SPATIAL AND TEMPORAL DISCONTINUITIES OF BIOLOGICAL PROCESSES IN
PELAGIC SURFACE WATERS

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ABSTRACT. The classical paradigm of an unproductive, nutrient-poor
pelagic zone where primary production is fueled almost exclusively by
nutrient regeneration processes, appears at odds with the contemporary
view that new primary production, supported by a stoichiometric input
of oxidized nutrients into the euphotic zone, is considerably higher
than previously thought. One way to accommodate both scenarios is to
invoke the two layer concept in which the bulk of new primary
production occurs at or near the base of the euphotic zone in response
to pulsed injections of NO$_3^-$ and PO$_4^{3-}$. Productivity in the upper
euphotic zone where nutrients and biomass are trapped would be
regulated almost exclusively by regenerative and degradative processes
that occur within the microbial food loop. Since the microbial food
loop which consists of a tightly-knit assemblage of phototrophic and
heterotrophic nanno- and picoplankton persists throughout the euphotic
zone, most of the energy and carbon processed by these small microbes
would be lost through respiration and thus would not contribute to new
production exiting to deeper waters. This raises the perplexing
question of how biological processes are coupled to the input of new
nutrients which, in turn, is controlled by physical events that occur
on greatly varying temporal and spatial scales. Possibly, short-lived,
local mixing events provide the right combination of light and new
nutrients to allow rapid and undetected bursts of growth of larger
phytoplankton species, in effect, creating ephemeral eutrophication
zones. The resulting food chain may be short and simple so that newly
fixed carbon can exit the euphotic zone rapidly while leaving behind
an oxygen signal.

1. INTRODUCTION

It has been suggested recently by a number of researchers that marine
primary production is far greater than has been measured by the
classical $^{14}$C incubation technique (Johnson et al., 1981;
Schulenberger and Reid, 1981; Jenkins, 1982; Jenkins and Goldman,
1985). Some of these newer estimates, based on integration of water

column oxygen measurements over long time and space scales, have not
gone unchallenged, however (Platt, 1984; Platt and Harrison, 1985,
1986). At the core of the resulting controversy is the question of how
the old 14C measurements, which often are presumed to represent
estimates of total primary production (the sum of new and regenerated
production) (e.g. Eppley and Peterson, 1979; Platt and Harrison, 1985)
and are performed on short temporal and spatial scales, can be
reconciled with the newer oxygen measurements that only are of new
production.

In trying to sort out the distinguishing characteristics of the
two types of measurements and what each represents it is instructive
to define first some important terms. Dugdale and Goering (1967) in
their now classical paper distinguished new (P_N) from regenerated
primary production (P_R) on the basis of the relative uptake of NO_3^-
and NH_4^+ by phytoplankton populations. By a simple mass balance
calculation, and using nitrogen as an example, new production was
defined as photosynthetically derived particulate organic nitrogen
that exited the euphotic zone to deeper waters. This new production
was balanced over long time scales by the quantity of dissolved
nitrogen (primarily NO_3^-) that was transported into the euphotic zone
by physical processes and was taken up by phytoplankton during growth.
Regenerated production, in contrast, was fueled solely by reduced
nitrogen sources (primarily NH_4^+ but also dissolved organic N
including urea) that originated from excretion and degradation
processes of heterotrophs that grazed primary producers within the
euphotic zone. Thus the sum of these forms of production equalled
total production (P_T).

The early view that the pelagic ocean was a biological desert
(Ryther, 1969) gained considerable support during the 1970's and early
1980's from numerous researchers who used the 15N tracer incubation
technique in field studies. Two major conclusions were that the
percentage of total production derived from regeneration processes [R
= P_R/P_T(100)] frequently was as high as 80-100% in surface waters of
the open ocean (Eppley and Peterson, 1979) and that the very small
(<10 μm) size class of microbes played a major role in the recycling
process (Glibert, 1982). Thus the contemporary view that new
production is considerably higher than previously thought appears at
odds with the classical paradigm of an unproductive, nutrient-poor
pelagic zone in which primary production is fueled almost exclusively
by nutrient regenerative processes.

A major difficulty in accepting the possibility of a highly
productive open ocean is that our knowledge of how nutrients are being
supplied to the euphotic zone and how the biology responds to this
input is limited. Based on traditional sampling practices, there is
little evidence for either the enhanced nutrient input or the higher
phytoplankton biomass required to support the quantity of oxygen that
accumulates seasonally in some oceanic locales. Hence we are either
dealing with a major artifact in the oxygen numbers or else we have
failed to characterize adequately all the important physical and
biological processes that are occurring at the interface between the
aphotic and euphotic zones of the open ocean. In support of the latter
possibility, Knauer et al., (1984) and Jenkins and Goldman (1985) suggested that the euphotic zone could be divided into an upper and lower layer. In the upper layer where new nutrients were scarce regeneration would be high and new production low. The lower layer, in contrast, would be a zone of high new production and low regeneration, supported by episodic inputs of new nutrients that were difficult to identify with conventional sampling techniques. In effect, nutrient regeneration, when integrated over the entire euphotic zone, would be considerably lower than the values extrapolated from $^{15}$N studies. In this paper I will expand on this concept and suggest that very different biological processes are responsible for regeneration and new production. In dealing with this question I will emphasize that the appropriate temporal and spatial scales upon which each of the processes function may be very different.

2. RELATIONSHIP BETWEEN NEW PRODUCTION AND REGENERATION

2.1. The $f$ ratio and Available NO$_3^-$

Following the lead of Dugdale and Goering (1967), many researchers have attempted to determine the regeneration efficiency $R$ by measuring the relative rates of NH$_4^+$ and NO$_3^-$ uptake by phytoplankton with $^{15}$N techniques (Eppley et al., 1979; Glibert, 1982; Glibert and McCarthy, 1984; Harrison et al., 1983; Harrison et al., 1987). Eppley and Peterson (1979) used the term $f$ ratio" which is $(1 - R/100)$ to describe the ratio of new to total production ($P_N$:$P_T$). In practice,

$$f = \frac{\Delta$NO$_3^-}{\Delta$NH$_4^+ + \Delta$NO$_3^-$}$$ (1)

in which is NO$_3^-$ and NH$_4^+$ are, respectively, the $^{15}$NO$_3^-$ and $^{15}$NH$_4^+$ uptake rates of the phytoplankton populations during the course of shipboard incubations on discrete and confined samples. Adjustments to Eq. 1 to account for urea uptake by phytoplankton and isotope dilution of $^{15}$NH$_4^+$ by grazer excretion of unlabelled NH$_4^+$ during the course of the incubation are necessary but difficult to make (Glibert et al., 1982; Harrison et al., 1987). A far more serious technical problem is that ambient NO$_3^-$ and NH$_4^+$ concentrations in surface waters of the open ocean frequently are below detection limits (~0.03 $\mu$g atoms/liter) (McCarthy and Goldman, 1979). Under such conditions $^{15}$N is not a true tracer and addition of even the smallest possible quantity of $^{15}$N-labelled substrate (typically 0.03-0.1 $\mu$g atoms/liter) increases the substrate concentration greatly, leading to anomalously high uptake rates. Past difficulties in making accurate measurements of NO$_3^-$ and NH$_4^+$ at these low concentrations have compounded this problem.

The recent attempts by Platt and Harrison (Platt and Harrison, 1985; Harrison et al., 1987) to show a general relationship between the $f$ ratio and ambient NO$_3^-$ concentration provide a clear example of the difficulties in using the $^{15}$N tracer method to determine regeneration efficiencies. As seen in Figure 1 from Harrison et al.
(1987), plots of $f$ versus ambient NO$_3^-$ for individual data sets from 8 field studies (mostly those from productive coastal or near-shore waters) appear to give reasonably good exponential fits of the data. On close scrutiny, however, it is evident that the bulk of the data in most of the plots fall into two distinct groups, one for ambient NO$_3^-$ concentrations below or near the detection limit where $f$ varies greatly from zero to close to the maximum values attained, and the other where $f$ is maximum at concentrations of NO$_3^-$ above several µg atoms/liter. The variability of the data in the first group presumably occurs because of enhanced uptake due to the pulsing effect of the tracer addition.

The problem of variable $f$ at very low NO$_3^-$ concentration is seen clearly in one of the data sets from the Middle Atlantic Bight study of Harrison et al. (1983). By replotting the data on appropriate scales, it is evident that the absolute uptake rates for NO$_3^-$ (Figure 1A) and NH$_4^+$ (Figure 1B) at ambient concentrations below 0.2 µg atoms/liter were highly variable and greatly influenced by the addition of $^{15}$N tracer (0.1 µg atoms/liter in this case): NO$_3^-$ varied from 0.1 to 6.9 µg atoms/m3/h and NH$_4^+$ from 0.3 to 11.8 µg atoms/m3/h when ambient NO$_3^-$ or NH$_4^+$ was undetectable. The resulting $f$ ratios ranged from 0.10 to 0.79 at concentrations of ambient NO$_3^-$ between undetectable and 0.25 µg atoms/liter (Figure 1C). For most of the other data sets analyzed by Harrison et al. (1987) there was a similar variability in $f$ when ambient NO$_3^-$ concentrations were at the detection limit. Glibert and McCarthy (1984) experienced the same difficulty in their diurnal study at a station in the Sargasso Sea: $f$ varied from 0.07 to 0.36 when ambient NO$_3^-$ and NH$_4^+$ concentrations which were <0.05 µg atoms/liter were increased greatly by addition of 0.03 µg atoms/liter of $^{15}$N tracer.

Thus, while plots of $f$ versus NO$_3^-$ may give the appearance that a quantitative relationship exists between the two variables (e.g. Figure 1B), a potentially serious bias is introduced when the resulting curve is fit from data sets representing the two extreme portions of the curve where, in fact, no real relationships exist between $f$ and NO$_3^-$. When NO$_3^-$ concentrations are very low $f$ is indeterminate and when NO$_3^-$ concentrations are very high $f$ plateaus at a saturating value. For this and other reasons (Jenkins and Goldman, 1985) the $^{15}$N technique simply may be unsuitable for determining regeneration efficiencies in oceanic waters when nutrient concentrations are at or near undetectable levels.

2.2. The Accuracy of Regeneration Measurements

The importance of having an accurate estimate of $R$ is seen in Figure 2 which is simply a plot of the ratio $P_T/P_N (= 1/f)$ and $R (= 1 - f)$. When $R$ is less than 60% the ratio of total to new production is relatively insensitive even to large errors in $R$. However, when $R$ is in the range 80-90% then the difference between total and new production becomes highly sensitive to small experimental errors in the determination of $R$. Given that the prevailing view has been that regeneration efficiencies in the open ocean are >90% (Eppl
Peterson, 1979), ironically determined by $^{15}\text{N}$ methodologies, and that the ratio $P_T: P_N$ really is the ratio of production measured by the $^{14}\text{C}$ and water column $O_2$ techniques, it is easy to see why great emphasis has been put on having an accurate estimate of $R$.

![Figure 1](image)

**Figure 1.** Absolute uptake rates for $\text{NO}_3^-$ (A) and $\text{NH}_4^+$ (B) and the resulting f ratio (C,D) as a function of $\text{NO}_3^-$ concentration from the study of Harrison et al. (1983). Panel C is the expanded version ($\text{NO}_3^-$ concentration between 0-5 $\mu$g atoms/l) of the full data set shown in Panel D ($\text{NO}_3^-$ concentration between 0-16 $\mu$g atoms/l). Open symbols represent data for which ambient $\text{NO}_3^-$ concentrations were $>0.25$ $\mu$g atoms/l. 15N tracer addition of 0.1 $\mu$g atoms/l were added to ambient $\text{NO}_3^-$ or $\text{NH}_4^+$ concentration in Panels A, B, and C, whereas only ambient $\text{NO}_3^-$ concentration is presented in Panel D. Numbers in Panels A and B indicate number of data points for experiments in which ambient $\text{NO}_3^-$ or $\text{NH}_4^+$.

Jenkins and Goldman (1985), in advocating the two layer system, actually were suggesting that the biological processes of regeneration and new production were distinctly different, the former involving a highly dynamic microbial food web where energy was wasted and the latter a simple and efficient food chain where energy was conserved. In the balance of this paper I will compare these two different systems and show that there is no incompatibility in the two systems existing simultaneously. In fact, the primary producers involved in new production may simply go unnoticed because of their small numbers but large size and because their growth is tightly coupled to episodic nutrient input into the euphotic zone.
Figure 2. Relationship between the ratio of total to new primary production $P_T/P_N$ and the efficiency of regeneration $R$. See text for details of calculations.

3. THE MICROBIAL FOOD LOOP

3.1. Size Structure in the Microbial Loop

Pomeroy (1974) provided the first clues that the classical marine food chain consisting of diatoms, copopods, and fish was not the only major pathway by which energy and materials were channelled in the ocean. He viewed the complicated microbial food web consisting of small phototrophs, bacteria, and protozoa as playing a vital, if not major role in these processes. Several discoveries in recent years have added further fuel to this argument. First, there is little doubt now that photosynthetic picoplankton (<2 μm in size) are ubiquitous in the world’s oceans in very large numbers (Johnson and Sieburth, 1979; Waterbury et al., 1979). On the basis of size fractionation studies with $^{14}C$, these phototrophs appear to contribute greatly to total primary production (Li et al., 1983; Platt et al., 1983). And second, evidence is mounting that the bulk of nutrient regeneration in pelagic surface waters occurs within the highly dynamic and complicated microbial food web first described by Pomeroy (the "microbial food loop") (Azam et al., 1983; Goldman and Caron, 1985). The actual structure of this food web and the types and sizes of the microbes involved have been exceedingly difficult to characterize. Small
protozoa are believed to play important roles in grazing the
phototrophs, and, along with bacteria, in processing nutrients and
dissipating energy. Pfenchel (1982), in fact, has argued that the
dominant predators of bacteria (and presumably of photosynthetic
ultraplankton) in the microbial food loop are phagotrophic
flagellates, microbes that generally are smaller than 10-20 μm in
size. Sieburth et al. (1978) distinguished two size classes of
microbes among the smaller organisms, the picoplankton (0.5-2 μm) and
the nanoplankton (2-20 μm), whereas Murphy and Haugen (1985), in
finding that small (2-5 μm) eucaryotic phototrophs were widely
distributed in large numbers in the North Atlantic along with the
picoplankton, enlarged the smaller size group to include all organisms <5 μm in size (the ultraplankton).

3.2. The Spinning Wheel Concept

Based on evidence that phytoplankton in the open ocean may be growing
at their maximum possible growth rates (Goldman et al., 1979),
together with the view that regeneration efficiencies in this system
are very high, the microbial food loop has been likened to a "spinning
wheel" that turns at a speed controlled by the maximum possible growth
rate of the phototroph component (Goldman, 1984a,b). I have previously
argued that the relative growth rate μ/μ(10) of the phytoplankton in
this wheel approaches 1 in which μ is the specific growth rate and
μ(10) is the maximum specific growth rate for a particular light
intensity (Goldman, 1980; 1986). Thus because light intensity varies
with depth, the absolute growth rate of phytoplankton is expected to
decrease with depth, but without a change in the physiological state
of the cell population. The size of the wheel (i.e. the biomass of
both phototrophs and heterotrophs), however, while a function of the
total nutrients added to the system, should be independent of the rate
at which the wheel spins (Goldman, 1984a,b).

3.3. New Production in the Microbial Loop

As the pendulum has swung from paradigm of the diatom-copopod-fish
linkage to that of the microbial loop, there is a growing perception
that the bulk of primary production in the open ocean occurs among the
ultraplankton. Little distinction is made between the sources of new
and regenerated production. Yet the only data in support of this
argument comes from 14C incubation studies on size-fractionated
samples (Li et al., 1983; Platt et al., 1983; Takahashi and Bienfang,
1983; Glover et al., 1985; Iturrraga and Mitchell, 1986). It must be
recognized, however, that such results provide no information on how
phototrophs of the microbial loop may contribute to new production.
Because of the extremely small size of the microbes involved, sinking
rates of individual untraplankton cells are very low (<0.1-0.2 m/d)
(Smayda, 1970; Bienfang, 1985); hence, we would expect these small
phototrophs to contribute negligible quantities of organic material
directly to new production. Results from sediment trap studies tend to
confirm this conclusion (Silver et al., 1986). Thus there are only two
alternative ways in which biomass within the loop could possibly sink out of the euphotic zone, either by efficient grazing by metazoan and release of large fecal material, or by physical aggregation of the microbial populations comprising the "loop" into larger particles.

Direct metazoan grazing on ultraplankton probably is not a major pathway by which biomass is passed up the marine food chain. Retention efficiencies for particles less than a few microns in size by most suspension-feeding metazoan generally is very low (Jorgensen, 1984). It is now generally believed that protozoa, particularly phagotrophic microflagellates because they are the main grazers of the ultraplankton, are a link between the very small components of the microbial loop and the larger zooplankton (Conover, 1982; Sherr et al., 1986). It must be recognized, however, that as the number of grazing steps between the ultraplankton and the metazoan increases, the total food chain efficiency decreases. Even considering that protozoa have gross growth efficiencies as high as 50-60% (Fenchel, 1982; Sherr et al., 1983; Caron et al., 1985), with only two grazing steps in a microbial food chain (e.g. small phototroph - flagellate - ciliate) only 25% of the initial biomass remains. To account for the very high nutrient regeneration efficiencies found in the microbial loop at least 3 grazing steps are required if at each step the gross growth efficiency is 50% (Goldman and Caron, 1985; Goldman et al., 1985). Such a food chain would leave even less prey biomass for metazoan grazers. Clearly, new production, at the levels suggested, does not occur by way of a grazing link between the microbial loop and larger marine animals.

Physical aggregation of particles into flocculent masses occurs in the ocean at many scales, ranging from the formation of microaggregates that are microns to tens of micron in size (Riley, 1970), to macroaggregates ("marine snow" that are hundreds to thousands of microns in size (Trent et al., 1978), and up to floating mats of large phytoplankton that are meters to tens of meters in size (Carpenter et al., 1977; Alldredge and Silver, 1982). These organic aggregates, formed by complex physical-chemical-biological interactions (McCave, 1975; 1984), often are enriched by orders of magnitude over the bulk fluid with nutrients and a diverse flora of bacteria, photosynthetic ultraplankton, and protozoa (Trent et al., 1978; Silver et al., 1978; Shanks and Trent, 1979; Caron et al., 1982). I have suggested in the past that aggregates of all sizes act as oases in the desert where the bulk of photosynthesis, grazing, and nutrient regeneration within the microbial loop may occur (Goldman, 1984a,b). Alldredge and Cohen (1987) recently showed that marine snow particles, indeed, had a very different chemical environment than the bulk fluid and could be important sites of microbial processes in the ocean.

Sinking rates of marine snow particles can vary from 1-350 m/d and frequently are over 100 m/d (Silver, 1986). These rates are substantial compared to sinking rates of most phytoplankton species in the ocean (<10-20 m/d) (Smayda, 1970); hence the microbial loop potentially could be an important source of new production if the photosynthetic ultraplankton were a significant component of the
floculent mass sinking out of the euphotic zone. This does not seem
to be the case, however, as only a few percent of the total population
of photosynthetic ultraplankton in the euphotic zone have been found
as intact cells within marine snow material (Silver et al., 1986).

4. SOURCES OF NEW PRODUCTION

4.1. Large Phytoplankton Species and New Production

A very distorted picture of global production may occur if the rare,
but potentially important biological events in the ocean are ignored.
The $^{14}$C and $^{15}$N incubation methods, by relying on a few discrete grab
samples to represent the entire euphotic zone, simply cannot provide
the necessary temporal and spatial coverage for measuring annual
production and nutrient cycling accurately over large areas of the
ocean. Results from size fractionation studies with both techniques,
although instrumental in furthering our understanding of the microbial
loop, still are of limited value because only relative information is
obtained on the captured populations.

Although the classical view that primary production was
restricted to diatoms left little room for the contribution of the
ultraplankton, neither does the contemporary view, emphasizing the the
importance of the ultraplankton, leave any room for a role for the
diatoms. Yet if the arguments presented above are correct, that is,
phototrophs of the microbial loop are not major contributors to new
production, then the only other source of this production must be the
larger phytoplankton species. It is my own contention that the great
flurry of recent interest over the ultraplankton and the microbial
loop has caused us to lose sight of two simple but crucial points.
First, one very large phytoplankton cell can equal the biomass of
ultraplankton orders of magnitude greater in number. And second,
biological events in the ocean are patchy on temporal and spatial
scales that are not amenable to quantitative measurement. For example,
the number of 1 μm cells required to equal the carbon content of one
diatom cell increases almost by three orders of magnitude for every
order of magnitude increase in the diameter of the diatom (Figure 3).
Thus in one liter of oceanic water it would take either a single 1000
um diatom or 100 diatoms 100 μm in size to equal the carbon content of
the entire population of photosynthetic picoplankton (~106-107 cells
according to Waterbury et al., 1986). Clearly, the chances of
adequately representing primary production in the ocean by dividing a
captured population into size fractions and incubating each fraction
in a bottle would be proportional to the chances of capturing all the
contributors to that production.

To dramatize the potential importance of larger phytoplankton
cells to new production and the difficulties that might be encountered
in recognizing and measuring this contribution, consider the extreme
scenario in which the microbial loop is a completely closed system:
the wheel spins at its maximum possible rate and regeneration is 100% efficient. The loop operates throughout the euphotic zone and is
Figure 3. Relationship for the number of 1 μm picoplankton cells that equal the carbon content of one diatom cell of a varying diameter. The Strathmann equation (Strathmann, 1967) \( \log C \text{ (pg carbon)} = 0.758 \log V \text{ (μm}^3) - 0.422 \) was used to convert cell volume to cell carbon.

essentially a steady state system. Superimposed on this zero production system is an independent production system comprised of large phytoplankton cells that grow rapidly in response to an episodic input of new nutrients and then sink out of the euphotic zone, leaving behind an integrated oxygen signal. Hence, the microbial loop and the system responsible for new production are entirely separated, both spatially and temporally (Figure 4).

For this new production system it can be shown that only a small number of larger phytoplankton cells are necessary to account for all the new production and that, with current sampling practices, this production easily could go unnoticed. As an example, consider that this new production occurs in a typical oligotrophic water such as the Sargasso Sea at a rate of 5 M O₂/m²/yr, as reported by Jenkins and Goldman (1985) (equivalent to 2.8 M C/m²/yr, assuming a photosynthetic quotient of 1.8). Next, consider that all of this production is limited either to the bottom 25 m or bottom 50 m of the euphotic zone and occurs continuously (steady state) or in one of several episodic sequences.
Figure 4. Schematic views of the extremes of the microbial loop and the system for new production. The microbial loop is portrayed as a spinning wheel where the rates of phytoplankton growth (μ), protozoan grazing (G), and nutrient regeneration (R') are equal and the relative phytoplankton growth rate as a function of light intensity [μ:μ(I0)] approaches 1 and where regeneration efficiency (R) is 100% so that new production (PN) is zero. This system is dominated by ultraplankton and small protozoa and occurs throughout the euphotic zone. The new production system is fueled by episodic inputs of NO₃⁻ and an inoculum cell population (X₀) into the lower portion of the euphotic that leads to blooms of large phytoplankton (Xₚ). The large phytoplankton are not readily grazed and thus sink to deeper waters.

New production in the steady state system simply is:

\[ P_N = \mu X \]  

(2)

in which μ and X respectively are the steady state growth rate (1/d) and cell concentration (cells/l) of the phytoplankton population. It is assumed that there are no losses and all cells sink out of the euphotic zone. Then, by converting cell carbon to cell volume (for diatoms in this example) (Strathmann, 1967), it is possible to determine the required steady state population of phytoplankton cells of different diameters necessary to produce all of the new carbon as a function of specific growth rate (Figure 5). Considering a realistic range of specific growth rates for phytoplankton in the water column of 0.1 to 1.5/d (Eppley, 1972; Goldman et al., 1979; Goldman, 1986), new production by 1 μm size picoplankton at the levels suggested could be maintained only with steady state populations of about 3 \times 10^6 to 4 \times 10^7 cells/l if production occurred only in the bottom 25 m (Figure 5A) and between 10^6 and 2 \times 10^7 cell/l if it occurred in the bottom 50 m (Figure 5B). While these picoplankton concentrations are about equal to those found commonly in oligotrophic waters (Waterbury et al., 1986), it must be recognized that much higher cell concentrations would be required to sustain total production.

The picture changes drastically, however, if very large cells are responsible for new production. For example, all of the new production...
in the bottom 25 or 50 m could be achieved with a steady state cell concentration of only 305 cells/l if the cells were 1000 µm in diameter and were growing at a rate of 0.1/d; even lower cell concentrations would be required if growth rates were higher (Figure 5). Cell concentrations this low, even of very large species, may be exceedingly difficult to quantify. For the steady state situation there is no temporal and spatial variability in cell number, but capturing and counting the few large cells that potentially could account for a large fraction of new production becomes a major challenge.

Figure 5. Nomographs of the steady state phytoplankton populations required for diatom cells of varying diameters as a function of specific growth rate to support new production at a rate of 5 M O₂/m²/yr if production occurred only in the bottom 25 m (A) or 50 m (B) of the euphotic zone. See text for explanation of calculations.

The problem of identifying the contribution of large phytoplankton cells to new production becomes more evident if production is tightly connected to episodic inputs of new nutrients. For example, consider four arbitrarily chosen episodic situations, the first two in which all of total yearly new production (2.8 M C/m²/yr) occurs during one continuous bloom period, one for 3.7 days duration (1% of the time) and the other for 18.3 days (5% of the time). Production in the
remaining two situations occurs during repetitive bloom periods, one involving five 10-day periods, and the other ten 5-day periods. For this analysis, it is assumed that an inoculum ($X_0$) of only 1 cell/l for each bloom of phytoplankton is recycled back into the euphotic zone with the new nutrient water (Figure 4). Also, new production only occurs in the bottom 25 m and all of the cells produced during the bloom ($X_F$) sink out of the euphotic zone immediately after each bloom ends. Annual new production thus is proportional to $X_F - X_0$ or $X_0(e^{ut} - 1)$ and can be expressed as:

$$P_N = 25 \times n \times C \times X_0(e^{ut} - 1)(10^3)$$

(3)

in which $n$ is the number of bloom periods per year, $t$ is the duration of each bloom period, and $C$ is the conversion factor from cell number to cell carbon for cells of different diameters (once again, using the Strathmann equation for diatoms). Regeneration in this new production system simply is $(X_0/X_F)100$.

From the resulting nomograph for the four situations (Figure 6), it is evident that the required growth rates to support yearly new production vary tremendously from one scenario to the other. Both the one 3.7 day bloom and the ten 5-day bloom scenarios require unrealistically high growth rates (>3/d) for small cells (10 $\mu$m) and approach the limits of attainability (<2/d) only when cells >50-250 $\mu$m in size are involved. Growth rates for all size classes considered (10-1000 $\mu$m) in the other two scenarios, however, are well within the attainable range (0.3-1.4/d) even at the reduced light levels expected in the bottom 25 m of the euphotic zone (Chan, 1978; Brand and Guillard, 1981). The cell populations attained at the end of each bloom period likewise varies greatly among the different scenarios, ranging from 7.4 x $10^6$ cells/l in the single growth period of 3.7 days and involving 10 $\mu$m size cells to 20 cells/l for each of the ten 5-day periods when 1000 $\mu$m size cells are involved (Table 1). Regeneration in each of these cases is essentially zero.

The above examples were meant to be gross exaggerations of how new production might occur. My purpose in presenting them solely is to highlight two main points:

1) Under both steady state and transient conditions the contribution of large phytoplankton cells to new production can be disproportionately large relative to that of the smaller cells and that this production could easily go unnoticed without intense sampling;

2) The required growth rates during these blooms are well within the known physiological limits of the phytoplankton.

4.2 Rare Events and Variability in Food Chain Structure

Ryther (1969) in his classical study of the factors governing fish production in the ocean pointed out that the size of the primary producers was the key factor in determining the number of links in the marine food chain. Coastal and upwelling regions where nutrients are in greatest supply have long been recognized as major sites of global
Figure 6. Nomograph of the required specific growth rate of diatoms as a function of cell diameter for four different hypothetical situations where 5 M O₂/m²/yr are produced through episodic events in the bottom 25 m of the euphotic zone and the inoculum for each bloom period is 1 cell/l. See text and Table 1 for details of calculations and description of episodic events.

Table 1. Final phytoplankton cell concentration resulting from episodic blooms of different durations and yearly frequencies and for cells of varying diameters when the inoculum (X₀) is 1 cell/l. See text and Figure 6 for details of analysis.

<table>
<thead>
<tr>
<th>Yearly Frequency</th>
<th>Bloom Duration (days)</th>
<th>Final Cell Concentration (cells/l)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>10 µm</td>
<td>100 µm</td>
</tr>
<tr>
<td>1</td>
<td>3.7</td>
<td>7.4x10⁶</td>
</tr>
<tr>
<td>1</td>
<td>18.3</td>
<td>7.4x10⁶</td>
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<tr>
<td>5</td>
<td>10.0</td>
<td>1.5x10⁶</td>
</tr>
<tr>
<td>10</td>
<td>5.0</td>
<td>7.4x10⁵</td>
</tr>
</tbody>
</table>

fish production because they sustain the growth of larger phytoplankton species leading to short and relatively efficient food chains. The notion that large phytoplankton species and species that
aggregate into large colonies by forming gelatinous or filamentous masses are relatively more abundant in nutrient enriched regions than they are in impoverished waters often is advocated (Ryther, 1969; Malone, 1971). Some factors which seem to favor the production of the larger species, e.g. heterogeneous nutrient supply (Harrison and Turpin, 1982) and high turbulence (Eppley et al., 1978; Margalef, 1978), are characteristic of nutrient enriched environments. Additional factors that might favor the larger species include reduced respiration rates (Laws, 1975), large storage vacuoles (Grenny et al., 1973), and temporal lags in the growth of grazers (Steele and Frost, 1977).

Large phytoplankton species are not restricted to seemingly productive coastal and upwelling waters. In fact, the extremely large species often are cosmopolitan species. It is well established that a diverse array of large diatom and dinoflagellate species are ubiquitous in oceanic waters in greatly varying background numbers (<1/m² to >100/1) (Belayayeva, 1972; Semina, 1972; Guillard and Kilham, 1977). However, recognition of the importance of the large (>60-100 µm) species to food chain dynamics and new production in oceanic waters has been hampered because of the difficulty in identifying and enumerating these plankton; quantitative analyses of these phytoplankton species can only be made after collection in net hauls (Belayayeva, 1972) or in sediment traps (Takahashi, 1986).

Truly huge species such as the diatom Ethmodiscus rex (up to 2000 µm in size) and the dinoflagellate Pyrocystis noctiluca (350-450 µm in diameter) generally are found in very low numbers (<1-200/m³), but they are distributed over large areas of the pelagic environment. (McHugh, 1954; Belayayeva, 1970; Swift et al., 1976). Somewhat smaller (50-100 µm) diatoms such as Hemiaulus hauckii, Mastogloia (Stigmaphora) rostrata and a variety of Rhizosolenia species (which vary greatly in size) frequently are the dominant diatoms found in oligotrophic waters (Guillard and Kilham, 1977). Semina (1972), on the basis of numerous net hauls in the Pacific Ocean, found that the average diameter of phytoplankton cells captured was >80 µm in an extensive area between about 200S and 200N; species of Pyrocystis and Rhizosolenia were the dominant forms. Blooms of many of these large diatom species have been observed on occasion with numbers reaching up to 103-104/1 (Clemons and Miller, 1984; Riley, 1957; Venrick, 1974).

Why large phytoplankton species are ever present in in oceanic waters in background numbers and why they bloom on occasion when nutrients seem not to be available are unanswered questions that have plagued biological oceanographers for a long-time (Guillard and Kilham, 1977; Clemons and Miller, 1984). Thus, because of the difficulties in collecting the large species and the sparcity of sampling, the few anecdotal accounts of such blooms really provide no information on the actual frequency and extent of their occurrence in the open ocean. From a few long term studies on phytoplankton distributions and particulate flux at specific oceanic stations, however, we can gain some perspective of the episodic nature of these blooms and their potential significance to new production. For example, from the two year study of Riley (1957) on weekly
phytoplankton distributions at a station in the North Central Sargasso Sea (Figure 7), it is evident that, aside from the expected spring diatom bloom which extended vertically throughout the euphotic zone, there were several periods when intense but short-lived blooms occurred at about 100 m resulting in cell concentrations between $10^4$-4 x $10^4$/l. The bloom period during early September, 1950 is of particular interest. During this period when the water was still thermally stratified the diatom *Rhizosolenia hebetata f* semispina (~150 µm long and 10 µm wide) reached a cell concentration of 2.1 x $10^4$/l, accounting for 65% of the total water column diatom population sampled on that date. The short-lived nature of the bloom and its occurrence in proximity to the base of the euphotic zone is suggestive of the episodic nutrient pulse-large phytoplankton species bloom scenario described earlier. Given that only 400 ml samples were obtained from 5 discrete depths for each sampling, the extent and magnitude of all the blooms indicated in Figure 7 are conservative, at best.

The fate of large phytoplankton species in oceanic waters is of crucial importance to their role in new production. It is becoming increasingly evident that sinking rates of bloom species often are much greater than would be predicted by the simple Stokes settling equation. Takahashi (1986), for example, estimated the sinking rates of a wide assortment of diatoms to be about 175 m/d in the subarctic Pacific. Similarly, the presence of photosynthetically-active phytoplankton cells at thousands of meters can be accounted for only by invoking accelerated sinking rates (Smayda, 1971; Platt et al., 1983). These accelerated sinking rates can only be accounted for by cell aggregation. Smetacek (1985), in fact, has suggested that rapid sinking of diatoms through aggregation is a survival strategy whereby cells switch from a growth phase when nutrients and light both are available to a resting dark stage and also to obtain shelter from grazing when the nutrient supply is exhausted; in this scenario cells not only avoid stress brought on by nutrient limitation, but also act as the seed population when nutrients are brought into the euphotic zone. This scenario dove-tails exactly with the scenario I have proposed earlier (Figure 4). For short-lived oceanic blooms triggered by episodic nutrient inputs, grazing, chiefly by copepods, simply can not keep pace with phytoplankton growth because the resident copepod population is too small and the growth rates of these grazers are low compared to those of the phytoplankton growth rates. If aggregation is a major mechanism by which bloom cells form large masses that can sink rapidly out of the euphotic zone then it is not necessary that the bloom species be large. For example, small coccolithophores which often are the dominant species in oligotrophic waters (Hulbert et al., 1960, Smayda, 1980) frequently appear in sediment traps as aggregated masses of intact cells (Honjo, 1982; Cadee, 1985).

The most dramatic evidence for direct and rapid transport of intact cells to great depth directly following a bloom and the uncoupling between primary and secondary production comes from time series photographs of massive accumulations of diatomaceous material
at depths between 1300 and 4500 m in the northeast Atlantic over periods of a few days (Billett et al., 1983; Lampitt, 1985; Rice et al., 1986). Accelerated sinking rates of 100 m/d were estimated from the time interval between the bloom and the deposition of the material at the sea floor (Billett et al., 1983). Sinking thus must be a common and major way in which new production exits the euphotic zone. The resulting food chain is short and simple and the $f$ ratio during these periods is very low.

Just how important relatively rare events may be to new production can be seen in the long-term (eight year), time-series study by Deuser (in press) of total particulate flux at 3200 m at Station S in the Sargasso Sea. Based on the first two to three years of bi-monthly measurements of particulates collected at the site, Deuser and Ross (1980) and Deuser et al. (1981) found a seasonal cycle in flux that matched closely (with an approximate one month lag) the seasonal trend in $^{14}$C-based primary productivity measured earlier by Menzel and Ryther (1961) at the same location. Subsequently, when eight years of data were analyzed the same yearly trends in flux were evident, but there were three sampling periods (one each in 1981, 1982, and 1983) in which unusually high particulate fluxes were recorded. These fluxes were in excess of the averaged data for the entire study (with the three periods excluded). In fact, the average daily flux for the period April 8-May 26, 1981 (117 mg dry wt/m$^2$/d) was higher by a factor of 2-3 than for any similar time of year during the eight years
of measurements. By including the three bi-monthly periods, the eight year average flux (based on 43 individual measurements of accumulated sediment trap material over two month periods) was increased by 8.2%. Since organic material was a relatively constant fraction of total particulates (Deuser, 1986), it can be assumed that the observed trends in the fluxes of total particulates were paralleled by those of biogenic material. Although the cause of these "rare events" has yet to be determined, it is evident that episodic and significant new production at this location could easily have gone unnoticed without adequate long-term sampling and that even a two-month sampling interval in this case may have been too long to represent quantitatively the true nature of the pulses.

5. SCALES OF REGENERATION AND NEW PRODUCTION

A major objective of this paper has been to show that two rather separate biological processes may be involved in new and regenerated production and that the temporal and spatial scales upon which each process functions are very different. The microbial loop dominates when nutrients are scare, which is the condition in any parcel of water in the euphotic zone of pelagic environments most of the time. The new production system, in contrast, may be dominated by large phytoplankton species which are not readily grazed and which occurs only when ephemeral patches of nutrients are introduced into the euphotic zone. The two systems operate side by side and are not, as proposed by Platt and Harrisson (1985), at variance with one another.

The microenvironment is the major domain of the microbial loop (Goldman, 1984a,b; Sieburth, 1984). The microbes in this system most likely lead a feast or famine existence where the bulk fluid is basically void of nutrients and prey. To survive, an individual ultraplankter or protozoan must search for food on temporal scales of seconds to days and over spatial scales of microns to thousands of microns. If this search occurs only in the bulk fluid where all microbes are randomly dispersed then molecular diffusion and viscosity become major physical barriers to success. For example, using a standard molecular diffusion coefficient of $10^3 \mu m^2/sec$ and a seawater kinematic viscosity value of $10^6 \mu m^2/sec$, and by assuming random distributions of organisms in the water column, it is easy to demonstrate the limitations of the proposal of McCarthy and Goldman (1979) regarding the importance of rapid nutrient uptake by phytoplankton in the presence of ephemeral point sources of nutrients (Jackson, 1980; Williams and Muir, 1981; Currie, 1984a,b). Yet, if we consider that organic aggregates of varying sizes (from tens to thousands of microns in size) are sites of nutrient enrichment because of their unique surface and bulk chemical properties (more viscous environments and hence lower molecular diffusion rates), and that organisms are attracted to these sites by chemical cues, then the microenvironment becomes an oasis in the desert where much of microbial activity may occur (Goldman, 1984b). Bulk fluid properties under such conditions provide no real clues as to the important
processes of nutrient acquisition, predation, and nutrient regeneration.

The "needle in the haystack" scales of the new production system are in marked contrast to the pertinent micro scales of the microbial loop. In this case we are dealing with physical and biological events on spatial scales of meters to hundreds of meters (and greater) and temporal scale of days to weeks, both well within our conceptual frame of reference and both easily measurable. But now the limiting factor is that we must be at the right place at the right time, in essence, we must know how to locate the needle in the haystack. The vastness of the ocean has, in effect, made it impossible until now to sample the rare events that may be a major source of nutrient enrichment of the euphotic zone and the new production that follows (Jenkins and Goldman, 1985). Clearly, Ryther (1969) was correct in assessing the need for short simple food chains to sustain fish production in the oceans. The application of this principle to reconciling the microbial loop constraints on new production with the actual measurements based on integrated O2 in the water column becomes evident only when the appropriate scales of the two systems depicted in Figure 4 are considered.

6. ACKNOWLEDGEMENTS

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