{P} \), or oscillating \( K_{P} \), is relatively easy using standard techniques for ordinary differential equations.

It is important to note that \( \tau_{g} \) is not the phytoplankton growth rate \( \mu \), but is rather the net rate of change of the population in response to environmental changes. In general, \( \tau_{g} \approx 1/\mu \), since it includes the various mortality and physical loss terms.

The model to explore the time scale hypothesis is developed on the premise presented above: the phytoplankton community \( P \) responds to changes in the environmentally controlled carrying capacity \( K_{P} \) with an inherent time scale \( \tau_{g} \). In addition, the phytoplankton are grazed by a zooplankton community \( Z \) with clearance rate \( \alpha \) and a grazing pressure or grazing rate is given by \( \alpha Z \).

The steady-state zooplankton biomass is set as a fraction \( \beta \) of the phytoplankton biomass \( P \). The zooplankton respond to changes in \( P \) with a response time scale \( \tau_{z} \). The grazing pressure or grazing rate is given by \( \alpha Z \).

The Lotka–Volterra model was applied to this problem in the same manner as described below. The strongly oscillating character of the Lotka–Volterra equations (for reasonable parameter ranges) gave highly unrealistic, and somewhat uninterpretable results for this problem.

\[ \frac{dP}{dt} = \frac{E_{s} - P}{\tau_{g}} - \alpha Z \]  

(2a)

\[ \frac{dZ}{dt} = \beta P \frac{P}{\tau_{z}} \]  

(2b)
The steady-state solutions, $\hat{P}$ and $\hat{Z}$, to equations (2a) and (2b) are:

$$\hat{P} = \frac{1}{\beta + \omega \tau_P} + \frac{\hat{K}_P}{\alpha + \beta \tau_P} \quad (3a)$$

$$\hat{Z} = \beta \hat{P} = \frac{1}{\beta + \omega \tau_P} + \frac{\hat{K}_P}{\alpha + \beta \tau_P} \quad (3b)$$

Notice that neither of these equations involves $\tau_P$, the zooplankton response time scale. The phytoplankton concentration at steady state is less than the carrying capacity $K_P$ due to the zooplankton grazing (see $Z$). The degree to which $\hat{P}$ approaches $K_P$ at steady state is controlled by the parameter group $\beta \hat{P}$. If $\beta \hat{P}$ is small, the steady-state $\hat{P}$ will be quite near $K_P$; while if $\beta \hat{P}$ is large, the steady-state $\hat{P}$ is only a small fraction of $K_P$. $\beta \hat{P}$ is the product of the zooplankton clearance rate $\beta$, the zooplankton biomass fraction $\beta$, and the phytoplankton response time scale $\tau_P$. The minimum phytoplankton response time scale $\tau_P$ is set by the inverse of the maximal intrinsic growth rate $\mu$, which is $\approx 1$ day$^{-1}$. Thus, we expect $\tau_P$ to be $\approx 1$ day. The zooplankton biomass fraction probably varies between $\approx 0.1$ and 10 (dimensionless). The zooplankton clearance rate can vary over several orders of magnitude, depending on the type of grazer: protist or metazoan [e.g. Hansen et al., 1997]. Thus, the largest variability in $\beta \hat{P}$ probably lies in $\beta$, the zooplankton clearance rate, and $\beta$, the zooplankton biomass fraction. High clearance rates and/or relatively high zooplankton biomass and/or a long phytoplankton response time scale will force the phytoplankton to be a small fraction of what the environment could support ($K_P$). At steady state, then, the zooplankton response time scale has no role in determining the phytoplankton biomass. Rather, it is the zooplankton grazing parameters that are the strongest determinant of the ambient phytoplankton concentration.

To run the model, a basic set of state variables and parameters was chosen to represent a range of phytoplankton/zooplankton communities. The phytoplankton response time scale $\tau_P$ was set to 1 day for all types of phytoplankton. The zooplankton response time scale was assumed to reflect the generation time of the organisms (or, more accurately, their $e$-folding time scale), and was varied between 1 day (representative of protists) and 30 days (representative of adult copepods). The zooplankton clearance rate was varied between 0.01 and 0.1 $\mu$g C l$^{-1}$ day$^{-1}$ (Hansen et al., 1997), while the zooplankton biomass fraction was set at 0.5. The exact choice of these parameters is not critical to understanding the model dynamics, since $\alpha$, $\beta$, and $\tau_P$ appear as a group in most solutions of the equations. The phytoplankton carrying capacity $K_P$ was initially set at 50 $\mu$g C l$^{-1}$, which is equivalent to $\approx 1$ $\mu$g chlorophyll l$^{-1}$.

**MODEL RESPONSE TO INCREASING $K_P$**

The temporal dynamics of the model are forced by changes in the carrying capacity $K_P$. There is an infinite variety of forcing functions that could be used to drive the model. For the purposes of this paper, the forcing will be restricted to a step change of magnitude $\Delta K_P$ in carrying capacity $K_P$. The model behavior under oscillating $K_P$ and non-linear changes in $K_P$ was explored (not shown); however, the fundamental dynamics are readily apparent with a step function forcing.

The temporal response of the phytoplankton to a step increase in carrying capacity can be understood in terms of three time scales. Two of these time scales relate to the rate of increase of the phytoplankton, the other to the increase in zooplankton (and consequent decrease in phytoplankton). While the intrinsic time scale of change of the phytoplankton is $\tau_P$, there are two effective time scales that arise due to grazing. The first effective time scale is the rate of change of the phytoplankton when there is no change in grazing pressure. This time scale, $\tau_P$, determines the rise in the phytoplankton biomass to the value it would have $P_{max}$ if the zooplankton did not change from their initial steady-state value $P_{o}$. Substituting the constant $P_{o}$ into equation (2a) makes it linear, and solvable using standard methods. The value of $P_{max}$ is given by:

$$P_{max} = \frac{E_Y + \Delta E_P}{1 + \alpha \tau_P \tau_P}$$

$$\hat{Z}_{o} = \frac{1}{\tau_P}$$

$$\hat{P}_{o} = (1 + \alpha \hat{P})^{-1}$$

This time scale is found using the same techniques as above. The steady-state biomasses are given by equations (3a) and (3b) with $K_P$ increased to $K_P + \Delta K_P$.

$$\hat{P} = \frac{E_Y + \Delta E_P}{1 + \alpha \tau_P \tau_P} + \frac{\hat{K}_P}{\alpha + \beta \tau_P}$$

$$\hat{Z} = \beta \hat{P} = \frac{1}{\beta + \omega \tau_P} + \frac{\hat{K}_P}{\alpha + \beta \tau_P}$$

$$\hat{P} = \frac{1}{\hat{P} + \omega \tau_P} + \frac{\hat{K}_P}{\alpha + \beta \tau_P}$$

$$\hat{Z} = \beta \hat{P} = \frac{1}{\beta + \omega \tau_P} + \frac{\hat{K}_P}{\alpha + \beta \tau_P}$$
The actual phytoplankton increase can be achieved more quickly than the plankton overshoot stage is the transient bloom, during which the phytoplankton begin to increase in biomass. The second stage is the enhanced final phytoplankton biomass \( P_f \), which is set by the new carrying capacity \( K_P + \delta K_P \), the phytoplankton response time scale \( \tau_P \), and the zooplankton parameters \( \alpha \) and \( \beta \) [see equation (7a)]. The maximal potential phytoplankton bloom is thus \( P_{\text{max}} \), while the steady-state value is \( P_s \). The difference between \( P_{\text{max}} \) and \( P_s \) determines the potential magnitude of the transient bloom; the degree to which this bloom magnitude \( (P_{\text{max}}) \) is reached is controlled by the ratio of the phytoplankton response time scale \( \tau_f \) (or \( \tau_Z \) or \( \tau_o \)) and the zooplankton response time scale \( \tau_Z \). If \( \tau_f > \tau_Z \), the zooplankton respond relatively slowly and \( P_{\text{max}}/P_s \) will be relatively large. However, for reasonable values of \( \alpha \) and \( \beta \), the transient bloom is only a small increase over the steady-state bloom \( P_s \). (Figure 2), typically 10% or so. For large \( \delta K_P \) and large \( \alpha/\beta_k \), the ratio of \( P_{\text{max}}/P_s \) can be \( >1.5 \). However, this potential \( P_{\text{max}} \) is never achieved, because the large \( \alpha/\beta_k \) implies strong grazing pressure, or a slow phytoplankton response, and the transient bloom is grazed as it occurs. Thus, to a good approximation, both the transient and steady-state bloom magnitudes are controlled by \( \delta K_P \), \( \tau_f \), \( \alpha \) and \( \beta \), and only weakly by \( \tau_Z \).

DEFINING A PHYTOPLANKTON BLOOM

There are two stages to phytoplankton blooms produced by the model’s response to a step increase in \( K_P \). The first stage is the transient bloom, during which the phytoplankton overshoot \( P_f \) as they tend toward \( P_{\text{max}} \) (Figure 1).

BLOOM CONTROLS: RESPONSE TIME SCALE VERSUS GRAZING

Examples of the influence of the zooplankton response time scale \( \tau_Z \) and clearance rate \( \alpha \) in determining the phytoplankton biomass are shown in Figure 3, for an increase in carrying capacity \( \delta K_P = 100 \mu g \text{C l}^{-1} \) (a potential tripling of the original biomass). A longer zooplankton response time scale \( \tau_Z > \tau_f \) allows the phytoplankton to
grow somewhat uncoupled from the zooplankton, and approach $P_{\text{max}}$. As the zooplankton respond, their grazing pressure ($\gamma Z$) increases, and the phytoplankton are grazed back to their new steady-state value $\hat{P}_f$ (Figure 3b, d). A long zooplankton response time scale relative to the phytoplankton response time scale thus allows a transient bloom of the phytoplankton in response to the environmental change. A short zooplankton response time ($\tau_Z \approx \tau_P$) increases the coupling between the changes in the phytoplankton and zooplankton biomasses. The fast zooplankton response allows the grazers to track the changes in phytoplankton, decreasing the extent to which they reach $P_{\text{max}}$ (Figure 3a and c), and decreasing the magnitude of the transient bloom. The ratio of the phytoplankton and zooplankton response time scales $\tau_P/\tau_Z$ thus controls the transient phytoplankton bloom dynamics in response to a change in the environment. However, as noted above, the transient bloom is only a small increase over the steady-state bloom ($\hat{P}_f$) (see Figure 2), and $\tau_Z$ has no influence on the magnitude of $\hat{P}_f$ [see equation (7a)].

Unlike $\tau_Z$, the zooplankton clearance rate, $\alpha$ has a strong contribution to both $\hat{P}_f$ and $P_{\text{max}}$, as it appears in the denominator of both equations. It thus has the potential to be a strong determinant of the bloom magnitude throughout the bloom (Figure 3). Low clearance rates allow significantly increased phytoplankton biomass in response to increased carrying capacity, although the relative magnitude of the transient bloom is decreased. The increase in phytoplankton biomass with decreases in $\alpha$ is quite marked, and considerably greater than the transient increases in phytoplankton driven by increases in zooplankton response time scale $\tau_Z$.

These dynamics are summarized in Figure 4, which shows the maximal increase in phytoplankton $[\max(\Delta P)]$.

Fig. 3. Response of phytoplankton (thick solid line) and zooplankton (thin solid line) to a step increase and decrease in carrying capacity $K_P$ (thick dashed line). Left panels: $\tau_Z = 1$ day. Right panels: $\tau_Z = 30$ days. Top panels: $\alpha = 0.1$ (µg C l$^{-1}$ day)$^{-1}$. Bottom panels: $\alpha = 0.01$ (µg C l$^{-1}$ day)$^{-1}$. Note the enhanced transient bloom for large $\tau_Z$, but higher $\hat{P}_f$ for low $\alpha$. 
times the zooplankton biomass fraction 

the transient bloom max

Fig. 4. Ratio of the change in magnitude changes in

phytoplankton blooms than similar

maximum magnitude of the bloom. For example, at

increases in 

changes in zooplankton grazing (\( \tau_z \)) have a pronounced effect in decreasing the

rate is low and/or the biomass of zooplankton is low), the

have little effect on the magnitude of the phytoplankton bloom. On the other hand, for a given value of \( \tau_z \), increases in \( \alpha \) have a pronounced effect in decreasing the maximum magnitude of the bloom. For example, at \( \alpha = 0.02 \) (µg C l –1 day) –1, the phytoplankton reach 80–90% of their potential biomass for a range of \( \tau_z = 1–30 \) days. However, for \( \tau_z = 1 \) day, changing \( \alpha \) from 0.01 to 0.1 (µg C l –1 day) –1 decreases the maximal phytoplankton biomass from 80% to <50% of its potential. Thus, changes in \( \alpha \) have much more pronounced effects on the magnitude of phytoplankton blooms than similar magnitude changes in \( \tau_z \).

This model suggests, then, that for a given increase in carrying capacity, changes in zooplankton grazing (\( \alpha \)) or biomass (\( \beta \)) have a more significant effect on the resultant magnitude of the phytoplankton bloom than changes in the zooplankton response time scale \( \tau_z \).

**APPLICATION TO IRONEX II**

This simple model [equations (1) and (2)] is easily applied to data, given measurements of concentrations of phytoplankton and zooplankton in appropriate units, and an estimate of \( K_P \). If any one of \( \tau_P \), \( \alpha \) or \( \beta \) is known, the other two can be estimated using the data, assuming a steady-state system. In applying the model to the data from IronEx II (Coale et al., 1996), it was assumed that the time scales \( \tau_P \) and \( \tau_z \) were known, and the model was used to estimate \( \alpha \) (the zooplankton clearance rate) and \( \beta \) (the fraction of zooplankton relative to phytoplankton) using data gathered prior to the iron enrichment.

The model was used to explore the different responses of the picoplankton and netphytoplankton to iron enrichment in an iron-limited system. In such a system, the carrying capacity \( K_P \) is set by the amount of available iron. Addition of suitable forms of iron should then act as a sudden increase in \( K_P \). As discussed in Coale et al., enrichment of iron-limited waters with acidic iron sulphate led to approximately a doubling of the picophytoplankton biomass (from ~7 to ~12 µg C l –1) and their microheterotrophic grazers (from ~5.5 to ~9 µg C l –1) over 5 days (Coale et al., 1996). The netphytoplankton increased from ~10.5 to ~59.5 µg C l –1 over the same time period, while the mesozooplankton increased from ~4 to ~7 µg C l –1. Using these data, and assuming a steady state prior to the enrichment, the zooplankton clearance rates \( K_P \) were set to 1 day for mesozooplankton and 30 days for the mesozooplankton.

The picoplankton/microheterotroph and netplankton/mesozooplankton food webs were treated as relatively separate communities. The two phytoplankton types interacted through the carrying capacity: the picoplankton were allowed to utilize their portion of the carrying capacity without interference from the netplankton. The netplankton then had access to the remaining carrying capacity. This simulates the enhanced competitive capacity of the picoplankton over the netplankton [e.g. (Moloney and Field, 1991)]. The picoplankton \( K_P \) was set equal to the total phytoplankton biomass prior to the
enrichment, while the netphytoplankton $K_P$ was set to the difference between the total phytoplankton biomass ($K_P$) and the picoplankton biomass. After enrichment, the $K_P$ for both groups was set to the total phytoplankton biomass (72 $µg$ C l$^{-1}$). That iron limitation determined $K_P$ before and during the bloom is supported by evidence that the phytoplankton were iron stressed throughout the field experiment (Erdner and Anderson, 1999). Making these assumptions, $/\alpha$ and $/\beta$ can now be calculated from the data prior to the bloom using equations (8a) and (8b) (Figure 5).

The calculated biomass fractions $/\beta$ were reasonably similar (0.78 for the picoplankton/microheterotrophs and 0.38 for the netplankton/mesozooplankton). The clearance rates, $/\alpha$, on the other hand, differed by an order of magnitude [0.25 (µg C l$^{-1}$ day)$^{-1}$ for the microheterotrophs and 0.0231 (µg C l$^{-1}$ day)$^{-1}$ for the mesozooplankton] (Figure 5). These values are quite reasonable for ciliates and copepods, respectively [e.g. (Hansen et al., 1997)], and suggest that the model is giving realistic results.

Using the parameters calculated from the data prior to the enrichment, the model was run from an initial steady state with a step increase in carrying capacity ($K_P + \delta K_P = 72$ $µg$ C l$^{-1}$) to generate the time series of picoplankton/microheterotrophs and netplankton/mesozooplankton (Figure 5). The model performs remarkably well at predicting the biomass 5 days after enrichment. It overpredicts the picoplankton/microheterotrophs by 30–40%, but predicts the netplankton/mesozooplankton very accurately. In particular, the model captures the very different dynamics of the picoplankton/microheterotrophs versus the netplankton/mesozooplankton. The picoplankton bloom is strongly attenuated; the increase in biomass is constrained to little more than a doubling. The netplankton, on the other hand, show an increase of almost 6-fold in response to the same enrichment.

To test whether the differences in the two systems were due to the zooplankton response time scales, the microheterotroph $/\tau_2$ was set to 30 days, while the mesozooplankton $/\tau_2$ was decreased to 1 day (i.e. a factor of 30 changes; Figure 6, dotted lines). The effect of these changes is clearly in the direction predicted by the original hypothesis: the picoplankton bloom increases and the netplankton bloom decreases. However, the changes are not pronounced: an ~20% decrease in the netplankton and a 50% increase in the picoplankton. Far larger changes in the bloom magnitudes are generated by changing the clearance rates, $/\alpha$ (Figure 6, dashed lines). Swapping the microheterotroph and mesozooplankton $/\alpha$ (i.e. a factor of 10 changes) leads to an ~50% decrease in the netplankton biomass and an increase of 150% in the picoplankton biomass. Thus, as predicted above, the zooplankton grazing parameters are a much stronger determinant of the phytoplankton bloom magnitude than the zooplankton response time scales.

Given the results of this model, it is useful now to revisit the arguments surrounding the original IronEx experiment (Martin et al., 1994; Limnol. Oceanogr., 36(8), 1991, special issue). These arguments centered around the relative contributions of grazing and iron limitation in allowing excess levels of ambient macronutrients in concert with low levels of chlorophyll (HNLC) in certain regions of the ocean [e.g (Cullen, 1995)]. These arguments can now be recast in terms of the carrying capacity and other parameters of the present model. If grazing were causing the HNLC region, then the phytoplankton biomass is held well below the carrying capacity $K_P$, which is set by the amount of macronutrient. In this scenario, the parameter group $/\delta K_P$ would be large, i.e. high clearance rate, high relative zooplankton biomass and/or slow phytoplankton

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**Fig. 5.** Application of the model to IronEx II. Upper panel: picoplankton/microheterotrophs; lower panel: netplankton/mesozooplankton. Thick solid lines: phytoplankton; thin solid lines: zooplankton; thick dashed lines: $K_P$. Zooplankton ($/\tau_2$) and phytoplankton ($/\tau_1$) biomass before and during the bloom from Coale et al. (Coale et al., 1996). The parameters $/\alpha$ and $/\beta$ were diagnosed from the data prior to the bloom using equations (8a) and (8b).
response time scale. On the other hand, if iron limitation caused the HNLC condition, then the carrying capacity \( K_P \) is set by the available iron, not the macronutrient, and the phytoplankton concentration is at or near the carrying capacity. This situation implies a small \( K_P \)—low clearance rate, relatively low zooplankton biomass and/or short phytoplankton response time scales. All the evidence from IronEx II suggests the latter case in the HNLC region of the equatorial Pacific [e.g. (Coale et al., 1996)].

However, as suggested by the present model, it is possible for one phytoplankton group to be held well below the carrying capacity by a high \( n_B \) (the picoplankton), while a co-existing group (the netplankton) is allowed to grow very close to the carrying capacity due to a low \( n_B \) of the zooplankton predators. A diagnosis, then, for a trace metal-induced HNLC versus a grazer-induced HNLC would be to compare the total phytoplankton biomass to the carrying capacity of the system, \( P = K_P \) implies environmental control, while \( P < K_P \) implies grazing control. This, of course, requires an estimate of \( K_P \), which is easier said than done.

The challenge is to estimate or perturb \( K_P \) and \( n_B \) accurately, independently and unequivocally. Various techniques have been used to assess \( K_P \), the biomass the phytoplankton could maintain in the absence of grazing. Dilution (Landry and Hassett, 1982), grazer exclusion (Rassoulzadegan and Sheldon, 1986) and the addition of polystyrene beads (Price et al., 1994) have all been used to attempt to disrupt the grazing losses in bottle incubations. Martin and Fitzwater added iron to HNLC water to attempt to show that iron limitation set the phytoplankton carrying capacity, i.e. that \( P = K_P \) even though there was excess macronutrient available (Martin and Fitzwater, 1988). While the iron additions allowed increased phytoplankton biomass, it was not possible to disprove the alternate hypothesis that the bottle effects changed \( n_B \), by simultaneously decreasing the zooplankton clearance rate or biomass. It was the controversy surrounding these experiments that led to the massive IronEx I and II field experiments.

Analyses of the HNLC condition in the Subarctic Pacific Gyre [e.g. (Strom et al., 2000)] indicate that the system is grazer controlled, i.e. \( P < K_P \) and \( n_B \) is relatively large. The strong grazer control severely limits the amplitude of fluctuations in phytoplankton biomass. In contrast, wind-driven upwelling systems are a transient condition with \( P < K_P \), and relatively low \( n_B \). These conditions are strongly favorable for pronounced blooms of phytoplankton [e.g. Figure 4]. Similar conditions exist during the spring bloom in many temperate waters, as the water stratifies and \( K_P \) increases due to the alleviation of mixing-induced light limitation [e.g. (Sverdrup, 1953)].

The concepts embodied in this simple model, then, are widely applicable in planktonic systems. The explicit inclusion of zooplankton and phytoplankton response time scales and grazing pressure has allowed clarification of the relative effects of these two dynamics in controlling phytoplankton blooms. The model supports the hypothesis that a long zooplankton response time scale may allow phytoplankton blooms, but additionally suggests that it is the strength of the grazing pressure that most strongly controls the magnitude of the bloom in response to environmental perturbations.

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P. J. S. FRANKS PHYTOPLANKTON BLOOMS IN A FLUCTUATING ENVIRONMENT