SVERDRUP’S CRITICAL DEPTH CONCEPT &
THE VERNAL PHYTOPLANKTON BLOOM

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Assignment

TOPICS

- What controls the timing of the spring bloom?
- What is Sverdrup’s critical depth concept?
- Interpreting non-dimensional critical-depth plots.
- Can we predict the timing of the spring bloom in MA Bay?
- Why is there no phytoplankton spring bloom in the Subarctic Pacific?

REQUIRED READINGS

Sverdrup, H. U. 1953. On conditions for the vernal blooming of phytoplankton. J. Conseil perm. int. Explor. Mer. 18: 287-295. [This is an important paper, but some of the terms have changed in the last 5 decades.]


RECOMMENDED

Evans, G. T. and J. S. Parslow. 1985. A model of annual plankton cycles. Biological. Oceanogr. 3: 327-347. [*This paper was a major conceptual advance for biological oceanography, explaining the lack of spring blooms in the North Pacific with a new theory and model]*


Parsons, T. R., L. F. Giovando, and R. J. LeBrasseur. 1966. The advent of the spring bloom in the eastern subarctic Pacific Ocean. J. Fish. Res. Board Can. 23: 539-546. [Just skim this article for now to see how Sverdrup’s (1953) critical depth has been applied. Millions of dollars of research has been funded since 1966 to determine the causes of the patterns noted in this paper. We will read ‘the latest’ after the midterm.]

Siegel, D. A., S. C. Doney, and J. A. Yoder. 2002. The North Atlantic spring phytoplankton bloom and Sverdrup’s critical depth hypothesis. Science 296: 730-733. [They use the SeaWifs data to estimate the community compensation light intensity, see Table of compensation light intensities below] [24]


Definition of terms & concepts

Most of these terms are defined in Appendix I, definitions and terms. This is just a checklist.

Compensation depth (hourly & diel)

Compensation light intensity. \( I_c \) or \( I_e \). The compensation light intensity is the primary unknown in the critical-depth calculation. Riley’s (1957) estimate of 40 ly/d is probably based on his knowledge of when blooms occurred on the New England shelf, and probably includes the effects of grazing.

Critical depth

Dimensional analysis

Ectocrine matter

Hourly & diel compensation depth

Mixed layer depth

Optical depth
ON THE SPRING BLOOM

Predicting the timing of the spring bloom is one of the major problems in biological oceanography. Since the 1920s, biological oceanographers have attempted to solve the riddle of what controls the spring bloom. Bigelow (1926) describes his fascination with the spring bloom in the Gulf of Maine:

“Perhaps no phenomenon in the natural economy of the Gulf so arrests attention (certainly none is as spectacular) as the sudden appearance of enormous numbers of diatoms in early spring, and their equally sudden disappearance from most of this area after a brief flowering period.”

The classic explanation for the timing of the spring bloom is Sverdrup’s (1953) critical depth concept. However, this conceptual model is obviously not the last word on the subject. Harris (1980) argued that no one has provided an adequate explanation of the timing of the spring bloom:

“Can we predict the timing and magnitude of algal blooms? Can we identify the likely dominant species in advance? Despite the claims of the modeling fraternity, I believe the answers to these questions are at present no, no, and no.”

Smetacek & Passow (1990) argue that Sverdrup’s (1953) explanation of the bloom is so badly flawed, that professors of biological oceanography should stop inflicting this concept on their students. Obviously, I don’t agree.

Mills (1989) reviews the early history of phytoplankton ecology, focusing on the Kiel School in Germany, the Plymouth Marine Biological Laboratory, and Gordon Riley in the US. The Kiel School led by Brandt, led the way in focusing on the nitrogen cycle, and nitrogenous limitation of phytoplankton production in the sea. The Kiel group did not make major contributions to our understanding of the spring bloom; the Norwegians led by Gran introduced the role of physical mixing to understanding phytoplankton growth. Gran in his Norwegian Ph.D. work first quantitatively described the spring bloom. Gran & Braarud (1935) led the way in focusing how light and water-column stability affect the timing and magnitude of the spring bloom. This study was conducted in the Bay of Fundy and Gulf of Maine, when the Norwegian Gran was funded by the Canadian government.

Riley modeled these processes quantitatively in the 1940's (Riley 1942, Riley 1946). Mills (1989) discusses Riley’s models of the bloom, and only mentions Sverdrup’s (1953) critical depth paper in a single footnote. He argues that Riley had presented the key concepts earlier. Riley had identified most of the key concepts, later used by the physical oceanographer Sverdrup.
in his model, but Riley made several mathematical errors in his equations. Sverdrup is given the lion’s share of credit for explaining the timing of spring blooms.

**SVERDRUP (1953): “ON CONDITIONS FOR THE VERNAL BLOOMING OF PHYTOPLANKTON.”**

Sverdrup’s paper is one of the cornerstones of biological oceanography. His critical-depth model was based on the earlier work of Gran & Braarud (1935) in the Gulf of Maine. Gran & Braarud (1935) introduced the idea of a critical depth, the depth to which phytoplankton could be mixed and still grow. They concluded that the critical depth was 5 to 10 times the compensation depth. Sverdrup made this concept more rigorous. Mills (1989) reviews this early history of biological oceanography and argues that Sverdrup is given undo credit for determining the factors controlling the spring bloom.

In Sverdrup’s words, the compensation depth is defined as the depth at which the energy intensity is such that the production by photosynthesis balances destruction by respiration. The critical depth is the depth above which daily integrated net production is zero. Thus the compensation depth refers to the net growth at a single depth, and the critical depth refers to the integrated water column production from the surface to the critical depth. The assumption is made that a phytoplankton population mixed to the critical depth will have zero net growth, just as the integrated net production from a uniformly distributed, but stationary, phytoplankton population from the surface to the critical depth will have zero net growth.

Sverdrup verified his model with data from Station M in the Norwegian Sea. Some question whether the critical depth model can ever be ‘tested’. I mean testing in the Popperian sense, which is to say, ‘attempting to falsify’. Parsons et al. (1966) apply the Sverdrup’s concept to the onset of zooplankton biomass increase in the North Pacific.

**AFTER SVERDRUP**

Townsend & Spinrad (1986) apply Sverdrup’s concept to the Gulf of Maine. They argued that in relatively shallow coastal areas such as Massachusetts Bay (depth = 35 m), the spring bloom begins in March when the critical depth reaches the bottom or when the water-column becomes stratified for a few days or weeks. The spring bloom, or series of small blooms, is pretty much over before the relatively permanent density stratification becomes pronounced in mid-April. Most of the available dissolved inorganic nitrogen is stripped from the water column by the Massachusetts Bay spring bloom.

Harris (1980), quoted above, offered a pessimistic assessment of simulation models of the spring bloom. Nevertheless, several models have done a good job of predicting the onset of the spring bloom. None so far have been able to predict the species succession during and after the bloom. Evans & Parslow (1985) showed that a shallowing of the mixed layer is not a necessary condition for the onset of the spring bloom. Spring blooms can occur even with a constant mixed
layer depth. However, Sverdrup (1953) never stated that a shallowing of the mixed layer was required for a spring bloom, only that the critical depth should exceed the mixed depth.

Smetacek & Passow (1990) criticized the Sverdrup critical depth concept. They argue that it focuses too much attention on the respiratory losses of phytoplankton. They point out that most textbook versions of the critical depth concept assume that the compensation light intensity used in the model is equivalent to the x-intercept of the P vs. I curve. Conventionally, it is assumed that phytoplankton respire at a constant rate of 10% $P_{\text{max}}$ no matter what the light intensity. The conventional choice for the compensation light intensity is 40 langley d$^{-1}$. This is the compensation light intensity Townsend & Spinrad (1986) used in their model of Gulf of Maine phytoplankton blooms. This estimate is purely empirical and is based on Riley’s work on the Sargasso Sea. Empirically, if one calculates the mean mixed-layer light intensity at the time of the spring bloom, it is roughly 40 langleys per day. This is not the light intensity needed to counteract the costs of phytoplankton respiration. This is the light intensity required to produce enough gross photosynthesis to counteract all losses of phytoplankton photosynthate. These losses include phytoplankton respiration, mesozooplankton grazing, microzooplankton grazing, vertical advection (sinking), mixing losses, and horizontal dispersion (advection and eddy diffusion). It may turn out that phytoplankton respiration costs are a very minor term in this set of loss terms.

A DIMENSIONAL ANALYSIS OF THE SPRING BLOOM IN THE GULF OF MAINE

Platt (1981) introduced the use of dimensional analysis to biological oceanographers. Legendre & Legendre (1983) give a particularly good introduction to dimensional analysis.

Figure 1 shows the basic dimensionless graph for the variables involved in critical depth: Dimensionless light vs. dimensionless depth. Dimensionless depth is $k*z$, where $k$ is the light attenuation coefficient and $z$ is water depth (from the surface). Dimensionless light can be plotted in a number of different ways. In one type of plot the dimensionless light variables $\frac{I_z}{I_c}$ and $\frac{I_z}{I_c}$ can be plotted. This type of plot should be generated for every date on which $I_c$ changes. The critical depth is the depth at which $\frac{I_z}{I_c} = 1$ and the compensation depth is the depth at which $\frac{I_z}{I_c} = 1$.

These two curves have exactly the same shape no matter what the incident light intensity ($I_o$). Changes in $I_o$ and $I_c$ cause the curve to be shifted up or shifted down. Such shifts will have a much greater effect on the critical depth than it will on the compensation depth.

A generalized critical and compensation depth plot can be generated for all water columns and all combinations of incident light intensity by plotting the value of $I_o/I_c$ as another dimensional variable. This will vary as a function of site and compensation depth.
CHANGES IN PHYTOPLANKTON SPECIES COMPOSITION

Margalef (1958) proposed that the typical temperate phytoplankton succession has three stages:

I. fast growing, small-celled diatoms
II. occurrence of a community of larger diatoms with lower growth rates
III. stage III is determined by the presence of large dinoflagellates with still lower growth rates.

The progression from Stage I to Stage III follows the progressive depletion of nutrients, while intense destabilization of the water column determine the end of a succession or the beginning of a new one.

Smyda (1980) remains the definitive review of marine phytoplankton succession. Hutchinson’s treatise on limnology, Reynolds (1984 a & b), Kalff & Knoechel (1978) are the best descriptions of aquatic phytoplankton succession. Kalff & Knoechel (1978) present a simple mathematical analysis, showing that while competition for nutrients is undoubtedly involved in the succession during the spring bloom, it is unlikely that later succession species simply outgrow the early succession species.

Allen & Starr (1982), Williams et al. (1981), and Legendre et al. (1985), in separate publications, have stressed the stochastic nature of phytoplankton succession. Deterministic models have been proposed for phytoplankton succession, especially by Tilman, but these have not had great predictive success in the field.

Dimensionless critical depth

INTRODUCTION

Sverdrup’s (1953) critical-depth model is one of the foundations of biological oceanography. His model explains the timing of the spring phytoplankton bloom as the result of seasonally increasing gross photosynthesis and water-water column stability. He introduced the concept of the critical depth, the depth above which the average net phytoplankton growth is zero. Stated most simply, the spring phytoplankton bloom can occur only when the mixed-layer depth is shallower than the critical depth.

The most famous applications of the model include Sverdrup’s (1953) own explanation of the timing of the bloom at weather-station M in the North Atlantic and Parsons et al. (1966) explanation of the timing of the spring bloom in the Subarctic Pacific. More recently, Townsend & Spinrad (1986) applied the critical-depth model to explain the timing of phytoplankton blooms in the Gulf of Maine. In important extensions of the critical depth model, Nelson & Smith (1991) and Mitchell et al. (1991) showed how the critical depth model can explain the low Chl a concentrations found in parts of the Southern Ocean. In the Southern Ocean, the mixed
layer depth is sufficiently deep that phytoplankton become light limited before \( \text{NO}_3^- \) or other nutrients can be depleted.

Mills’ (1989) excellent scientific history of biological oceanography has a wonderfully readable section on the search for the explanation of the spring bloom. This history reads like Judson’s (1979) description of the Watson & Crick’s discovery of the structure of DNA and Provine’s (1986) history of Sewall Wright’s development of the adaptive landscape model. The critical-depth, adaptive-landscape, and DNA models are foundations of their respective fields, but all have an element of controversy associated with them.

One controversy surrounding the critical-depth model is whether Sverdrup deserves full credit for its creation. Mills’ (1989) argues that the ideas were largely Gran’s and the mathematics was largely solved by Gordon Riley. Both should share the credit for the ideas behind the critical-depth model. Building on Gran & Braarud’s (1935) work, Riley (1942) described the role of water-column stability in controlling the spring bloom on Georges Bank. In 1942, Riley did not deal with the effects of light intensity on photosynthetic rate. However by 1946, Riley had calculated the mean photosynthetic rate in a well-mixed water column using equations very similar to Sverdrup’s (cf., Riley’s eq. (2) or Equ. 1 below and Sverdrup’s eq. (6)). Riley (1946) should not be given credit for the critical-depth model, because his equation representing the effects of mixing on net phytoplankton growth was wrong. Riley’s equation (5), shown here as Equ. 1, is identical to Sverdrup’s solution for the mean photosynthetic rate in the euphotic zone:

\[
P_h = \frac{p I_0}{k z_l} \left( 1 - e^{-k z_1} \right) \left( 1 - N \right) \left( 1 - V \right).
\]

where, \( P_h \) = mean photosynthetic rate in euphotic zone \[
\frac{\text{g C fixed}}{\text{g C phyto. biomass Time}}.
\]

\( p = \) proportionality constant between photosynthesis and light intensity, \( L \)

\( I_0 = \) surface light intensity.

\( k = \) light attenuation coefficient \( = \frac{1.7}{\text{Secchi-disk depth}}. \)

\( z_l = \) depth of the euphotic zone.

\( = \) depth at which \( I = 0.0015 \text{ g cal cm}^{-2} \text{ min}^{-1}. \)

\( = 1\% \) of \( I_0 \) at the time of the spring bloom.

\( (1 - N) = \) factor reducing photosynthetic rate due to nutrient limitation.

\( (1 - V) = \) factor reducing photosynthetic rate due to vertical water movements.

\( = \frac{z_1}{z_2}. \)

\( z_2 = \) the depth of the mixed layer.

However, in this equation Riley calculated the effects of mixing with the \((1-V)\) coefficient, which grossly overestimates the effects of water column mixing in reducing photosynthetic rate. In Equation 1 if the compensation depth were 5 m \( (z_1) \) and the mixed-layer depth \( (z_2) \) was 50 m, the average gross photosynthetic rate should be multiplied by factor of 0.1. It is clear that Riley
intended $P_h$ to measure gross, not net production, because a temperature-dependent phytoplankton respiration term is added later in his equation (8) which includes all of the major loss terms for phytoplankton growth:

$$\frac{dP}{dt} = P \left[ \frac{P_l}{kz_1} (1 - e^{-kz}) (1 - N) (1 - V) - R_o e^{rt} - gZ \right],$$

where, $P =$ phytoplankton biomass [g C m$^{-2}$].

$t =$ time [d].

e = base of Naparien logarithms.

$R_o =$ phytoplankton respiration at 0° C (= 0.0175 d$^{-1}$).

$r = \frac{\ln(2)}{10}$, scales $R$ to have a $Q_{10}$ of 2.

$T =$ temperature in °C.

g = rate of grazing by a unit quantity of zooplankton [d$^{-1}$].

$z_1 =$ depth of the euphotic zone.

$Z =$ zooplankton biomass in g C m$^{-2}$.

In the story of the critical-depth model, Sverdrup plays the role of Watson & Crick to Gordon Riley’s Rosalind Franklin. Mills (1989, p. 290) states “Riley was annoyed that Sverdrup did not mention his work [the 1946 paper].” Sverdrup had cited Riley’s earlier 1942 paper but had not cited the key 1946 paper. Riley had justification for being annoyed since he had missed the full explication of the what we now call the critical-depth model only by miscalculating the effects of a deep mixed-layer depth with his faulty (1-V) factor. Mills (1989) rectifies this slight by presenting the key contributions of Riley’s work to biological oceanography. Because of his error in using the (1-V) factor, the field was open for Sverdrup in 1953 to create a simple quantitative model that tied the roles of seasonally increasing light intensity and water-column stability into a predictive model of the spring bloom.

Smetacek & Passow’s (1990) review somewhat shockingly points out that many biological oceanographers have misinterpreted Sverdrup’s model. The further argue that it should no longer be inflicted on graduate students:

“The fact that most scientists are not even aware of the discrepancy between Sverdrup’s original model and its latter-day versions strongly suggests that it is put to little if any practical use. Its predictive ability in the context of spring bloom growth has, to our knowledge, been explicitly challenged by only a few workers ... Its implicit acceptance is reflected in the way it is routinely cited and in the prominence it receives in teaching programs and textbooks. It is time we adopted a more critical attitude toward this model instead of continuing to inflict it as a matter of course on innocent graduate students.”
Smetacek & Passow’s (1990) criticism of the intellectual value of Sverdrup’s critical depth model is similar to Provine’s (1986) criticism of Sewall Wright’s adaptive landscape. Provine (1986, p. 316) concluded, “It should give pause to consider that for over fifty years the majority of evolutionary biologist have believed Wright’s 1932 diagrams of the adaptive landscape to be the most heuristically valuable diagrams in all of evolutionary biology, yet to discover that the surface as he conceived it is unintelligible.” Sewall Wright’s last published paper in 1988 addressed Provine’s (1986) criticism. He knew what his adaptive landscape represented, even though others did not. Certainly Sverdrup and Riley knew that zooplankton grazing played a role in the critical-depth model, even if the modern presentation of the model to graduate students ignores it.

I was assigned Sverdrup’s original paper in my biological oceanography course (taught by Dr. Karl Banse in 1976), and I in turn have assigned this paper to each biological oceanography class that I’ve taught. The critical depth concept plays an important role in biological oceanography (and my class), since it explaining the concept is akin to a full midterm examination.

In preparing a midterm examination for my class, I developed a non-dimensional representation of the critical-depth model. This analysis produces a simple dimensionless semi-logarithmic plot that reveals the key features of the critical depth model. One plot can be used to show the compensation and critical depths for any water column at any time of year.

**Blooms, Compensation & critical depths: some definitions**

One of the pedagogical appeals the critical-depth model is that to understand it students must know the definitions of many of the biological oceanographic terms used to define primary production. Explaining the model is an all-in-one midterm examination.

There are three terms involved in Sverdrup’s (1953, p. 287) statement, “...there must exist a critical depth such that blooming can occur only if the depth of the mixed layer is less than the critical value.” I found “spring bloom” to be the most difficult to define. The conventional definition of spring bloom is the rapid increase in phytoplankton biomass with time, or high $\frac{dC}{dt}$.

Table 1 defines C and all other variables.
Table 1. Base units and variables used in the critical-depth concept. c.g.s. units used wherever possible

<table>
<thead>
<tr>
<th>Fundamental quantity</th>
<th>Quantity Symbol</th>
<th>Dimension Symbol</th>
<th>Base Unit</th>
<th>Unit symbol</th>
</tr>
</thead>
<tbody>
<tr>
<td>mass of carbon</td>
<td>C</td>
<td>[M&lt;sub&gt;c&lt;/sub&gt;]</td>
<td>gram carbon</td>
<td>g C</td>
</tr>
<tr>
<td>mass of chlorophyll a</td>
<td>Chl a</td>
<td>[M&lt;sub&gt;cha&lt;/sub&gt;]</td>
<td>gram chl a</td>
<td>g Chl a</td>
</tr>
<tr>
<td>photons of light</td>
<td>photons</td>
<td>[hv]</td>
<td>mol photon</td>
<td>E (Einstein)</td>
</tr>
<tr>
<td>light energy</td>
<td>watts</td>
<td></td>
<td>watts</td>
<td>W</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Variable</th>
<th>Variable Symbol</th>
<th>Dimension Symbol</th>
<th>Base unit</th>
<th>Unit symbol</th>
</tr>
</thead>
<tbody>
<tr>
<td>Water depth</td>
<td>z</td>
<td>[L]</td>
<td>centimeter</td>
<td>cm</td>
</tr>
<tr>
<td>Specific growth rate</td>
<td>µ</td>
<td>[T&lt;sup&gt;-1&lt;/sup&gt;]</td>
<td>gram carbon</td>
<td>s&lt;sup&gt;-1&lt;/sup&gt;</td>
</tr>
<tr>
<td>Specific grazing loss</td>
<td>G</td>
<td>[T&lt;sup&gt;-1&lt;/sup&gt;]</td>
<td>&quot;</td>
<td>&quot;</td>
</tr>
<tr>
<td>Other specific losses</td>
<td>l</td>
<td>[T&lt;sup&gt;-1&lt;/sup&gt;]</td>
<td>&quot;</td>
<td>&quot;</td>
</tr>
<tr>
<td>Gross Photosynthesis at depth z</td>
<td>P&lt;sub&gt;g&lt;/sub&gt;&lt;sub&gt;z&lt;/sub&gt;</td>
<td>[M&lt;sub&gt;c&lt;/sub&gt;L&lt;sup&gt;-2&lt;/sup&gt;T&lt;sup&gt;-1&lt;/sup&gt;]</td>
<td>gram carbon</td>
<td>g Ccm&lt;sup&gt;-3&lt;/sup&gt;s&lt;sup&gt;-1&lt;/sup&gt;</td>
</tr>
<tr>
<td>Net photosynthesis at depth z</td>
<td>P&lt;sub&gt;n&lt;/sub&gt;&lt;sub&gt;z&lt;/sub&gt;</td>
<td>&quot;</td>
<td>&quot;</td>
<td>&quot;</td>
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<tr>
<td>Max. gross photosynthesis</td>
<td>P&lt;sub&gt;max&lt;/sub&gt;</td>
<td>&quot;</td>
<td>&quot;</td>
<td>&quot;</td>
</tr>
<tr>
<td>Depth-average gross photosynthesis from the surface to depth z</td>
<td>P&lt;sub&gt;f&lt;/sub&gt;&lt;sub&gt;z&lt;/sub&gt;</td>
<td>&quot;</td>
<td>&quot;</td>
<td>&quot;</td>
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<tr>
<td>Phytoplankton respiration</td>
<td>R</td>
<td>&quot;</td>
<td>&quot;</td>
<td>&quot;</td>
</tr>
<tr>
<td>light attenuation coefficient for PAR</td>
<td>k</td>
<td>[L&lt;sup&gt;-1&lt;/sup&gt;]</td>
<td>1/centimeters</td>
<td>cm&lt;sup&gt;-1&lt;/sup&gt;</td>
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<tr>
<td>Photosynthetically Available Radiation (PAR)</td>
<td>I</td>
<td>[hvL&lt;sup&gt;-2&lt;/sup&gt;T&lt;sup&gt;-1&lt;/sup&gt;]</td>
<td>E/centimeter&lt;sup&gt;2&lt;/sup&gt;second or W/centimeter&lt;sup&gt;2&lt;/sup&gt;</td>
<td>E cm&lt;sup&gt;-2&lt;/sup&gt;s&lt;sup&gt;-1&lt;/sup&gt; or W cm&lt;sup&gt;-2&lt;/sup&gt;</td>
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<tr>
<td>Variable</td>
<td>Variable Symbol</td>
<td>Dimension Symbol</td>
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<tr>
<td>Net downwelling irradiance just below the water surface</td>
<td>$I_o$</td>
<td>“”</td>
<td>“”</td>
<td>“”</td>
</tr>
<tr>
<td>Net downwelling irradiance at depth $z$</td>
<td>$I_z$</td>
<td>“”</td>
<td>“”</td>
<td>“”</td>
</tr>
<tr>
<td>Average light intensity from surface to depth $z$</td>
<td>$\overline{I_z}$</td>
<td>“”</td>
<td>“”</td>
<td>“”</td>
</tr>
<tr>
<td>Compensation light intensity</td>
<td>$I_c$</td>
<td>“”</td>
<td>“”</td>
<td>“”</td>
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</tbody>
</table>

Unfortunately, Parsons et al.’s (1966) application of the critical depth model to the subarctic North Pacific does not fit this definition. In the subarctic Pacific, phytoplankton biomass remains relatively constant ($\frac{dC}{dt} = 0$). Parsons et al. (1966) predicted the timing of the bloom in grazer biomass, not phytoplankton biomass. Their application of the spring bloom model was apparently consistent with Sverdrup’s since grazer biomass is indeed coupled to phytoplankton biomass through equations of the following sort (Frost 1980):

$$\frac{dC}{dt} = C(P_2 - R_p) - CG - CI. \quad (3)$$

Sverdrup (1953), and most authors, defined the spring bloom solely in terms of increasing phytoplankton biomass (term 1 above). Others modeled the spring bloom in terms of a period of positive gross photosynthesis (term 2). Parsons et al. (1966) applied the spring bloom model to the bloom in macrozooplankton biomass, which is coupled to term 4, the grazing loss term.

Is an increase in phytoplankton biomass ($\frac{dC}{dt}$) a prerequisite for the application of the spring bloom model, or would the following definition be acceptable? “The spring increase in phytoplankton net areal production, expressed as $g C m^2$, can occur when the mixed-layer depth is shallower than the critical depth.” I really can’t accept this definition. First, it is inconsistent with Gran & Braarud (1935), Riley (1942, 1946), and Sverdrup (1953). Bloom means an increase in biomass not production. When Riley described the spring bloom, he was not describing the gradual increase in net photosynthesis observed form January through April. He wanted to explain the sharp spike in phytoplankton biomass observed in April. By abandoning the definition of the spring bloom as being analogous to the increase in net production, we must dismiss Parsons et al.’s (1966) study as a true application of the spring bloom model.
Sverdrup’s critical depth can be defined in two ways. First, it is the depth above which the daily average water column light intensity \( I_d \) equals the compensation light intensity. Second, the critical depth is the depth above which depth-integrated daily gross photosynthesis equals respiration. Sverdrup (1953) showed how the critical depth can be calculated. He based included a factor of 0.18 to reduce the amount of radiation to that utilizable by phytoplankton. As Nelson & Smith (1991) note, most later authors incorporated this factor of 0.2 erroneously in applications of the critical depth model.

Sverdrup (1953) made the following assumptions in developing an equation to predict the critical depth:

1. Thoroughly mixed top-layer of thickness \( D \).
2. Turbulence strong enough to distribute the plankton
3. Production not limited by the lack of plant nutrients.
4. Within the mixed layer, the extinction coefficient, \( k \) is constant.
5. Wavelengths in the range 420 to 560 nm only considered [too narrow a range for current estimates of PAR]
6. Production of organic matter by photosynthesis is proportional to the energy of the radiation at the level under consideration
7. The energy \( I_c \) at the compensation depth is known.

Given these assumptions, the following equation can be used to calculate the critical depth:

\[
\frac{D_{cr}}{1 - e^{-k_eD_{cr}}} = \frac{I_e}{I_c k_e},
\]

where, \( D_{cr} \) = critical depth in meters.
\( k_e \) = extinction coefficient.
\( I_e \) = avg. energy passing sea surface per unit time (PAR).
\( I_c \) = energy at the compensation depth.

The compensation light intensity is the light intensity at which net photosynthesis is zero. The compensation depth is the depth corresponding to the average daily light intensity is equal to the compensation light intensity. At this light intensity, phytoplankton respiration balances gross photosynthesis.

Spring blooms can occur when the critical depth is greater than the mixed layer depth. Riley (1942 & 1946) and Sverdrup (1953) defined the mixed-layer depth in terms of the density gradient, \( \frac{dp}{dz} \). Riley (1946) explicitly defined mixed layer depth: “the depth of the mixed layer ...is arbitrarily defined as the maximum depth at which the density is no more than 0.02 of a \( \sigma \) unit greater than the surface value.”

Smetacek & Passow (1990) note that most biological oceanographers have assumed that the compensation light intensity is defined as the depth at which gross photosynthetic rate is
balanced by phytoplankton respiration. However, Sverdrup (1953) included grazing and other phytoplankton loss terms in “respiration.” Sverdrup stated: “The compensation depth...must for instance, lie higher for a mixed population of phyto- and zooplankton than for a pure phytoplankton population.” This implied zooplankton grazing was probably included in most applications of the critical depth model by specifying a compensation light intensity sufficient to balance not only phytoplankton respiration but also the ubiquitous microzooplankton grazers present. Riley (1957) estimate for $I_c$ of 40 langley d$^{-1}$ is often used in critical depth calculations (e.g., Townsend & Spinrad 1986). Riley’s estimate of 40 langley d$^{-1}$ probably included zooplankton grazing (1 langley=1 watt cm$^{-2}$). Table 2 shows some of the values that have been used for the compensation light intensity in the literature. It is amazing that there is a 40-fold range in compensation light intensities from the literature.
Table 2. Estimates of compensation light intensity, $I_c$, from the literature. As noted by Siegel et al. (2002), most of these compensation light intensities are community compensation light intensities, which include the effects of loss terms, especially grazing. Units are converted when possible, using the following relationships and assumptions (from Parsons et al. 1984, p. 68):

- Photoperiod = 12 h
- $1 \text{ langley} = \frac{1 \text{ g cal}}{\text{cm}^2} = \frac{4.185 \times 10^7 \text{ ergs}}{\text{cm}^2} = \frac{4.185 \text{ Watt sec}}{\text{cm}^2}$
- $1 \text{ Ein} = 6.02 \times 10^{23} \text{ quanta} = \frac{2.86 \times 10^4 \text{ g cal}}{\text{Angstroms}}$
  - 1 Angstrom=$10^{-10}$ m
  - If average wavelength of PAR = 550 nm:
    - $1 \text{ Ein} = (2.86 \times 10^4 \text{ g cal} / 5500) = 52 \times 10^3 \text{ g cal}$
- 1 Joule = mks unit of work = $10^3 \text{ g cm s}^{-2}$
- 1 electron volt = $1.6 \times 10^{-19}$ joules (Falkowski & Raven 1997, p. 34)

<table>
<thead>
<tr>
<th>$I_c$</th>
<th>Original Units</th>
<th>$\frac{\mu E}{m^2 s}$</th>
<th>$\frac{E}{m^2 d}$</th>
<th>$\frac{\mu E}{m^2 s}$</th>
<th>Original citation</th>
<th>Used by</th>
</tr>
</thead>
<tbody>
<tr>
<td>2.48 $\mu E$</td>
<td>m$^2$s</td>
<td>2</td>
<td>0.2</td>
<td>1</td>
<td></td>
<td>Smetacek &amp; Passow (1990)</td>
</tr>
<tr>
<td>0.0015 g cal</td>
<td>cm$^2$ min</td>
<td>5</td>
<td>0.4</td>
<td>1</td>
<td></td>
<td>Riley (1946)</td>
</tr>
<tr>
<td>0.17 ly/h</td>
<td>langley</td>
<td>9</td>
<td>0.6-0.8</td>
<td>2</td>
<td></td>
<td>Jenkins (1937) Sverdrup (1953)</td>
</tr>
<tr>
<td>0.17 ly/h</td>
<td>langley</td>
<td>9</td>
<td>0.8</td>
<td>2</td>
<td></td>
<td>Jenkins (1937) Parsons et al. (1966)</td>
</tr>
<tr>
<td>0.96-1.97</td>
<td>Einstein (mol photon)</td>
<td>12-17</td>
<td>1-1.5</td>
<td>5-8</td>
<td></td>
<td>Siegel et al. (2002) Siegel et al. 2002</td>
</tr>
<tr>
<td>1.5-1.7 W m$^{-2}$</td>
<td>Watt</td>
<td>31</td>
<td>2.7</td>
<td>7</td>
<td></td>
<td>Mann &amp; Lazier (1991, p. 86)</td>
</tr>
<tr>
<td>35 $\mu E$ m$^{-2}$s$^{-1}$</td>
<td>Einstein</td>
<td>35</td>
<td>3.0</td>
<td>8</td>
<td></td>
<td>Nelson &amp; Smith (1991)</td>
</tr>
<tr>
<td>40 ly/d (Total light, not PAR)</td>
<td>langley</td>
<td>ER R</td>
<td>??</td>
<td>40</td>
<td></td>
<td>Riley (1957) Townsend &amp; Spinrad (1986)</td>
</tr>
<tr>
<td>9.375 J m$^{-2}$s$^{-1}$</td>
<td>PAR</td>
<td>Joule</td>
<td></td>
<td></td>
<td></td>
<td>Gieskes &amp; Kraay (1975)</td>
</tr>
</tbody>
</table>
In order to understand, the role of respiration and grazing losses, I’ll start with the definition of specific growth rate ($\mu$). We’ll assume that there is one type of phytoplankton cell with growth characteristics defined by $\mu$:

$$\mu = \frac{1}{C} \frac{dC}{dt}. \quad (5)$$

What is the relationship between respiration and grazing loss? It can be defined in terms of $\mu$:

$$\frac{dC}{dt} = P_g - R - C (G - L),$$

where, $C$ = Phytoplankton concentration.
$G$ = Specific growth rate.
$L$ = Other phytoplankton losses.
$P_g$ = Gross photosynthesis.
$R$ = Phytoplankton respiration. \quad (6)$

What is meant by *the spring bloom*? The spring bloom can be defined as the rapid increase in phytoplankton standing stock, $dC/dt$, or it can be defined as the rapid increase in phytoplankton net production, $P - R$. Sverdrup (1953) used the former definition and Parsons et al. (1966) used the latter interpretation.

The compensation depth in the water column is the depth at which downwelling irradiance ($I_z$) is equal to the compensation light intensity. In shallow waters, such as Massachusetts Bay (35-m depth), the spring bloom can occur when the critical depth exceeds the bottom depth. In the subarctic Pacific a spring bloom results in increased primary production and biomass of mesozooplankton, but with no net increase in phytoplankton standing stock.

**Dimensional analysis**

Bowman et al. (1981), Platt (1981), Platt et al. (1984), Lewis et al. (1985) and Legendre & Legendre (1983) use dimensional analysis and dimensionless variables to analyze phytoplankton growth. Bowman et al. (1981), Platt et al. (1984), and Lewis et al. (1985) are closest to the analyses presented here, but no one appears to have couched the critical depth problem explicitly in terms of dimensionless depth, light and production variables.

The first step in dimensional analysis is defining the relevant variables. The critical depth model can be described using a subset of the variables defined in Table 1.
I can create 7 independent dimensionless variables from this set:

\[ \frac{kz}{I_o} = \text{dimensionless depth = optical depth.} \]

\[ \frac{I_z}{I_o} = \text{dimensionless light intensity at depth } z. \]

\[ \frac{I_z}{I_o} = \text{dimensionless average light intensity.} \]

\[ \frac{I_z}{I_o} = \text{dimensionless compensation light intensity.} \]

\[ \frac{P_z}{P_{\text{max}}} = \text{dimensionless gross photosynthesis at depth } z. \]

\[ \frac{P}{P_{\text{max}}} = \text{dimensionless average gross photosynthesis.} \]

\[ \frac{R}{P_{\text{max}}} = \text{dimensionless respiration.} \]

In Table 1, a variety of units could be used for light intensity (Watts, Joules, Einsteins).

The two definitions of critical depth give rise to two types of dimensionless critical depth plots. The semi-logarithmic dimensionless critical depth plot shows dimensionless light at depth \( z \) and dimensionless average light from the surface to depth \( z \) versus optical depth \( kz \). I assume that the light attenuation coefficient, \( k \), is constant with depth. Light intensity declines exponentially with depth in accordance with Beers’ Law:

\[ I_z = I_o e^{-kz} \]  \hspace{1cm} (8)

The average light intensity from the surface to depth \( z \) was solved by Sverdrup (1953) and is found in Parsons et al. (1984, Equation 57, p. 94) (Note that Parsons et al. (1984) include a 0.5 conversion factor to convert from total solar irradiance to PAR:

\[ \frac{\overline{I_z}}{I_o} = \frac{1}{z} \int_0^z e^{-kz} \, dz = \frac{1}{kz} (1 - e^{-kz}). \]  \hspace{1cm} (9)
Figure 1. A plot of dimensionless light intensity vs. dimensionless depth (optical depth). The upper line shows Beer’s law, $I_z = I_o e^{-kz}$. The curve is described by Equ. 9 (see text).
If \( k \) is constant with depth, Figure 1 shows how all water-column light profiles can be plotted on one dimensionless graph of dimensionless light vs. dimensionless depth \((kz)\). Figure 1 is based on Townsend & Spinrad’s (1986) equation for PAR for the Gulf of Maine:

\[
E_a = \alpha + \beta \sin \omega t.
\]

where, \( \alpha = 150 \text{ langley per day} \), \( \beta = \text{beta} = 550 \text{ langley per day} \),

\[
E_a = \text{Light at surface (PAR)}.
\]

\[
\omega = \Omega = \frac{\pi}{365} \frac{d}{d}.
\]

\( t = \text{day of year (day 0 is 12/21)} \).

The compensation light intensity, \( I_c = 40 \text{ ly/d} \), was taken from Riley (1957). Riley’s relatively high \( I_c \) value is based on empirical observations of when spring blooms occur on the New England shelf. It is higher than laboratory estimates of the light intensity at which gross production equals zero.

Figure 2 shows two light profiles: the light level at depth \( z \), and the average light level from the surface to depth \( z \). To find the compensation depth and critical depths using this plot, plot \( I_c/I_0 \) as a vertical line on this graph. The \( I_c/I_0 \) values are specific to specific regions; the Gulf of Maine values are shown in Fig. 1. Figure 1 also shows how the \( I_c/I_0 \) values for each date can be plotted as vertical lines on the critical dimensionless depth plot. The intersection of these horizontal lines with the lines showing \( I_c/I_0 \) are the compensation and critical depths respectively. Compensation depth on December 21 is approximately 1.3 optical depths, and critical depth is approximately 3.7 optical depths. The seasonal maximum compensation and critical depths are 3 and 16.5 optical depths. These dimensionless depths can be converted to depth in m if the light attenuation coefficient for the water column is known.
The second definition of the critical depth model is expressed in terms of depth-integrated photosynthesis. Critical depth is the depth above which water-column net photosynthesis is zero. Smetacek & Passow (1990) use this way of defining critical depth, plotted in Fig. 2, in their discussion of the critical depth concept. As a ‘back-of-the-envelope’ approximation, respiration can be assumed to be 10% of \( P_{\text{max}} \) (Burris 1980). The compensation depth corresponding to that rate is the intersection of the vertical line with the solid curve in Fig. 1. The critical depth is the depth at which depth-averaged production equals respiration, and is shown by the intersection of the vertical lines, representing respiration rate and the dashed curve in Fig. 1. Smetacek & Passow (1990) argued that the calculated critical depth is very sensitive to the respiration rate. Figure 2 shows that changing the respiration rate from 10% of \( P_{\text{max}} \) to 5% of \( P_{\text{max}} \) changes the compensation depth by only a few meters, but doubles the critical depth (from 150 m to 200 m in Fig. 2).

Figure 3 shows a dimensionless critical depth plot using production rather than light intensity. If gross photosynthesis is linearly proportional to light intensity, as Sverdrup (1953) assumed, and light attenuation, \( k \), is constant with depth, then a dimensionless plot of \( \frac{P}{P_{\text{max}}} \) vs. \( \frac{z}{P_{\text{max}}} \) can be applied to all water columns. This plot is similar to Platt et al.’s (1984) Fig. 1, where relative photosynthesis was plotted vs. optical depth. If one assumes that respiration is a fixed percentage of \( P_{\text{max}} \), then the compensation and critical depths (as optical depths) can be quickly read from the graphs. One conventional assumption is that phytoplankton respiration is 10% of \( P_{\text{max}} \) (see review by Burris 1980). If critical depth is defined in this way,
calculation of the critical depth is particularly simple. A horizontal line corresponding to $\text{Resp}/P_{\text{max}} = 0.1$ is plotted. The critical depth is the optical depth at which this vertical line intersects the average gross photosynthesis to that point (Fig. 3). If respiration is 5% of $P_{\text{max}}$, the critical depth is 20 optical depths.

It is not coincidental, that the critical depth doubles as respiration as a percentage of $P_{\text{max}}$ is halved. Figure 3 shows that the critical depth, expressed as optical depths, is simply $\frac{P_{\text{max}}}{R}$. The critical depth itself is simply $\frac{P_{\text{max}}}{k\, R}$.

Thus, it is particularly uninformative to define critical depths using respiration as a fixed percentage of $P_{\text{max}}$. The critical depth defined in this way is independent of geographic region and light intensity.

**Figure 4.** The same relationships shown in Fig. 3 are shown with a grid to show that the critical depth, as $kz$, is simply $\frac{P_{\text{max}}}{R}$. If respiration is 10% $P_{\text{max}}$, the critical depth is 10 optical depths.

**DISCUSSION**

These analyses say nothing about the validity of *Sverdrup’s (1953) critical depth model*, but they do clarify some of the issues. Fig. 5 shows that one conventional form of the critical depth model is equivalent to saying, “*Spring blooms occur when the mixed layer depth is shallower than 10 optical depths.*”

The real value in the displays is the elucidation of the key features of the critical depth model. Fig. 4 shows clearly why the ratios of compensation depths to critical depths change so radically with increasing light intensity in the late winter and spring in temperate latitudes. Fig. 2 shows why slight changes in respiration can have such dramatic effects on critical depth.

In short, these dimensionless plots may have considerable pedagogical appeal for those of us who continue to inflict the critical depth model on our graduate students.
Outlines of papers

REQUIRED


I. Photosynthesis and growth of phytoplankton in the sea.
   A. Methods of Estimating Primary Production
      1. Steemann-Nielsen’s C-14 method discussed
      2. \( k_c = 1.7/T \), where \( T \) is the Secchi disk depth in meters.
      3. Platt’s (1971) equation used to transform semi-diel rates into daily rates.
      4. Short incubations may not be best
         - Photosynthetic rate may change
      5. Light intensity and quality may change throughout the day
      6. Nighttime respiration losses difficult to estimate
         a. light-dark bottle \( O_2 \) method
         b. Simulated in-situ method discussed.
   B. \( P \) vs. \( I \) curves
      1. Steele’s equation [note Jassby-Platt more commonly used]
         \[
         P_g = P_{\text{max}} \frac{I}{I_{\text{opt}}} \exp\left(1 - \frac{I}{I_{\text{opt}}}\right).
         \]
         (37, p. 89)
         a. \( I_c \): intersection of initial slope and \( P_{\text{max}} \)
         b. \( P_{\text{max}} \) varies as a function of environmental variables and the physiological state of the algae
      2. diel net photosynthesis (p. 91 right.)
         \[
         P_{\text{net}} = P_{\text{g}} e^{-24R}
         \]
         (50)
      3. Compensation depth (p.91 rt. col): The depth at which net photosynthesis is zero.
      4. diel vs hourly
         a. The hourly compensation depth will change during the day and will be maximum at noon and zero during darkness.
         b. The diel compensation depth will change with season.
      5. specific versus total production
         a. In order to obtain the actual photosynthesis, the \( P \) vs. \( I \) relationship must be multiplied by the amount of phytoplankton biomass
         b. “When chl a is not uniformly distributed, the expression for photosynthesis per unit of chl a must be obtained by multiplying the photosynthesis by the actual amount of chl a at different depths in the water column.”
         c. specific growth rate: (p. 92) Table 19 provides measured values of \( \mu \) for the world’s oceans. 0.26 divisions \( d^{-1} \) in the gyres to over 1 per day in the African and Western Arabian seas.
   C. CRITICAL DEPTH:
      CRITICAL-DEPTH CONCEPT: The depth to which plants can be mixed and at which the total photosynthesis for the water column is equal to the total respiration is known as the “critical depth”. Or the depth above which the average light intensity for the water column equals the compensation light intensity.
      Equations:
      \[
      I_c = 0.5 I_e e^{4D_c}
      \]
      (56)
      \[
      \int_{avg(I_c)} = 0.5 I_c \int_{D_{cr}} e^{4D_c} \delta D/D_{cr}
      \]
      \[
      D_{cr} = 0.5 I_c / [kD_c] \cdot (1-e^{4D_c})
      \]
      (57)
where, \( D_{cr} \) is large, (57) reduces to:

\[
D_{cr} = 0.5 \frac{I_0}{[\text{avg}(I) \times k]}
\]  

(58)

See Figure 41 (page 94).

1. It is possible from equation (57) p. 94 to calculate the critical depth if one knows the extinction coefficient, the solar radiation and assuming some value for the compensation light intensity.

2. Five critical-depth concept assumptions:
   a. plants are uniformly distributed in the mixed layer
   b. there is no lack of plant nutrients
   c. extinction coefficient of light is constant
   d. production proportional to light intensity [is this assumption correct?]
   e. respiration constant with depth

D. Factors affecting light extinction (p. 95)

\[
k' = 0.04 + 0.0088 \text{C} + 0.054 \text{C}^{3/2}
\]

where C is Chl a concentration.

E. Factors affecting the quantity and quality of light

"(p. 97-8) In high productivity areas generally characterized by thin euphotic zones, and if not influenced by land runoff or tidal mixing, most of the light is attenuated by phytoplankton."

Fig. 42: Excellent schematic of the seasonal change in production and phytoplankton standing stock.

F. Compensation light intensity = 1% of \( I_o \), compensation depth = depth at which light is 1% of surface light, or 4.6 light attenuation depths.

\[
\frac{I}{I_o} = e^{-kz}
\]

\[
ln(0.01) = -kz
\]

\[
-4.6 = kz
\]

4.6 = kz, where kz is the dimensionless light attenuation depth.

Compensation depth = \( z_c = 4.6/k \)

[n.b., The compensation light intensity is not really 1% of \( I_o \). This is just a very rough approximation]

G. p. 97, footnote: 3 times the Secchi depth is sometimes employed as an estimate of the euphotic depth.

**Table 21:** Diel net photosynthesis for various amounts of Chl a under different levels of irradiance. (assumed a \( P_{max} \) of 1 mg C/mg Chl a/hr. It would be better to measure the actual \( P_{max} \) in any environment in order to obtain better prediction of the in situ productivity. In highly productive areas, \( P_{max} \) may be greater than 5 mg C/mg Chl a/hr

**light utilization efficiency** the ratio of photosynthetic production to the total incoming solar radiation. This **ecological efficiency** should not be confused with the **quantum efficiency**. The photosynthetic production is generally converted into energy units from carbon content and this is defined as PSR. According to Platt, 1977, the light-utilization efficiencies fluctuated between 0.02 and 0.9%, being an average of 0.26%.


I. Introduction

A. Based on the earlier work of Gran & Braarud (1935)

B. **Compensation depth:** \( dp = dr \)

Fig. 1. Schematic representation of the variation with depth of organic matter.

C. Gran & Braarud (1935) concluded that the critical depth was 5 to 10 times the compensation depth.

D. Riley (1942)

II. Analytical model:

A. Seven assumptions:

1. Thoroughly mixed top-layer of thickness D.
2. Turbulence strong enough to distribute the plankton
3. Production not limited by the lack of plant nutrients.
4. Within the mixed layer, the extinction coefficient, $k$ is constant.
5. Wavelengths in the range 420 to 560 nm only considered [too narrow a range for current estimates of PAR]
6. Production of organic matter by photosynthesis is proportional to the energy of the radiation at the level under consideration
7. The energy $I$, at the compensation depth is known.

“The compensation depth is defined at the depth at which the energy intensity is such that the production by photosynthesis balances destruction by respiration....It must for instance, lie higher for a mixed population of phyto- and zooplankton than for a pure phytoplankton population.”

B. n.b. Sverdrup only uses 20 percent of $I_c$ but PTH and most authors use 50% as the conversion to PAR from $I_c$ determined from the solar radiation-latitude equation.

C. Double integral (depth and time) of gross production

$$D_{c}/[1-e^{-kDcr}]=1/k\cdot[@avg(I)/I_c]$$  \(6\)

where $I_c$ is the effective light passing the sea surface.

III. Tests of the analytical model.

Table 1. Mixed layers at station M, off East Greenland

Table 2. Phytoplankton per liter at station M.

Fig. 2: prediction of spring bloom at station 'M'

A. Interpretation of Fig. 2.
1. until the final week of April, mixed layer depth $> z_c$
2. after middle May, $z_c >$ mixed-layer depth

B. Gran and Braarud’s (1935) generalization confirmed.


515-529. [T & S’s model can predict the timing of the spring bloom as the period when critical depth exceeds bottom depth.] [14, 15, 16, 23, 24, 28]

I. Introduction:

Bigelow (1926) quote. “Perhaps no phenomenon in the natural economy of the Gulf so arrests attention (certainly none is as spectacular) as the sudden appearance of enormous numbers of diatoms in early spring, and their equally sudden disappearance from most of this area after a brief flowering period.” (p. 465)

A. Spring bloom in early March
B. Gran & Braarud (1935)
C. Sverdrup (1953)
D. Riley (1957): 40 langley per day is $I_c$

II. Results

III. Discussion

A. 3 mechanisms for stratification
1. fresh-water runoff along the coast
2. doming of slope water intrusions in the offshore basins
3. local bathymetry.

B. 4 to 8 $\mu$M DIN

$$E_o = \alpha + \beta \sin \omega t.$$  \(4\)

where, $\alpha = 150$ langley per day.

$\beta = \text{beta} = 550$ langley per day.

$\omega = \text{omega} = \frac{\pi}{365 \text{ d}}$.

$t = \text{day of year} (0 \text{ corresponds to 12/21}).$

C. $k$ in these waters ranged from 0.1 to 0.15.

Fig. 12. Plots of critical depth where depth averaged irradiance is 40 $\text{ly d}^{-1}$. Depth vs. date.
SUPPLEMENTAL


[Mills reviews the work of the Kiel School, Plymouth Biological Laboratory and Riley. These groups laid the foundation for the study of phytoplankton ecology, especially the cause of the vernal phytoplankton bloom.]

IV. “The Water Blooms”: The discovery of the spring bloom and its control.
A. Early history
   1. Brandt
   2. philosophy
B. H. H. Gran.
   1. 1902 Ph.D. described the spring bloom
   2. 1932 study of Bay of Fundy and Gulf funded by the Canadian govt.
   3. Gran & Braarud (1935)
C. Lohman: spring bloom the result of interactions between temperature and light, not nutrients.
D. Whipple’s Boston waterworks studies

IV. Hydrography and the control of plankton abundance: solving the problem of plankton blooms.
A. Gran: between 1912-1915 estimated the depth at which photosynthesis was balanced by respiration - later called the compensation depth.
B. Gardner and Gran used the light-bottle dark-bottle method, introduced by Whipple
C. Increased vertical mixing in northern latitudes refutes Brandt’s denitrification hypothesis.
   “the explanation is so evident that my explanation of 1899 that denitrifying bacteria are the case of plankton deficiency in the tropical oceans is invalidated by it. However, I still maintain the view “that denitrifying bacteria break down an excess of nitrogen compounds and that it is they that maintain the existing equilibrium in nature.”
D. Gran proposed iron could limit phytoplankton growth in coastal waters (p. 166)
E. “Nonetheless, by 1935 vertical circulation was well established as a complex factor governing the bloom. The ideas of the Kiel school became of merely historical interest.” (Mills concluding sentence of Ch. 5, p. 171)


I. Critical depth: the depth at which the total production beneath a unit surface is equal to the total respiration.

\[
\frac{D_{cr}}{1 - e^{-k_s D_{cr}}} = \frac{I_e}{I_c k_s}.
\]

- \(D_{cr}\) = critical depth [meters].
- \(k_s\) = extinction coefficient.
- \(I_e\) = Avg. energy passing sea surface per unit time (PAR).
- \(I_c\) = energy at compensation depth.

Compensation depth: The depth at which the energy intensity is such that production by photosynthesis balances destruction by respiration.

Critical depth:
II. Station P data described

III. Methods used.
   A. extinction coefficient measured by Secchi disk $k = 1.7/D$
   B. Compensation depth taken from Jenkins (1937) as 0.13 ly/hr
   C. Light calculated from solar radiation *0.2
   D. Depth to the mixed layer were taken from Giovando and Robinson

Fig. 1. Critical depths and the depths of mixing
Fig. 2. Critical depths and depths of mixing.
Fig. 3. Copepod weight weights during April and the occurrence of the Spring bloom.

IV. Copepod biomass in the North Pacific


I. Abstract:
   A. Sverdrup’s (1953) model requires an estimate of $I_c$, the compensation light intensity where photosynthetic and community loss processes balance
   B. $I_c$ determined with satellite and hydrographic datasets.
   C. 1.3 mol photons m$^{-2}$ d$^{-1}$
       1. $2x$ light intensity for phytoplankton alone


I. Introduction
   A. Sverdrup (1953)
   B. Sverdrup implicitly included zooplankton in the terms “total population” and “total respiration” [Did he?]
   C. Gran & Braarud (1935)
      1. critical depth 5-10 times compensation depth
      2. included zooplankton respiration in respiration term
   D. their argument: algal respiration not particularly important in predicting spring blooms

II. Respiration
   A. 10% $P_{max}$
   B. Respiration = (photorespiration + dark respiration)
   C. Dark respiration = (maintenance + growth)
   D. $P$ vs. $I$ curves.
      1. intercept of 10% $P_{max}$
      2. newer observations indicate that the $P$ vs. $I$ curve curves to the origin.
      3. compensation point as low as 2.48 µmol quanta m$^{-2}$s$^{-1}$

III. Implications.
   A. what is the compensation depth?
   B. correcting respiration by a factor of 2 or 10 produces
      1. changes in $z_{comp}$ of 0.2 or 2 respectively.
      2. changes in $z_c$, of 2 to 10
Fig. 1. Sverdrup’s model in its modern rendition.
C. $z_c$ will be below the depth of winter mixing
D. species with low maintenance respiration are probably not those that thrive at the onset of seasonal phytoplankton succession, i.e., the bloom
E. “...the steepness of the slope of $a$ rather than the position of $I$, (on the $P$ vs $I$ diagram where $I$ is the light intensity at the compensation point) confers the competitive advantage during the early stages of the spring bloom.”
F. “Use of the critical-depth concept diverts attention to the lower reaches of the euphotic zone, whereas spring bloom induction is governed by processes occurring close to the surface.”

IV. Actual blooms
A. temporary stabilization is very important [observed in MA Bay]

Fig. 2. Population growth rates in a 50-m water column, with growth above 10, 20, 30, 40 and 50 m with $\mu’s = 1, .5, .25, and 0.1$ div.
B. reduced wind-induced kinetic energy causes blooms in shallow areas.
   “Thus, the critical depth, on an annual basis, lies below the depth of the biosphere; all ecosystems contribute at least some organic carbon to the sedimentary fossil record, even if it amounts to only a few $\mu gC m^{-2} y^{-1}$.”

V. Conclusion (p. 233):
“The fact that most scientists are not even aware of the discrepancy between Sverdrup’s original model and its latter-day versions strongly suggests that it is put to little if any practical use. Its predictive ability in the context of spring bloom growth has, to our knowledge, been explicitly challenged by only a few workers (e.g. Kaiser and Schulz 1978). Its implicit acceptance is reflected in the way it is routinely cited and in the prominence it receives in teaching programs and textbooks. It is time we adopted a more critical attitude toward this model instead of continuing to inflict it as a matter of course on innocent graduate students.”

I. Abstract
A. model exhibits a spring bloom as a repeating pattern
B. explains the lack of a spring bloom
C. bloom is a deviation from quasi-equilibrium behavior.

II. Introduction
A. blooms expected to recur each year.
B. mathematical models of blooms
   1. consequence of initial conditions
   2. Kremer & Nixon is an exception.
C. Cycle of phytoplankton driven by cycle of physical conditions

III. The model
A. didn’t model upper layer dynamics.
B. Equations: 4 equations.

Table 1. meanings and typical parameter values
Fig. 1. The annual cycle of model I phytoplankton and herbivores, mixed layer depth and photosynthetic rate.

IV. Intermezzo.

V. The reduced model

Fig. 2. The annual cycle for a mixed layer depth of 80 m.

VI. Reduced model

Fig. 3. Vertically integrated phytoplankton from Fig. 1 and Fig. 2.

Fig. 4. The annual cycle for a mixed layer depth of 25 m.

Fig. 5. The annual cycle for a mixed layer depth of 80 m.

Fig. 6. The annual cycle of Model 2 for a mixed layer depth of 25 m.

VII. Analysis
Fig. 7. The quasi-equilibrium cycle corresponding to Fig. 6.

VIII. The Subarctic Pacific

Fig. 8. The annual cycle for Model 1 for parameters appropriate to the subarctic Pacific

IX. Discussion
Levinton straw man: the stabilization of the water column causes the spring bloom.

X. Appendix: modeling phytoplankton growth rate.
XI. Vertical structure of the open ocean: biology of the mixed layer
   A. Introduction
   B. Vertical structure and phytoplankton production: tropical waters
   C. Vertical structure and phytoplankton production: temperate and polar waters
      1. Diurnal and seasonal changes in mixed layer depth
         a. The mechanism of the spring bloom
         b. Early history
            (1) Gran & Braarud (1935)
            (2) Riley 1949
         c. Sverdrup 1953
            (1) Station M figure from Sverdrup

References

BLOOMS


Legendre, L. 1990. The significance of microalgal blooms for fisheries and for the export of particulate organic carbon in the oceans. J. Plankton Res. 12: 681-699. [Blooms can be controlled by hydrodynamics through irradiance or nutrients. They are associated with high sedimentation of intact cells or fecal pellets. They have major effects on benthic and pelagic food webs and global carbon flux] {7, 29}


Mills, E. L. 1989. Biological Oceanography: An early history. Cornell University Press, Ithaca NY and London. [Mills reviews the work of the Kiel School, Plymouth Biological Laboratory and Riley. These groups laid the foundation for the study of phytoplankton ecology, especially the cause of the vernal phytoplankton bloom. The history of bloom studies and models is covered in chaps. 4 and 5]


Nelson, D. M. and W. O. Smith. 1991. Sverdrup revisited: critical depths, maximum chlorophyll levels and the control of Southern Ocean productivity by the irradiance-mixing regime. Limnol. Oceanogr. 36: 1650-1661. [The Southern Ocean has low Chl a year-round despite abundant DIN. Others had proposed iron limitation, but Nelson & Smith argue that the critical depth is only slightly deeper than the deep-mixed layer depth. Chl a can only increase slightly before the phytoplankton again become light limited (the critical depth shallows due to the absorption of light by phytoplankton to equal the mixed layer depth), see also Mitchell et al. 1991] {7, 13, 15, 29}


Sakshaug, E., K. Andersen, S. Myklestad and Y. Olsen. 1983. Nutrient status of phytoplankton communities in Norwegian waters (marine, brackish and fresh) as revealed by their chemical composition. J. Plankton Res. 5: 175-196 [They note that phytoplankton generally follow the Redfield ratio, but exhibit nutrient deficiency and slow growth at the termination of single species blooms]


Smetacek, V. 2000. The giant diatom dump. Nature 406: 574-575. [1000 species, Giant diatoms documented by Kemp et al., small chain formers settle rapidly in flocs. Kemp et al. document a fall dump of large diatoms, as opposed to small spring cells.]

Smetackek, V. and U. Passow. 1990. Spring bloom initiation and Sverdrup’s critical depth model. Limnol. Oceanogr. 35: 228-233. [A strong critique of the use of the critical depth concept as a pedagogical tool. They argue that it is largely misinterpreted (Sverdrup (1953) included grazers in his respiration term)]]


MODELS OF THE BLOOM

Evans, G. T. 1988. A framework for discussing seasonal succession and coexistence of phytoplankton species. Limnol. Oceanogr. 33: 1027-1036. [Evans adapts the E & P (1985) model to study succession between 2 phytoplankton species. Spring phytoplankton are given a lower $K_n$ for N, lower respiratory losses, lower $\mu_{max}$ and a higher $a$ and sinking rate. Three phytoplankton species groups are added for one run.]

Evans, G. T. and J. S. Parslow. 1985. A model of annual plankton cycles. Biolog. Oceanogr. 3: 327-347. [A simulation model which shows that a shallow year-round pycnocline can maintain winter primary production & grazer populations that can control spring blooms.]


Winter, D. F., K. Banse, and G. C. Anderson. 1975. The dynamics of phytoplankton blooms in Puget Sound, a fjord in the northwestern United States. Marine Biology 29: 139-176. [Nutrients are rarely limiting in the main basin of Puget Sound. Primary production is controlled largely by physical factors (advection and vertical mixing). This situation may apply to many temperate and arctic waters if Harrison & Platt’s 1986 analysis is borne out]

ON SINKING DIATOM BLOOMS


Boyle, E. 1998. Pumping iron makes thinner diatoms. Nature 393: 733-734. [Commentary on Hutchins & Bruland 1998 & Takeda (1998). Fe affects uptake of Si relative to nitrate. Hutchins & Bruland (1998) look at Big Sur, with a low river input and narrow continental shelf, Fe spikes increased phytoplankton growth. Low Si:C ratios in Fe enhanced experiments results in little increase in Si removal despite higher diatom growth. Fe-limited diatoms grow thicker silica frustules. Note that in the SOIREE experiment, diatoms that were Fe-replete didn’t sink; see Abraham et al. 2000]


Legendre, L. 1990. The significance of microalgal blooms for fisheries and for the export of particulate organic carbon in the oceans. J. Plankton Res. 12: 681-699. [Blooms can be controlled by hydrodynamics through irradiance or nutrients. They are associated with high sedimentation of intact cells or fecal pellets. They have major effects on benthic and pelagic food webs and global carbon flux.]


Smetacek, V. S. 1985. Role of sinking in diatom life-history cycles: ecological, evolutionary and geological significance. Marine Biology 84: 239-251. [28, 31, 36] [The mass sinking of diatoms at the end of the spring bloom may be an evolved response: the transition from a growing to a resting stage. Diatom slime production enhances sinking rates (= 100 m d⁻¹). Copepod grazing retards the vertical flux, because pellets are more likely to be recycled. Seeding strategies are discussed. The characteristic species of high-nutrient environments—the bloom diatoms—tend to be small and spiny in contrast to diatoms of the nutrient impoverished mid-oceanic gyres.]

Smetacek, V. and F. Pollehne. 1986. Nutrient cycling in pelagic systems: a reappraisal of the conceptual framework. Ophelia 6: 401-428. [An odd collection of natural history observations. Marine spring bloom diatoms either have large cells or the smaller cells form into larger chains. Copepods feed mainly on regenerated production; new production sinks to the benthos. Diatom slime production can lead to high sedimentation rates of Thalassiosira. New and regenerating N systems are discussed] [31]

Smetacek, V. 2000. The giant diatom dump. Nature 406: 574-575. [1000 species, Giant diatoms documented by Kemp et al., small chain formers settle rapidly in flocs. Kemp et al. document a fall dump of large diatoms, as opposed to small spring cells.]

PLANKTONIC SUCCESSION


Allen, T. F. H., S. M. Bartell, and J. F. Koonce. 1977. Multiple stable configurations in ordination of phytoplankton community change rates. Ecology 58: 1076-1084. [This is arguably the most poorly written paper in the entire ecological literature. For example, 'As the points on Fig. 1 represent species changes then the difference between points reflects changes in species changes. The regions of oscillation, however, restrict the changes in species changes and so amount to changes in the change of species change (p. 1083)'. Despite the style, some of the ideas are very interesting.]

Allen, T. F. H. and T. B. Starr. 1982. Hierarchy. University of Chicago Press, Chicago. [Hierarchy theory is applied to phytoplankton succession. These authors agree with Harris and O'Neill et al., that reductionist models of phytoplankton succession may be doomed to failure.]


Barnett, A. M. and A. E. Jahn. 1987. Pattern and persistence of a nearshore planktonic ecosystem off Southern California. Cont. Shelf Res. 7: 1-25. [Classification analysis (UPGMA sorting of correlations) is used to group zooplankton sampled in offshore transects. Barnacle larvae, Oithona, and Acartia dominate inshore; the offshore is dominated by Calanus pacificus, Eucalanus californicus, and Rhinocalanus.]


Carlucci, A. F. and P. M. Bowes. 1970. Production of vitamin B₁₂, thiamine, and biotin by phytoplankton. J. Phycol. 6: 351-357. [Later successional phytoplankton species may require early species to 'pave' the way through the release of vitamin B₁₂.]


Colebrook, J. M. 1984. Continuous plankton records: relationships between species of phytoplankton and zooplankton in the seasonal cycle. Marine Biology 84: 261-265. [Results from the Hardy continuous plankton recorders carried by ships of opportunity throughout the North Atlantic.]

Colebrook, J. M. 1986. Environmental influences on long-term variability in marine plankton. Hydrobiologia 142: 309-325. [Seasonal and year-to-year patterns in continuous plankton recorder data from the N. Atlantic are analyzed (includes PCA analysis)]

Cushing, D. H. 1989. A difference in structure between ecosystems in strongly stratified waters and in those that are only weakly stratified. J. Plankton Res. 11: 1-13. [The ocean consists of weakly stratified systems, dominated by small diatoms and dinoflagellates (>5µm) and stratified regions, which do not support major fisheries.]


Estrada, M., M. Alcarez, and C. Marrase. 1987. Effects of turbulence on the composition of phytoplankton assemblages in marine microcosms. Mar. Ecol. Prog. Ser. 38: 267-281. [Margalef's phytoplankton mandala is tested with lab cultures. The diatom to dinoflagellate transition is controlled by turbulence. PCA is used to analyze successional pattern.]


Gallagher, J. 1982. Physiological variations and electrophoretic banding patterns of genetically different seasonal populations of Skeletonema costatum (Bacillariophyceae). J. Phycol 18: 148-162. /S. costatum is often the dominant species in both spring and fall blooms. Gallagher (no relation) shows that there are at least 2 physiologically distinct sibling species of S. costatum/]


Harris, G. P. 1986. Phytoplankton ecology: Structure, function and fluctuation. Chapman & Hall, London. [Chapter 9 deals with seasonal patterns of distribution and abundance. This book is loaded with controversial ideas (i.e., nutrient limitation is rare for phytoplankton) and provides the best available review of phytoplankton succession. Extends the interesting discussion of spatial and temporal scales introduced in Harris 1980]}


Ibanez, F. 1984. Sur la segmentation des séries chronologiques planctoniques multivaroables. Oceanologica Acta 7: 481-491. [Uses a variety of multivariate statistical techniques, including a PCA with a beautiful Kendall’s horseshoe, to analyze zooplankton succession]


Legendre, P., S. Dallot, and L. Legendre. 1985. Succession of species within a community: chronological clustering with applications to marine and freshwater zooplankton. Amer. Natur. 125: 257-288. [Only chronologically contiguous samples are allowed to cluster; the technique allows key break points (.., due to water-column overturn) to be detected. Zooplankton succession is used as an example.]

O’Neill, R. V., D. L. DeAngelis, J. B. Wade, and T. F. H. Allen. 1986. A hierarchical concept of ecosystems. Princeton University Press, Princeton N J. [“It is difficult to explain successional changes in phytoplankton communities based on cellular physiology. The intervening levels of species, guilds and strategies attenuate the minute-to-minute changes in biochemistry and make it impossible to predict successional patterns solely on physiology. Any attempt to relate a macroscopic property to the detailed behaviors of components several layers lower in the hierarchy is bound to fail due to the successive filtering” (p. 80-81)]


Smetacek, V. S. 1985. Role of sinking in diatom life-history cycles: ecological, evolutionary and geological significance. Marine Biology 84: 239-251. {28, 31, 36} [The mass sinking of diatoms at the end of the spring bloom may be an evolved response: the transition from a growing to a resting stage. Diatom slime production enhances sinking rates (=100 m d⁻¹). Copepod grazing retards the vertical flux, because pellets are more likely to be recycled. Seeding strategies are discussed. The characteristic species of high-nutrient environments-the bloom diatoms-tend to be small and spiny in contrast to diatoms of the nutrient impoverished mid-oceanic gyres.] {28, 31, 36}

Smetacek, V. and F. Pollehne. 1986. Nutrient cycling in pelagic systems: a reappraisal of the conceptual framework. Ophelia 6: 401-428. [An odd collection of natural history observations. Marine spring bloom diatoms either have large cells or the smaller cells form into larger chains. Copepods feed mainly on regenerated production; new production sinks to the benthos. Diatom slime production can lead to high sedimentation rates of Thalassiosira. New and regenerating N systems are discussed] {31}

Sommer, U. 1986. Phytoplankton competition along a gradient of dilution rates. Oecologia 68: 503-506. [Succession and competitive exclusion in chemostat culture is studied under a variety of dilution (=specific growth) rates and combinations of P and Si limitation. The competitive dominant can switch with different environmental conditions, but cannot be predicted from Monod kinetics because of lack of precision in estimates of k. See also Tilman (1982)]

Sommer, U. 1988. Phytoplankton succession in microcosm experiments under simultaneous grazing pressure and resource limitation. Limnol. Oceanogr. 33: 1037-1054. [A light and zooplankton-containing dark reactor (141 polycarbonate container) are coupled. Freshwater phytoplankton from a eutrophic lake. Diatoms dominated initially, and their dominance related to Si:P ratios. Higher Si:P ratios are needed in the presence of pulsed additions and especially grazers. A filamentous green dominated the end of all experiments. Intense resource competition even with an unchecked predator is documented (a refutation of Hairston Smith and Slobodkin).]


Sverdrup, H. U. 1953. On conditions for the vernal blooming of phytoplankton. J. Conseil perm. int. Explor. Mer. 18: 287-295. [The most important paper on this list: A spring bloom occurs when the mixed-layer depth is shallower than the critical depth.] {3, 4, 7, 10, 12, 13, 14, 15, 16, 17, 20, 21, 24, 26, 28, 29, 30}

HARMFUL ALGAL BLOOMS


Tont, S. A. 1987. Variability of diatom species populations: from days to years. J. Mar. Res. 45: 985-1006. [Over 300,000 observations of diatoms at the Scripps pier are analyzed with PCA to separate seasonal, annual, and long-term cycles.]


Venrick, E. L. 1990. Phytoplankton in an oligotrophic ocean: species structure and interannual variability. Ecology 71: 1547-1563. [Variation on the annual to decade time scale is analyzed in the diverse (300-500 spp) oligotrophic ocean]

Comment

Volume 42, part 5 of Limnol. Oceanogr. is devoted to the ecology and oceanography of harmful algal blooms.


DIMENSIONAL ANALYSIS


Bowman, M. J., W. E. Esaias, and M. B. Schnitzer. 1981. Tidal stirring and the distribution of phytoplankton in Long Island and Block Island Sounds. J. Mar. Res. 39: 587-603. [Figure 3 presents Pingree’s s-kh diagram which plots water column depth using non-dimensionalized depth or kh. The mixing should have been presented in non-dimensional form, but was not.]

Legendre, L. and P. Legendre. 1983. Numerical ecology. Elsevier Scientific Publishing. 419 pp. [Their chapter on dimensional analysis is superb. They also provide a straightforward matrix approach for generating the set of orthogonal dimensionless variables. I have programmed a MATLAB algorithm called dimenal.m that will perform this analysis for any dimensional matrix. See outline above]


Platt, T., M. R. Lewis and R. Geider. 1984. Thermodynamics of the pelagic ecosystem: elementary closure conditions for biological production in the open ocean. Pp. 49-84 in M. J. Fasham, eds., Flows of energy and materials in marine ecosystems: theory and practice. Plenum. [Cited by Lewis et al. (1985). They review this paper (which I don’t have) which concludes that the P vs. I curve can be expressed with 3 dimensionless groups P/Pm, I/I0 and the integral of K from the surface to depth z.]


**MISCELLANEOUS**


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